

RESULTS OF THE ARCHBOLD
EXPEDITIONS. NO. 97
A REVISION OF THE FROGS OF
THE SUBFAMILY ASTEROPHRYINAE
FAMILY MICROHYLIDAE

RICHARD G. ZWEIFEL

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ABSTRACT

ASTEROPHRYINE FROGS are confined in distribution to the New Guinea region, from the Louisiade Archipelago on the east, westward through New Guinea proper to the Moluccas Islands. Members of this subfamily are not known to have reached Australia or the Bismarck Archipelago. The subfamily Asterophryinae is characterized by the diplasiocoelous condition of the vertebral column, upper and lower jaws symphygnathine in most genera, and the tongue broadly attached (less than one-quarter free behind). The closest relationship is with the Sphenophryinae, also limited largely to the New Guinea region, whose members are procoelous, eleutherognathine, and have the tongue more than one-quarter free behind. The last major reviser of the Microhylidae included five genera and 24 species in the Asterophryinae. In the present work seven genera (one new) are defined,

largely on the basis of features of the osteology of the skull, and 37 species (10 new) are recognized. Apparently all asterophryine (and all sphenophryine) frogs have direct embryonic development, omitting a free-living tadpole stage. All species for which information is available inhabit the floor of the rain forest, although structural features of some little-known forms suggest arboreal tendencies. None is known to be even partly aquatic. Various species are found at elevations from sea level to over 11,000 feet (3350 m.). The distribution of all species is shown on spot maps, and most species are illustrated. Keys to the genera and species are provided. Audiospectrograms illustrate the mating calls of five species. The chromosome number ($n=13$) is known for only one species of one genus.

INTRODUCTION

THE ANURAN FAUNA of New Guinea is incompletely known, but surely includes well over 160 species. Approximately half are members of the Microhylidae and belong to the subfamilies Asterophryinae and Sphenophryinae. The subfamily Asterophryinae is limited to the New Guinea region, from the Moluccas through New Guinea proper to the islands of the eastern tip of New Guinea. The subfamily Sphenophryinae also is centered in New Guinea, but a fringe of species extends into peripheral areas—to New Britain, northern Australia, Lesser Sunda Islands, Celebes, and the southern Philippines.

The goal of the present study is to define and diagnose the species and genera of the Asterophryinae and to present such information on variation, distribution, ecology, and relationships as can be gathered from preserved specimens and limited field experience. Studies of similar scope on the genera of the Sphenophryinae are under way.

It is hoped that the studies in progress will provide a solid systematic base for future work with more of an ecologic and zoogeographic bias. The fauna of New Guinea is of particular interest to students of evolution, for it has evolved in an area that combines virtually oceanic insularity with a large land mass (it is, after Greenland, the largest island in the world, being about 1500 miles in length) that offers habitats rang-

ing from tropical lowlands to recently glaciated alpine grassland. On the west the classic lines of Wallace and Weber emphasize the faunal differences between the New Guinea region and southeast Asia. Islands to the east of New Guinea—Admiralty Islands, Bismarck Archipelago, Solomon Islands—have been rather effectively isolated from New Guinea. Australia to the south has had land-bridge connections with New Guinea but perhaps because of the predominantly rain-forest environment of New Guinea and the more arid conditions of Australia, there has not been a massive exchange of faunas. As a result of this near isolation and ecologic diversity, the fauna offers unusual opportunities for the study of parallel and convergent evolution, for the relatively few invaders have been presented with more unoccupied niches than a continental mass of similar diversity would offer.

PREVIOUS STUDIES ON THE ASTEROPHRYINAE

The first asterophryine to be described was *Ceratophrys turpicula* Schlegel, 1837, and in the following 41 years only four species were added to the fauna. With the increased European interest in exploration and colonization of New Guinea in the late 1800s, more material became available to scientists, and in the period from

1888 to 1915 another 12 species that I regard as valid were described. The principal workers during these years were van Kampen in Holland, Méhely in Hungary, and Boulenger in England. Van Kampen's studies culminated in "Amphibia of the Indo-Australian Archipelago," published in 1923, which summarized the existing state of knowledge of Papuan microhylid frogs but added little if any new interpretation. Earlier, Méhely (1901) published a review (unfortunately not all-inclusive) of the New Guinea microhylids that included much anatomical information and established new subfamilies, genera, and species. It is regrettable that the writing and publishing of Boulenger's Catalogue (1882) antedated the flow of new material from New Guinea, for although Boulenger later described several asterophryine species, he never had occasion to synthesize data on the New Guinea microhylids. Nieden (1926) compiled much information on microhylids, but added nothing of consequence on the Papuan forms.

With one notable exception, the years between the first and second world wars saw only minor contributions to the literature on Papuan microhylid frogs. The exception was, of course, Parker's (1934) monograph of the Microhylidae. In this basic work he established or verified the anatomical basis for the definitions of the family and lower categories and, so far as the relatively limited material available made it possible, defined distributions and described the variation of the four genera and 24 species of the Asterophryinae that he recognized. He later (1936) described a new genus and species. Parker (1934) had only 92 specimens of asterophryine frogs available for examination, about 40 per cent of these of one species, and saw no specimens at all of five species.

Collections made between the two world wars by the Archbold Expeditions of the American Museum of Natural History, but not studied then, and by the same organization and other collectors during and following World War II formed the basis for papers by Zweifel (1956, 1960, 1963) and Loveridge (1948, 1955) in which new species of the Asterophryinae were described but did not include any significant revisionary material.

Thus, when the present study was undertaken, information on the Asterophryinae differed insignificantly from that available to Parker (1934, 1936) except for the addition of several

new species and for a scattering of data on distribution and life history (e.g., Brongersma, 1953; Tyler, 1963).

ACKNOWLEDGMENTS

The present study is cited as one of the results of the Archbold Expeditions in recognition of the large numbers of specimens collected on the seven expeditions to New Guinea and now in the collection of the Department of Herpetology, the American Museum of Natural History. Numerous other organizations and individuals also contributed in important ways. A grant from the National Science Foundation (GB-2217) enabled me to carry on field work in New Guinea in 1964 and to visit museums in London, Amsterdam, Leiden, Frankfurt, Sydney, Adelaide, and Honolulu. The National Geographic Society provided funds for my trip to New Guinea in 1968 and for study at museums in Genoa, Bogor, and Sydney. In 1969 I participated in the R/V "Alpha Helix" expedition to New Guinea (sponsored by the Scripps Institution of Oceanography, funded by the National Science Foundation) and had the opportunity to make additional field studies on microhylid frogs.

Among the individuals who have contributed to this study I first thank Mr. Fred Parker of Daru, Territory of Papua and New Guinea. Mr. Parker, with whom I have had the pleasure of working in the field, is an accomplished naturalist whose voluminous collections will, after they have been thoroughly studied, increase our knowledge of the Papuan herpetofauna more than those of any other individual. Most of Mr. Parker's specimens are in the Museum of Comparative Zoology, Harvard University, but he also has donated material to many other museums, including the American Museum of Natural History. Several other persons aided my work in New Guinea in a variety of ways. Mr. John Womersly, Chief, Division of Botany, made laboratory facilities available in Lae, arranged field trips, and helped in many ways. Mr. Angus Hutton, in charge of the Government Experimental Tea Plantation at Garaina, collected many worthwhile specimens and facilitated my work on two separate visits to Garaina. Mr. Roy D. Mackay, Preparator-in-Charge of the Papua and New Guinea Public Museum and Art Gallery, Port Moresby, took

me on collecting trips around Port Moresby, made specimens in his care available to me, and helped in ways that only a knowledgeable government official can. Mr. James Menzies of the University of Papua and New Guinea contributed a number of valuable specimens and permitted me the use of tape recordings of frog calls. Mr. Greenfield Sluder was an energetic and helpful field assistant. Dr. Jared Diamond contributed many valuable specimens.

Mrs. Margaret Shaw typed and brought order to a thoroughly scribbled-over, much revised, and almost indecipherable manuscript. All drawings of frogs and their skulls are the painstaking work of Mrs. Frances Zweifel.

Material borrowed from many collections was essential to this study (see Materials, below), but I single out Dr. E. E. Williams of the Museum of Comparative Zoology for special thanks. His museum received the bulk of the extremely numerous F. Parker specimens, and the microhylids were made available to me almost as soon as they arrived at Harvard University.

MATERIALS

I have examined approximately 1500 specimens of asterophryine frogs, including individuals of all species that I regard as valid. The vast majority of specimens are alcoholic, although many species are represented as well by cleaned and dried skeletons or skulls, or by specimens cleared and stained with alizarin red S.

I have examined the definitive type material (holotype, lectotype, or syntype specimens) on which 45 of the 50 trivial names formerly or herein proposed for asterophryines are based. The type-specimens of four of the remaining five species are lost or destroyed, and the fifth species is a synonym of a distinctive species and presents no problems.

Material used in this study is scattered in museums in several countries. Curators in charge of these collections were most generous with their time and specimens, and I am greatly indebted for their assistance. The abbreviations given here are used in the text to indicate the name of a museum presently (or in some cases, formerly) holding particular specimens cited in the text:

AM, Australian Museum, Sydney (Harold Cogger)
AMNH, the American Museum of Natural History,
New York

BBM, Bernice P. Bishop Museum, Honolulu (J. L. Gressitt; S. Nakata; A. Ziegler)
BMNH, British Museum (Natural History), London (A. Grandison)
FMNH, Field Museum of Natural History, Chicago (R. F. Inger; H. Marx)
HC, field numbers of H. Cogger, specimens in the Australian Museum
IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels (G. de Witte; A. Capart)
MCZ, Museum of Comparative Zoology, Harvard University (E. E. Williams)
MM, Macleay Museum, Sydney (specimens in the Australian Museum)
MSNG, Museo Civico di Storia Naturale, Genoa (E. Tortonese; L. Capocaccia)
MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia (K. Somadikarta)
RMNH, Rijksmuseum van Natuurlijke Historie, Leiden (L. Brongersma; M. Hoogmoed)
SAM, South Australian Museum, Adelaide (M. Tyler)
SMF, Senckenberg Natur-Museum und Forschungs-Institut, Frankfurt am Main (K. Klemmer; R. Mertens)
SW, field numbers of T. Schultze-Westrum, specimens in the Zoologische Staatssammlung, Munich
UPNG, University of Papua and New Guinea, Port Moresby (J. Menzies)
USNM, National Museum of Natural History, Smithsonian Institution, Washington, D. C. (J. Peters)
ZMA, Zoologisch Museum, Amsterdam (D. Hillenius; S. Daan)
ZMB, Zoologisches Museum an der Humboldt-Universität zu Berlin (G. Peters)

METHODS

At least superficial dissection is essential in working with microhylid frogs, and in many instances a more thorough examination of the skull is necessary. Specimens were examined by dissection, by use of cleaned and dried skulls, and by clearing and staining with alizarin red S. Aspects of color and pattern may be useful when working with living material and some features remain well-enough defined in preserved specimens (and are consistent enough) to be worth noting. Tape-recorded mating calls were analyzed by use of a Kay Electric Company audio-spectrograph, Sona-Graph model no. 6061A.

Measurements of external features are essential for the correct identification of specimens. Standardized measurements were made on most specimens as indicated in the following paragraphs. Abbreviations used in the text are given in parentheses. Measurements (all in

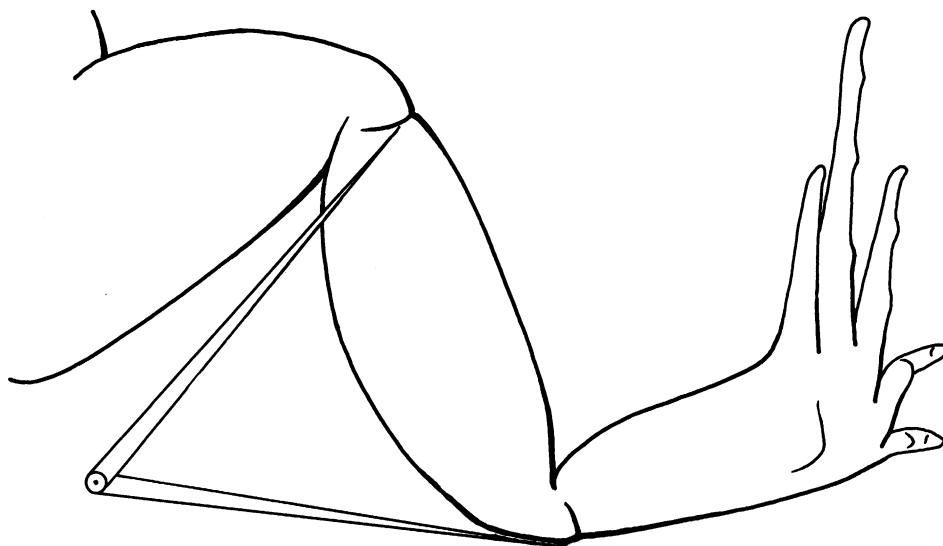


FIG. 1. Hind leg of frog in dorsal view; dividers show span measured as tibia length (TL).

millimeters) were made with dial calipers or ocular micrometer, as appropriate to the span being measured.

S-V, length from snout to vent from tip of snout to cloacal opening.

HW, head width at widest point, generally at level of eardrums or jaw angles.

TL, tibia length from heel to fold of skin on knee (fig. 1).

Eye, eye or orbit length from anterior to posterior corner of eye, with eye forced into a "natural" position if possible.

E-N, distance from eye to naris from anterior corner of eye to center (not posterior edge) of naris.

IN, internarial distance, distance between centers of external nares.

EAR, tympanum size, greatest diameter measured horizontally, including tympanic ring.

Digital discs (not abbreviated), greatest width measured at right angles to axis of toe.

Width of penultimate phalange (not abbreviated), measured at narrowest portion.

Fingers and toes were not measured in absolute units, but the relative lengths were determined by placing them parallel with, respectively, the third finger and fourth toe.

Where possible, I have used the type-specimen as the basis for the description of external morphology and have followed this description with a discussion of variation seen among other

specimens of the species. In instances where it was not possible to describe the type in detail I have utilized a specimen from near the type locality or presented a generalized description based on more than one specimen.

Some characteristics common to all astero-phryines (mentioned in the following section on morphology) are not repeated in the descriptions except for completeness in descriptions of new species.

I routinely made scatter diagrams comparing several other measurements with snout-vent length; these often served to call attention to differences that might otherwise have been overlooked. In many instances, least-squares lines of best fit were calculated in order that average differences in growth trends might better be visualized. Ratios were generated between various pairs of measurements (usually with snout-vent length as the denominator) and were used, with appropriate statistical reduction, in both intra- and inter-specific comparisons.

There are difficulties in using measurements. The most obvious involves consistency in results from specimen to specimen and from worker to worker. The soft, flexible nature of the material makes complete consistency an almost impossible goal. One source of error has hopefully been reduced as I made all the measurements myself. I trust that persons who have occasion to attempt to identify specimens and must utilize

measurements will be able to copy my methods sufficiently closely so that deviations will not be significant.

A problem inherent in using measurements to compare individuals or samples is that introduced by ontogenetic changes in proportions. In theory, this problem is easily resolved by comparing (with scatter diagrams, for instance) samples that include individuals at all stages of growth. Unfortunately, there are few species for which adequate samples are available. Thus, when ratios are used to compare aspects of morphology within or between species, the possibility that ontogenetic factors may influence apparent differences or similarities must be kept in mind.

The data for *Phrynomantis lousiadensis*, illustrated in figures 42–47, indicate the magnitude of the changes involved. Tibia length in juveniles averages about 51 or 52 per cent of snout-vent length of the Rossel Island population, but decreases to about 43 per cent in large adults. Head width shows the opposite trend, increasing from about 38 to 40 per cent in juveniles to about 44 to 47 per cent in adults. Eye size is a particularly difficult character to work with,

and the large amount of scatter seen in the data reflects variability of measurement as much as it does actual variation in eye size. In the sample plotted, the average eye size changes from almost 15 per cent of body length in juveniles to about 10 per cent in adults.

Samples generally are heavily weighted toward specimens in the adult size range. Thus, when faced with the task of identifying juvenile specimens one should expect that the proportions of the individual in hand will deviate from the averages given for the various species; eye size and tibia length tend to be at the high end of the range and head width at the low end. Because the distance from eye to naris is influenced by relative eye size, juveniles tend to have a lower E–N/IN ratio.

In presenting distributional data I have included literature records whose validity I do not question. In instances where I have examined one or more specimens from a locality already mentioned in the literature for that species, I have not appended the literature reference. I have examined all specimens cited by collection number in the paragraphs titled "Distribution and specimens examined."

STRUCTURE AND HABITS

MORPHOLOGY

DETAILS OF MORPHOLOGY pertinent to identification and systematic relationships are given in the generic and specific accounts. What follows are in the main generalities.

HABITUS: Although the asterophryines do not show the diversity in body form that the related sphenophrynines display, they do exhibit morphology that differs from the common concept of microhylids as small-eyed, rotund, short-legged, small-headed animals. Members of some genera, notably *Barygenys*, *Xenorhina*, and *Xenobatrachus* conform somewhat to this stereotype, but many species of *Phrynomantis* are more like *Bufo* in body shape and eye size. The species of *Phrynomantis* that have notably expanded digital discs are perhaps best compared to *Eleutherodactylus*, and *Asterophrys* resembles *Ceratophrys* and other broad-headed terrestrial forms.

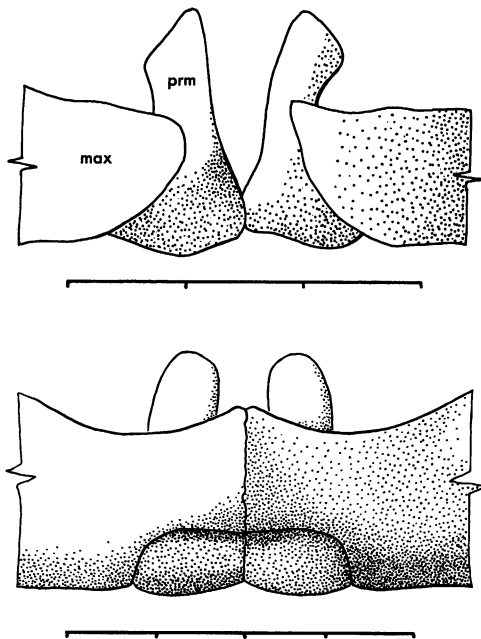


FIG. 2. Anterior ends of upper jaws seen from front showing eleutherognathine condition (upper, *Hylaphorbus rufescens myopicus*) and symphygnathine condition (lower, *Phrynomantis stictogaster*). Scale lines subdivided in millimeters.

Abbreviations: max, maxilla; prm, premaxilla.

SKELETON: The asterophryine skull is a relatively rigid, solid structure, more so than is the case in many frogs. The nasal bones are large, form a median suture (or are fused), and in most genera contact the frontoparietals as well, almost completely excluding the ethmoid from the dorsal surface of the skull. There is never a frontoparietal foramen. The maxillae in most species meet in front of the premaxillae (the "symphygnathine" condition; fig. 2, lower), strengthening the snout region. Similarly, in all but one species the anterior ends of the dentaries meet one another and are fused with the mentomeckelian bones. The quadratojugals are well developed and strongly attached to the maxillae. The vomers (fig. 3) are well-developed bones that invariably meet on the midline of the palate. In the forms that I consider more advanced, the bones are expanded mesially forming a longer, stronger line of contact. In some forms a projection from the maxillary shelf contacts the anterior end of the vomer and adds rigidity to the system. A sliver of bone projects anteriorly from the vomer mesial to the internal naris in some forms and may turn outward, almost surrounding the naris. A row of odontoids may be present on the vomer, and in *Xenobatrachus* there are one or two prominent spikes on each vomer. No asterophryine frog has true teeth on any bone. In the majority of species the roofing bones of the skull are smooth, but they characteristically are rugose in two monotypic genera (*Asterophrys* and *Pherohapsis*) and may be somewhat pitted in two species of *Phrynomantis*. Peculiarities in skulls include the compression of the upper parts of the frontoparietals into a dorsal crest in *Asterophrys*, the development of an arcade over the prootic region in *Pherohapsis*, and the presence of a postocular sheet of bone connecting the maxilla and squamosal in *Pherohapsis* (and, rarely, in *Asterophrys*).

The pectoral girdle is notable for its simplicity. The only bony elements in the ventral portion of the girdle are the coracoids. The cartilaginous sternum may show a slight degree of ossification (detectable only in cleared and stained specimens), but never is there a bony style. Omosternum, clavicles, and procoracoids are absent,

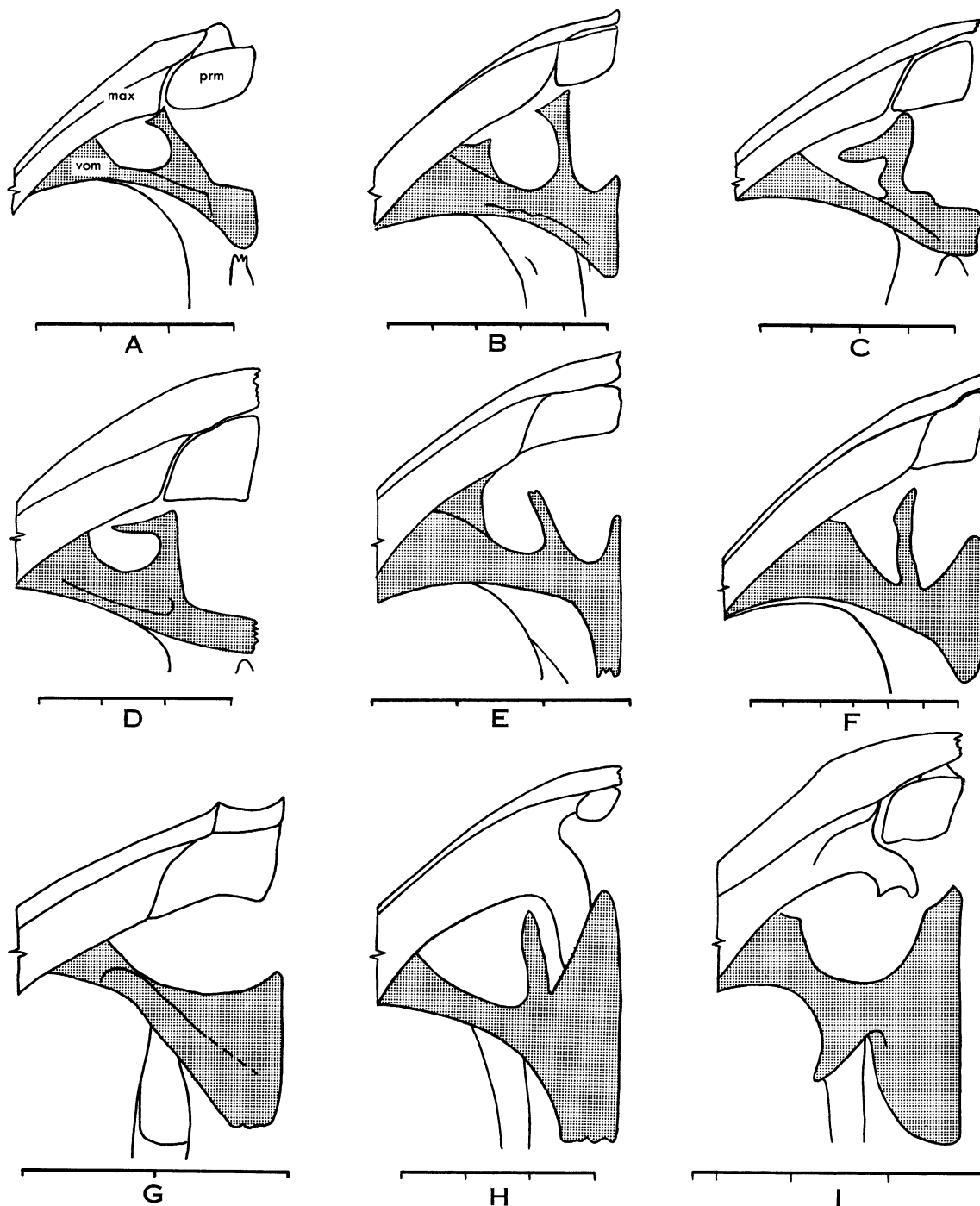


FIG. 3. Variation in shape of vomers; each figure represents the right vomer (and associated bones) seen in palatal aspect. Scale lines subdivided in millimeters. A. *Hylophorbus rufescens*. B. *Phrynomantis lateralis*. C. *Phrynomantis humicola*. D. *Phrynomantis wilhelmana*. E. *Pherohapsis menziesi*. F. *Asterophrys turpicula*. G. *Barygenys nana*. H. *Xenorhina oxycephala*. I. *Xenobatrachus rostratus*.

Abbreviations: max, maxilla; prm, premaxilla; vom, vomer.

represented neither by bone nor by cartilaginous tissue.

The vertebral column is diplasiocoelous. The sacral vertebra has diapophyses that are only slightly expanded (fig. 41), and articulates with the free urostyle by paired condyles.

The terminal phalanges generally bear at least a trace of transverse, T-shaped expansions but Parker (1934) stated that they may also be simple.

EAR: The ear appears to be well developed in all forms, although it is never conspicuously enlarged and the external part is generally ill-defined.

HANDS AND FEET: The tips of the digits range from bluntly rounded structures with no trace of expansion, to broad discs with circum-marginal grooves, up to three times the width of the penultimate phalanges. A few species have fairly prominent subarticular tubercles, although more often there is only a low, rounded elevation in their place or none. There is no outer metatarsal tubercle. The inner metatarsal tubercle, which in some species of other families is elaborated as a digging spade, is never more than a moderately low, rounded protuberance. Although the size of the digits relative to body size varies among the genera and species, there is little variation in relative lengths among fingers and toes. The third finger is invariably the longest and the first the shortest. The second and fourth generally are about equal in length but either (more commonly the fourth)

may be longer. There is no variation at all in relative toe length, the universal sequence being $4 > 3 > 5 > 2 > 1$.

PHARYNGEAL FOLDS: Typically two folds cross the palate just anterior to the pharynx; as a rule the anterior one is smooth, the posterior denticulate (fig. 4). According to Parker (1934, p. 6), folds of this sort are unique to the Microhylidae. The folds are not soft and flabby, but possess some rigidity. I suspect that by their backward orientation they may serve to prevent large, unwieldy items of prey such as earthworms from moving in the wrong direction in the throat.

EYES: In all species that I have observed alive the pupil forms a horizontal ellipse. So far as can be determined from preserved specimens, all species have this sort of pupil.

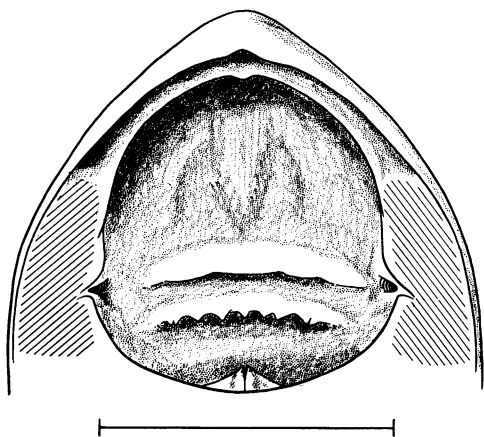


FIG. 4. Roof of mouth (lower jaw removed) of *Phrynomantis wilhelmana* to show palatal folds: anterior smooth, posterior serrate. Diagonal lines indicate transected muscle masses. Scale line represents 1 cm.

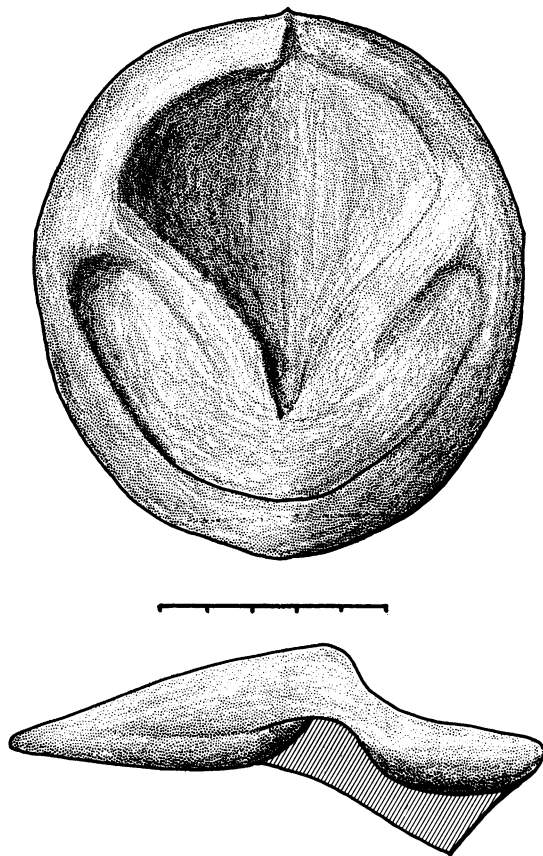


FIG. 5. Tongue of *Phrynomantis wilhelmana* in dorsal (upper) and lateral (lower) views. Anterior is down in dorsal view and left in lateral. Cross-hatched area is pedicle. Scale line subdivided in millimeters.

TONGUE: The asterophryine tongue is a thick structure with little free margin (fig. 5). It generally has a shallow median groove that passes posteriorly into a deeper pocket. Parker (1934, p. 6) suggested that the pocket is a post-mortem condition produced by a strong contraction of the hyoglossus muscle. Samuel McDowell (personal commun.) has pointed out the logical correlation of the tongue-tied condition of the Asterophryinae with the immobility of the mento-meckelian bones, as movement of these bones is involved in tongue ejection (Gans, 1961). The monotypic genus *Hylophorbus* combines the typical asterophryine tongue with the primitive, unfused condition of the lower jaw. Thus, it appears that fusion of the mento-meckelian bones with the dentaries and consequent strengthening of the lower jaw followed freeing of the mento-meckelian bones from their involvement in protrusion of the tongue.

VOCAL SAC: I have observed no diversity in vocal sac structure. It is consistently single and subgular, with slitlike openings in the floor of the mouth. The skin is not modified, so the presence of the sac is not obvious upon external examination.

HABITS AND HABITATS

All asterophryines whose habits are known inhabit the forest floor. Large-eyed forms such as *Hylophorbus* and *Phrynomantis* may be found at night active on the leaf litter or resting at the mouths of burrows. Probably the small-eyed genera (*Xenobatrachus*, *Xenorhina*, *Barygenys*) are more cryptic in their habits, but less is known about these forms than about the others. No known asterophryine has the toes webbed, so presumably none is even partly aquatic. In this respect the group shows less diversity than the Sphenophryinae, which includes riparian species. The presence of relatively large digital discs in three species of *Phrynomantis* implies that these species may be at least occasionally arboreal, perhaps inhabiting shrubs and low trees at night as do many *Cophixalus* (Sphenophryinae). There is nothing known to confirm this inference, however. The only specimen of *P. boettgeri* was under moss at the foot of a tree, and a *P. eurydactyla* was in a cave; there is no record for the third species, *P. slateri*.

I have made no effort to study food habits, although the material is preserved in hundreds

of stomachs for anyone who wishes to study it. Information in the literature and casual examination of specimens indicate that a diversity of food items is taken, and that the asterophryines do not conform to the view that microhylids are predominantly eaters of ants and termites. Lizards, insects, and earthworms all fall prey.

BREEDING HABITS

So far as is known, all frogs of the two Papuan subfamilies Asterophryinae and Sphenophryinae have direct development. Although direct evidence (terrestrial eggs associated with adult frogs or eggs from which identified young have hatched) is available for only a few species, there can be little doubt that this is the exclusive form of development. Gravid females are known for most of the species, and the well-developed ova invariably are large (as much as 5 mm. in diameter in large species) and yolky, never small and dark as is typical of aquatic eggs. Furthermore, no larva of the characteristic microhylid type has been reported in New Guinea.

The mating habits of New Guinea microhylids remain completely unknown. No external secondary sexual characters, such as the swollen thumbs or spiny, epidermal nuptial pads common to many male anurans, distinguish male from female asterophryines. In such distantly related microhylids as *Gastrophryne carolinensis* (subfamily Microhylinae; Conaway and Metter, 1967) and *Breviceps adspersus* (subfamily Brevicipitinae; Wager, 1965), the male is literally glued to his rotund mate by dermal secretions. I have seen no external indication of appropriate glandular proliferation in New Guinea frogs, but I have not made the histological examination of the skin that would provide surer evidence.

The eggs are laid in moist, sheltered places such as beneath or within rotting logs (see accounts of *Phrynomantis robusta* and *P. wilhelmana*) and undoubtedly also in burrows in the ground. In some instances, at least, the eggs are attached in rosary-like strings (above-mentioned species), but they also may be unattached (see account of *P. humicola compta*). In two instances male frogs were found with the eggs, and in one the frog appeared to be "guarding" (*P. robusta*).

The adaptive advantage of direct development in the New Guinea environment is obvious. Great areas of the island are mountainous,

and standing water breeding sites are rare or nonexistent. Highly specialized adaptations are needed to take best advantage of the streams for larval development (e.g., the sucker mouths of hylid tadpoles), and microhylid larvae are of the pond-type rather than stream-type. Divorce from an aquatic period of larval development enables the frogs to exploit areas far from surface water. Limestone regions, where even permanent streams are absent, can serve as breeding sites because of the water holding capacity of the forest-floor growth and litter.

Direct development requires large reserves of yolk and this drastically reduces the clutch size compared to that of a species that deposits its smaller eggs in water. Numbers of mature eggs noted within or laid by asterophryines range from 10 to 55. Obviously, there must be a great reduction in mortality to compensate for this low fecundity. Sheltered development within a hidden and possibly guarded nest substitutes for a risky period of free larval life, and this undoubtedly plays a large part in permitting lower fecundity. Another consideration is that adult frogs, relatively secure in their familiar forest-floor hiding places, are not exposed to the dangers of travel to and from aquatic breeding sites or to the possibility of predation while at the sites.

MATING CALLS

I have gathered little information on mating calls of asterophryine frogs. These terrestrial frogs do not form aggregations at aquatic breeding sites, but generally call singly and often sporadically from the shelter of leaf litter or from the mouths of burrows in the forest floor. Their habits make them difficult to find and still more so to record. I have tape-recorded or heard the calls of six species: *Hylophorbus rufescens*, *Pherohapsis menziesi*, *Phrynomantis lateralis*, *P. personata*, *P. robusta*, and *P. wilhelmana*. The calls are similar in that each consists of a series of short (ca. 0.1–0.2 sec.), discrete notes with little differentiation of notes within the series. *Phryno-*

mantis lateralis may utter 60 or more such notes in a series before pausing silently for several minutes. The other species of this genus produce fewer notes per call (less than 10 in those recorded), but also space the calls over long intervals. *Hylophorbus*, while producing calls that are qualitatively similar to those of *Phrynomantis*, seems less inclined to pause for long periods between calls. *Pherohapsis* produces longer series of notes than most others (being comparable to *Phrynomantis lateralis* in this respect), but I have no information on its persistence in calling. The calls are described in more detail in the species accounts.

The few species with which I am familiar call at night. *Xenobatrachus rostratus* calls in the daytime (see species account), although perhaps not exclusively. On many occasions I heard asterophryine-like calls issuing from the leaf litter in the daytime, but I was never able to associate frogs found in the leaf litter with particular calls.

The calls referred to here as mating calls may serve a territorial function as appears to be the case in a ground-dwelling ranid, *Platymantis papuensis* (Zweifel, 1969), but I did not have the opportunity to test this with playback experiments. One *Phrynomantis robusta* responded readily to my vocal imitation of its call by calling, but it moved deeper within its burrow rather than advancing to the source of the other call, as *Platymantis* would have done.

At least one species, *Phrynomantis lateralis*, gives a "distress call" (see species account).

The peculiar situation of two different-sounding calls, differing principally in their tuning, was observed in *Phrynomantis lateralis* and *Hylophorbus rufescens*. This is discussed in the respective species accounts.

Although the calls discussed here have much in common, they are too few to confirm what might be inferred—that there is a common character to the asterophryine call. I have recorded the calls of many more species of the subfamily Sphenophryninae and find considerable diversity there even within one genus.

SYSTEMATICS

DEFINITION OF THE ASTEROPHRYINAE

MÉHELÝ (1901) DIVIDED the New Guinean microhylids into two subfamilies, the Symphygnathinae and Eleutherognathinae, according to whether the anterior ends of the maxillary bones met in a sutural contact in front of the premaxillae (symphygnathine condition) or were separated (eleutherognathine). Nieden (1926) distinguished the subfamilies of Microhylidae ("Engystomatidae") on the presence or absence of teeth, and included all Papuan microhylids except *Genyophryne* ("Teeth present in lower jaw" based on an erroneous interpretation by Boulenger) in the Engystomatinae ("Upper- and lower jaw untoothed").

Parker (1934) reappraised the subfamilial arrangement of the Microhylidae and recognized two subfamilies in the Papuan region that corresponded in large part to those of Méhelý. The names Méhelý used did not follow the rules of nomenclature so were discarded and replaced by the names Asterophryinae and Sphenophryinae. Asterophryinae was first used by Fejérváry (1923) as a subfamily of the Astero-phryidae in a context that bears no resemblance to later and present classifications. The Sphenophryinae of Noble (1931) corresponded closely but not entirely to Parker's concept of that subfamily, but Noble distributed the astero-phryines among two subfamilies, the Cacopinae and the Symphygnathinae.

I have recently (Zweifel, 1971) examined the characteristics of the Asterophryinae and Sphenophryinae and have presented revised definitions. The Asterophryinae are defined as diplasiocoelous microhylid frogs that have the tongue broadly attached (less than one-quarter free posteriorly) and have direct embryonic development (no free-living tadpole stage). In most genera the upper and lower jaws show the symphygnathine condition. The Sphenophryinae, which may be regarded as the "sister group," are procoelous frogs with the tongue more than one-quarter free behind, also with direct embryonic development, but never with symphygnathine jaws. Parker (1934, p. 10) recognized the close relationship of these two groups: "Very possibly this group [Spheno-

phryinae] should be united with the Astero-phryinae." With the removal of *Genyophryne* from the Asterophryinae and its placement in the Sphenophryinae (Zweifel, 1971), the distinctness of the two groups (in terms of vertebral, skull and lingual characteristics) is enhanced, and I see no advantage in combining them into a single subfamily.

GENERA AND SPECIES OF THE ASTEROPHRYINAE

Thirteen generic names that are based on species of asterophryine frogs have been established, and in the present paper I add one more (table 1). Méhelý (1901) made the first attempt at synthesizing information on the generic status of New Guinean microhylids. Although his work is valuable in that he utilized and illustrated skeletal characters still deemed to be of systematic importance, he failed to treat several genera described prior to his work. The modern concept of genera of the Asterophryinae, therefore, dates from the works of Parker (1934, 1936).

Parker (1934) assigned four genera to the Asterophryinae: *Genyophryne*, *Metopostira*, *Xenobatrachus*, and *Asterophrys*; later (1936) he described *Barygenys*. I have elsewhere (Zweifel, 1971) presented reasons for removing *Genyophryne* from the Asterophryinae and placing it in the Sphenophryinae; hence, this genus is of no further concern here.

Parker differentiated the genera entirely on the basis of characteristics of the maxillary, dentary, and vomerine bones. Maxillae differed according to whether the anterior ends failed to make contact in front of the premaxillae (*Metopostira*, *Barygenys*), or whether they formed a suture (*Xenobatrachus*, *Asterophrys*). Dentaries differed similarly, either failing to make contact anteriorly and not fused with the mentomeckelian bones (*Metopostira*), or in contact and fused (the other three genera). The diagnostic difference in the vomers was whether one or two large spikes were present on each side (*Xenobatrachus*), or absent (*Asterophrys*, *Metopostira*, *Barygenys*).

In reassessing the generic limits I have considered the same skeletal characters as did

TABLE 1
GENERIC NAMES ESTABLISHED FOR ASTEROPHRYINE FROGS^a

| Name, Author, Date | Type-Species | Present Proposed Status |
|---|--|---------------------------------|
| <i>Asterophrys</i> Tschudi, 1838 | <i>Ceratophrys turpicula</i> Schlegel, 1837 | Valid genus |
| <i>Xenorhina</i> Peters, 1863 | <i>Bombinator oxycephalus</i> Schlegel, 1858 | Valid genus |
| <i>Phrynomantis</i> Peters, 1867 | <i>Phrynomantis fusca</i> Peters, 1867 | Valid genus |
| <i>Hylophorbus</i> Macleay, 1878 | <i>Hylophorbus rufescens</i> Macleay, 1878 | Valid genus |
| <i>Xenobatrachus</i> Peters and Doria, 1878 | <i>Xenobatrachus ophiodon</i> Peters and Doria, 1878 | Valid genus |
| <i>Callulops</i> Boulenger, 1888 | <i>Callulops doriae</i> Boulenger, 1888 | Synonym of <i>Xenorhina</i> |
| <i>Mantophryne</i> Boulenger, 1897 | <i>Mantophryne lateralis</i> Boulenger, 1897 | Synonym of <i>Phrynomantis</i> |
| <i>Choanacantha</i> Méhely, 1898 | <i>Choanacantha rostrata</i> Méhely, 1898 | Synonym of <i>Xenobatrachus</i> |
| <i>Gnathophryne</i> Méhely, 1901 | <i>Mantophryne robusta</i> Boulenger, 1898 | Synonym of <i>Phrynomantis</i> |
| <i>Metopostira</i> Méhely, 1901 | <i>Metopostira ocellata</i> Méhely, 1901 | Synonym of <i>Hylophorbus</i> |
| <i>Pomatops</i> Barbour, 1910 | <i>Pomatops valvifera</i> Barbour, 1910 | Synonym of <i>Phrynomantis</i> |
| <i>Pseudengystoma</i> Witte, 1930a | <i>Pseudengystoma bouwensi</i> Witte, 1930 | Synonym of <i>Xenorhina</i> |
| <i>Barygenys</i> Parker, 1936 | <i>Barygenys cheesmanae</i> Parker, 1936 | Valid genus |
| <i>Pherohapsis</i> , new genus | <i>Pherohapsis menziesi</i> , new species | New genus |

^aExcluded is *Genyophryne* Boulenger, 1890, formerly regarded as an asterophryine but now placed in the Sphenophryinae; see text.

Parker and have noted some other features of the skull that are useful in interpreting relationships. My decision to recognize seven genera where Parker recognized four may result in part from a greater tendency to emphasize minor variations, but I think it is due more to the greater number of species and specimens available to me, and the consequent opportunity for more thorough analysis.

For reasons of priority I find it necessary to substitute the name *Hylophorbus* for *Metopostira*, but my concept of the diagnostic characteristics of the genus is the same as that of Parker. I consider the genus to include only one species, whereas Parker first included three (1934) and later two (1936). However, Parker had not examined specimens of the second species, which I transfer to another genus.

Barygenys remains as diagnosed by Parker (1936), except that five rather than two species are now known. In addition to the unique combination of skeletal characters (upper jaw eleutherognathine, lower jaw symphygnathine), frogs of this genus are notable for their small eyes, short and bluntly pointed fingers, and vertical ridges on the snout.

The principal changes I propose affect the genus *Asterophrys* as it was conceived by Parker. On the basis of skull morphology and eye size three distinct groups may be recognized. The largest group (15 species) I assign to the genus

Phrynomantis. In these species the parasphenoid is narrow anteriorly (about half the width of the frontoparietals at the same level), the vomers show little expansion along their midline contact, and the eyes are large (Eye/S-V averages greater than 0.09).

The next largest group within Parker's *Asterophrys* includes six species for which the name *Xenorhina* is available. The skull is rather flattened compared with the condition in *Phrynomantis*, with the parasphenoid relatively much wider, almost as wide as the frontoparietals. The frontoparietals tend to expand downward, forming more of the lateral, anterior wall of the braincase than in *Phrynomantis*, in which more of the ethmoid is exposed laterally. The vomers are much expanded along their midline contact, especially anteriorly and may be supported anteriorly by a spur from the maxillary shelf. The eyes are small (Eye/S-V 0.09 or less in all species). *Xenobatrachus*, recognized by Parker as a valid genus, has the same features as *Xenorhina*, with the added specialization of one or two prominent spikes on each vomer. I recognize eight species in place of Parker's six.

Asterophrys stands as a monotypic genus. The frontoparietal bones are compressed into a high dorsal crest that has no counterpart in other asterophryines so far as I know. The nasal bones are fused, and the massive squamosals in some individuals (but not in all) connect anteriorly

TABLE 2
PRESENT STATUS OF TRIVIAL NAMES APPLIED TO FROGS OF THE SUBFAMILY ASTEROPHRYINAE

| Original Combination | Author, Date | Proposed Status |
|--|------------------------|---|
| 1. <i>amboinensis</i> , <i>Hylophorbus</i> | Mertens, 1930 | Synonym of <i>Phrynomantis fusca</i> |
| 2. <i>atra</i> , <i>Xenorhina</i> | Günther, 1896 | <i>Barygenys atra</i> |
| 3. <i>bidens</i> , <i>Xenorhina</i> | van Kampen, 1909 | <i>Xenobatrachus bidens</i> |
| 4. <i>boettgeri</i> , <i>Gnathophryne</i> | Méhely, 1901 | <i>Phrynomantis boettgeri</i> |
| 5. <i>bouwensi</i> , <i>Pseudengystoma</i> | Witte, 1930 | <i>Xenorhina bouwensi</i> |
| 6. <i>cheesmanae</i> , <i>Barygenys</i> | Parker, 1936 | Same combination |
| 7. <i>compta</i> , <i>Phrynomantis humicola</i> | — | New subspecies |
| 8. <i>doriae</i> , <i>Callulops</i> | Boulenger, 1888 | <i>Xenorhina doriae</i> |
| 9. <i>dubia</i> , <i>Xenorhina</i> | Boettger, 1895 | <i>Phrynomantis dubia</i> |
| 10. <i>eurydactyla</i> , <i>Phrynomantis</i> | — | New species |
| 11. <i>exsul</i> , <i>Barygenys</i> | Zweifel, 1963 | Same combination |
| 12. <i>extimus</i> , <i>Hylophorbus rufescens</i> | — | New subspecies |
| 13. <i>flavicularis</i> , <i>Barygenys</i> | — | New species |
| 14. <i>fusca</i> , <i>Phrynomantis</i> | Peters, 1867 | Same combination |
| 15. <i>gigantea</i> , <i>Xenorhina</i> | van Kampen, 1915 | <i>Xenobatrachus giganteus</i> |
| 16. <i>glandulosa</i> , <i>Phrynomantis</i> | — | New species |
| 17. <i>humicola</i> , <i>Phrynomantis humicola</i> | — | New species |
| 18. <i>infulata</i> , <i>Phrynomantis</i> | — | New species |
| 19. <i>kampeni</i> , <i>Liophryne</i> | Boulenger, 1914 | Synonym of <i>Phrynomantis robusta</i> |
| 20. <i>kopsteini</i> , <i>Hylophorbus</i> | Mertens, 1930 | <i>Phrynomantis kopsteini</i> |
| 21. <i>lateralis</i> , <i>Mantophryne</i> | Boulenger, 1897 | <i>Phrynomantis lateralis</i> |
| 22. <i>leopoldi</i> , <i>Asterophrys</i> | Witte, 1930 | Synonym of <i>Asterophrys turpicula</i> |
| 23. <i>louisianensis</i> , <i>Asterophrys</i> | Parker, 1934 | <i>Phrynomantis louisianensis</i> |
| 24. <i>macra</i> , <i>Metopostira</i> | van Kampen, 1906 | Synonym of <i>Hylophorbus rufescens rufescens</i> |
| 25. <i>macrops</i> , <i>Xenorhina</i> | van Kampen, 1909 | <i>Xenobatrachus macrops</i> |
| 26. <i>mehelyi</i> , <i>Choanacantha</i> | Boulenger, 1898 | <i>Xenobatrachus mehelyi</i> |
| 27. <i>menziesi</i> , <i>Pherohapsis</i> | — | New species |
| 28. <i>microtus</i> , <i>Mantophryne</i> | Werner, 1901 | Synonym of <i>Phrynomantis robusta</i> |
| 29. <i>minima</i> , <i>Asterophrys</i> | Parker, 1934 | <i>Xenorhina minima</i> |
| 30. <i>myopicus</i> , <i>Hylophorbus rufescens</i> | — | New subspecies |
| 31. <i>nana</i> , <i>Barygenys</i> | — | New species |
| 32. <i>neuhausi</i> , <i>Mantophryne</i> | Vogt, 1911 | Synonym of <i>Xenorhina doriae</i> |
| 33. <i>obesus</i> , <i>Xenobatrachus</i> | Zweifel, 1960 | Same combination |
| 34. <i>ocellata</i> , <i>Metopostira</i> | Méhely, 1901 | Synonym of <i>Hylophorbus rufescens rufescens</i> |
| 35. <i>ocellata</i> , <i>Xenorhina</i> | van Kampen, 1913 | <i>Xenobatrachus ocellatus</i> |
| 36. <i>ophiodon</i> , <i>Xenobatrachus</i> | Peters and Doria, 1878 | Same combination |
| 37. <i>oxycephalus</i> , <i>Bombinator</i> | Schlegel, 1858 | <i>Xenorhina oxycephala</i> |
| 38. <i>parkerorum</i> , <i>Xenorhina</i> | — | New species |
| 39. <i>personata</i> , <i>Phrynomantis</i> | — | New species |
| 40. <i>robusta</i> , <i>Mantophryne</i> | Boulenger, 1898 | <i>Phrynomantis robusta</i> |
| 41. <i>rostrata</i> , <i>Choanacantha</i> | Méhely, 1898 | <i>Xenobatrachus rostratus</i> |
| 42. <i>rufescens</i> , <i>Hylophorbus</i> | Macleay, 1878 | <i>Hylophorbus rufescens rufescens</i> |
| 43. <i>similis</i> , <i>Asterophrys</i> | Zweifel, 1956 | <i>Xenorhina similis</i> |
| 44. <i>slateri</i> , <i>Asterophrys</i> | Loveridge, 1955 | <i>Phrynomantis slateri</i> |
| 45. <i>steini</i> , <i>Asterophrys</i> | Ahl, 1932 | Synonym of <i>Asterophrys turpicula</i> |
| 46. <i>stictogaster</i> , <i>Phrynomantis</i> | — | New species |
| 47. <i>stresemanni</i> , <i>Xenorhina</i> | Ahl, 1932 | Synonym of <i>Xenorhina oxycephala</i> |
| 48. <i>turpicula</i> , <i>Ceratophrys</i> | Schlegel, 1837 | <i>Asterophrys turpicula</i> |
| 49. <i>valvifera</i> , <i>Pomatops</i> | Barbour, 1910 | Synonym of <i>Phrynomantis robusta</i> |
| 50. <i>wilhelmana</i> , <i>Asterophrys pansa</i> | Loveridge, 1948 | <i>Phrynomantis wilhelmana</i> |

with the maxillae in a broad sheet of bone. All the roofing bones of the skull including the maxillae are rugose. The new genus *Pherohapsis*, also monotypic, shares some of these characters with *Asterophrys* but lacks the dorsal crest and possesses unique squamosal-temporal arcades.

I recognize 37 species in the Asterophryinae, 10 of them new. Two species are considered polytypic—one with three subspecies, the other with two. Including the new names proposed herein, a total of 50 trivial names is available for frogs of this subfamily. These names, and their proposed status, are listed in table 2.

Synonymies: Generic synonymies include each new generic name that I regard as a synonym of the genus in question, but not every old name that has been applied in part to the genus. Information on the latter topic is given above and in generic accounts. Species synonymies include all new names applicable to the taxon treated as well as the first usage of all new combinations of old names.

RELATIONSHIPS

My concept of generic relationships within the Asterophryinae derives largely from features of the skull, because the postcranial skeleton exhibits no variation of significance on this level, and because I have made no detailed investigations of the muscular anatomy.

The symphygnathine condition of the maxillary bones (fig. 2, lower), in which the anterior ends (pars facialis) of the bones come together and may even be firmly sutured, is peculiar to certain asterophryine genera and may reasonably be considered the specialized condition. The primitive condition, typical of the vast majority of the Salientia, is the eleutherognathine condition found only in *Hylophorbus* (fig. 2, upper) and *Barygenys* among the Asterophryinae. Similarly, the condition in which the dentaries are fused with the mento-meckelian bones and are in contact is more advanced than the usual condition of nonfusion and noncontact. The latter situation is seen among asterophryines only in *Hylophorbus*.

Most of the asterophryines have the nasal bones extremely well developed. Not only are they in firm contact along the midline, but they also contact the anterior ends of the frontoparietals and exclude the ethmoid from the dorsal surface of the skull, or leave only a small

area of that bone visible. *Hylophorbus* is the exception; the nasals do not meet the frontoparietals, and in consequence there is an arc of ethmoid dorsally exposed. I am inclined to view the condition in *Hylophorbus* as more primitive, although the evidence for this is less compelling than it is for the upper and lower jaws.

The condition of the vomers in *Xenorhina* and *Xenobatrachus*, where these bones expand both anteriorly and posteriorly as the midline is approached and may be supported anteriorly by a projection from the maxilla is decidedly unusual in the Microhylidae, and can reasonably be regarded as a specialized condition. The presence of prominent vomerine spikes in *Xenobatrachus* is an additional specialization. Expansion of the vomers to a somewhat lesser degree occurs in *Barygenys*, *Asterophrys*, and *Pherohapsis*, and these genera lack the additional specializations of *Xenorhina* and *Xenobatrachus*. The vomers of *Hylophorbus* and *Phrynomantis* exhibit what is presumably the more primitive condition, with the mesial ends little or not at all expanded.

In the genera *Asterophrys*, *Barygenys*, *Xenorhina*, and *Xenobatrachus* the parasphenoid is relatively wide, typically more than half the width of the frontoparietals anteriorly, which contrasts to the relatively narrow parasphenoid of *Hylophorbus*, *Phrynomantis*, and *Pherohapsis*. The latter condition is probably the more primitive, as it occurs widely in the genera of the Sphenophryinae.

The ethmoid is broadly exposed laterally between the frontoparietals and parasphenoid in the genera *Hylophorbus*, *Phrynomantis*, and *Pherohapsis*, whereas in *Barygenys*, *Xenorhina*, and *Xenobatrachus* there is a tendency to downward, lateral growth of the frontoparietals, forming a more sturdy enclosure to the anterior part of the braincase. In some instances the frontoparietals almost reach the parasphenoids and cover much of the ethmoids. The situation in the latter group of genera is presumably the more specialized.

Some features of foot structure deserve consideration. Within the Asterophryinae (as well as within the Sphenophryinae) there is a broad spectrum of development of digital discs, from forms with no expansion of the terminal phalanges, to those in which there are discs almost three times the width of the penultimate phalanges. In most large groups of anurans it would be conventional to regard the forms without discs as primitive and those with discs as specialized. I do not think this is the case in

TABLE 3
COMPARISON OF ADVANCED (+) AND PRIMITIVE (—) STATES IN SEVEN GENERA OF THE ASTEROPHRYINAE

| | <i>Hylophorbus</i> | <i>Phrynomantis</i> | <i>Pherohapsis</i> | <i>Asterophrys</i> | <i>Barygenys</i> | <i>Xenorhina</i> | <i>Xenobatrachus</i> |
|--|--------------------|---------------------|--------------------|--------------------|------------------|------------------|----------------------|
| Maxillae symphygnathine (+) or eleuthernathine (—) | — | + | + | + | — | + | + |
| Dentaries symphygnathine (+) or eleuthernathine (—) | — | + | + | + | + | + | + |
| Nasals well developed (+) or less well developed (—) | — | + | + | + | + | + | + |
| Vomers expanded (+) or not expanded (—) | — | — | + | + | + | + | + |
| Vomerine spikes present (+) or absent (—) | — | — | — | — | — | — | + |
| Parasphenoid broad (+) or narrow (—) | — | — | — | + | + | + | + |
| Frontoparietals tend to en- close braincase laterally (+) or not (—) | — | — | — | — | + | + | + |
| With well-developed digital discs (—) or not (+) | — | — | — | — | + | + | + |
| With well-developed sub- articular tubercles (—) or not (+) | — | — | — | — | + | + | + |

the Asterophryinae, however. In forms in which the digital discs are scarcely or not at all developed there still may appear slight grooves on the tips of some digits, and the underlying bones bear slight lateral projections. I think it reasonable to interpret the grooves as vestiges of the terminal grooves so prominent in forms with well-developed discs, and the small projections as vestiges of the bony arms that lend the T-shape to the ultimate phalanges of forms with better-developed discs.

The other principal variation in foot structure involves the degree of development of subarticular tubercles. The virtual absence of tubercles under the digits and on the soles and palms may be regarded as the specialized condition and the presence of distinct, rounded tubercles as primitive.

Within each of the genera *Phrynomantis*, *Xenorhina*, and *Xenobatrachus*, there exist both species with and without discs, although in the last two genera the discs are never so well developed as in some *Phrynomantis*. *Hylophorbus*, *Asterophrys*, and *Pherohapsis* have distinct but not well-developed discs and compare favorably with many *Phrynomantis*. *Barygenys* has discless fingers and toes with or without small discs. Evidently, separate parallel trends toward reduction of digital discs

have taken place in *Phrynomantis*, *Xenorhina*, and *Xenobatrachus*. *Barygenys* is perhaps more specialized than the other genera in this respect.

Extensive development of subarticular tubercles is seen in *Hylophorbus*, *Pherohapsis*, *Asterophrys*, and several species of *Phrynomantis*. Tubercles are at best weakly developed in *Xenorhina*, *Xenobatrachus*, and *Barygenys*. The presence of tubercles is the most widespread condition in frogs, so their absence or weak development is regarded as a specialization. As is the case with digital discs, however, there appears to have been parallel loss of tubercles in different genera.

On the basis of the assumptions and information presented above (summarized in table 3), it appears that *Hylophorbus* is the most primitive of the living asterophryines. *Phrynomantis* could easily be derived from *Hylophorbus*, by development of the symphygnathine condition in upper and lower jaws and slight size increase in the nasals and frontoparietals to where they largely cover the ethmoid dorsally. The skull of *Pherohapsis* is basically similar to that of *Phrynomantis*, differing most obviously in the sculpturing of the roofing bones, nasal fusion, the extensive additional bone development in the squamosal and prootic regions, and slight broadening of the vomers. *Asterophrys* probably

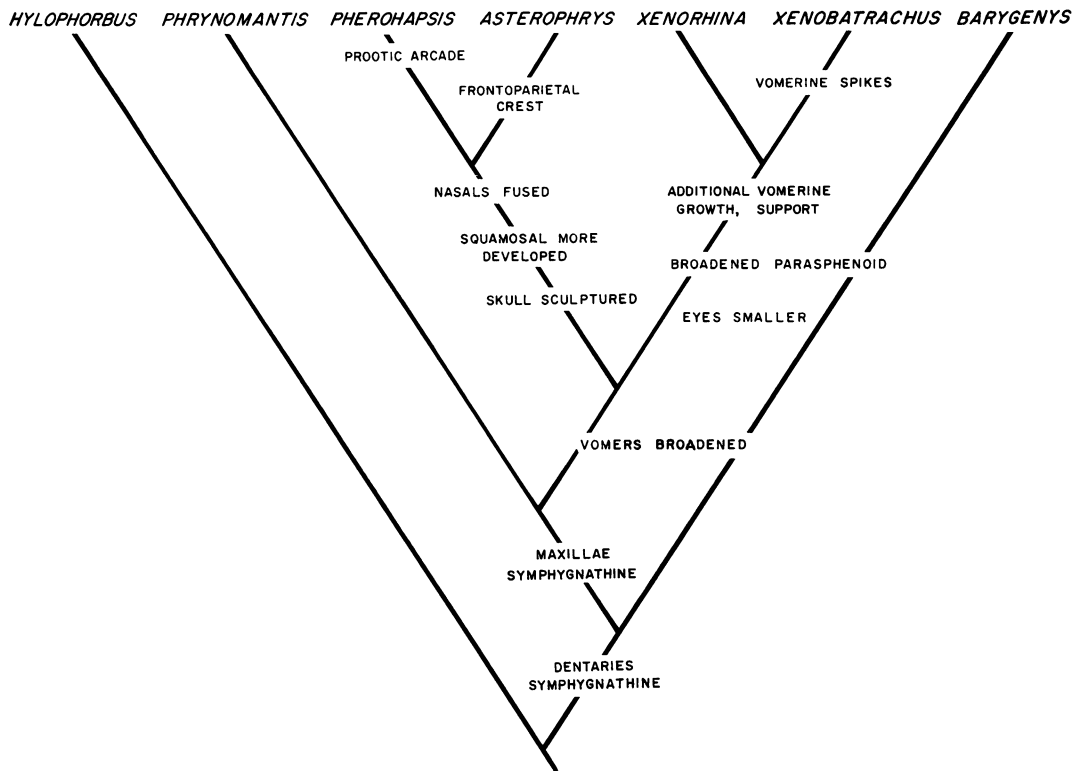


FIG. 6. Proposed phylogeny of asterophryine genera. Where one or more characters is indicated on a given branch, the alternate branch retains the more "primitive" character (see text).

also fits into this evolutionary sequence, having sculptured skull bones, fused nasals, heavy squamosals, and broadened vomers. Its broadened parasphenoid may be a parallel development to this condition in genera mentioned below.

Xenorhina and *Xenobatrachus* differ only in the possession by the latter of vomerine spikes. Presumably these genera developed from a *Phrynomantis*-like precursor through reduction in eye size and increased rigidity of the skull brought about by expansion and bracing of the vomers.

The place of *Barygenys* in the phylogenetic scheme is not at all clear. If the eleutherothine condition of the maxillae is primitive in this genus and does not represent a secondary return to the primitive condition, then the line leading to *Barygenys* must have split off early from the basic *Hylophorbus*-like stock and undergone an independent development that to some extent paralleled changes taking place in the line leading to *Xenorhina* and *Xenobatrachus* (reduction in

eye size, vomerine expansion, broadened parasphenoid).

An alternative is that *Barygenys* developed from a line in which the fully symphygnathine condition had developed but later was lost. This alternative disposes of the need for explaining the vomerine expansion, broad parasphenoid, and small eyes of *Barygenys* as parallel developments to similar characteristics seen in *Xenorhina* and *Xenobatrachus*. I see no way of deciding which alternative is the more likely, and undoubtedly others (less parsimonious) could be devised. The two alternatives I discuss are diagrammed in figures 6 and 7.

Parker (1934, p. 10) set forth the opinion that the Asterophryinae and Sphenophryinae are closely related. In a number of respects, such as the protrusile tongue, eleutherothine maxillae, and presence of a full complement of ventral elements in the pectoral girdle of some genera, the Sphenophryinae are less specialized than the Asterophryinae. The asterophryine genus

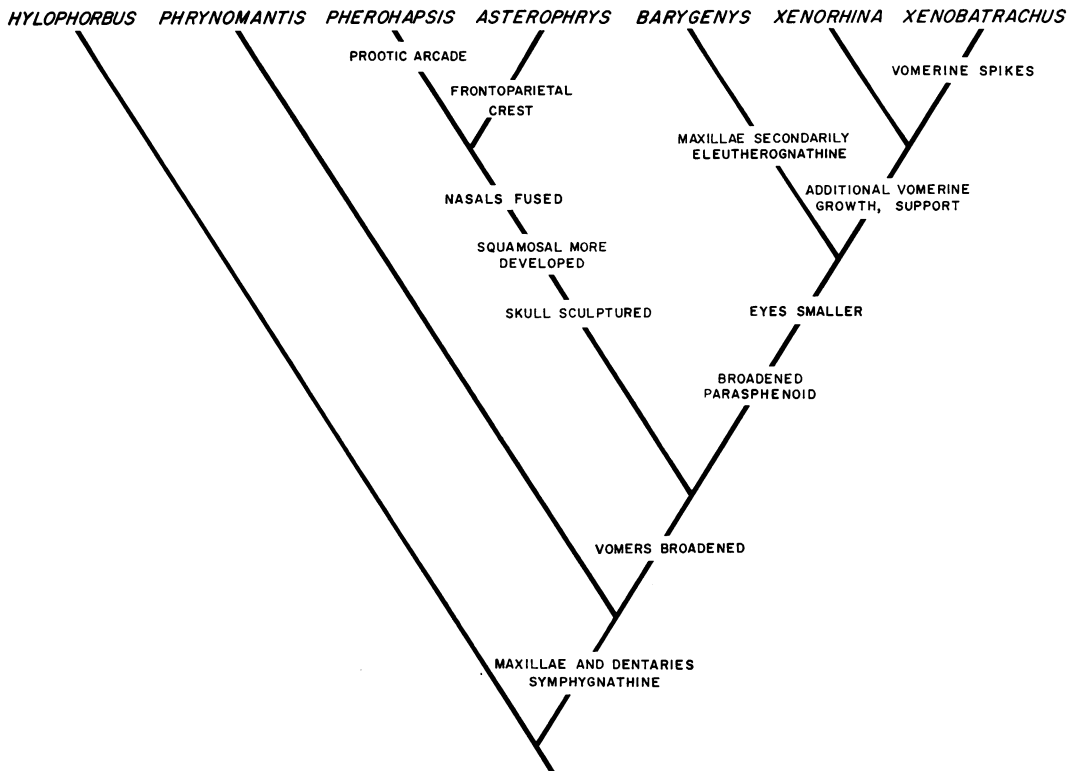


FIG. 7. Alternative proposed phylogeny of asterophryine genera. Where a label lies between or crosses two branches, parallel development of the same character is presumed (see text and fig. 6).

that I consider the most primitive, *Hylophorbus*, differs from *Cophixalus* of the Sphenophryninae only in having the tongue less free and in having a diplasiocoelous rather than procoelous vertebral column. Therefore, it may be that the Asterophryinae sprang from stock much like the present-day *Cophixalus*. I see no benefit in speculating at the present time on just when this might have occurred or what geographic relationships may have influenced the evolution of the two groups.

KEY TO THE GENERA OF THE ASTEROPHRYINAE

The genera are defined largely on the basis of features of the skull, some of which are not readily accessible to superficial dissection. I have utilized external features to as great an extent as possible, but some dissection will be necessary. The condition of the maxillae with respect to presence or absence of contact in front of the

premaxillae is easily determined by loosening the skin at the anterior edge of the upper jaw and reflecting it on the snout, whereupon the bones can be seen. The roof of the mouth is best observed (for presence or absence of vomerine spikes) by separating the skin and muscles from the margin of the lower jaw and folding the floor of the mouth out of the way. The presence or absence of a sheet of bone between squamosal and maxilla can be determined by probing with a needle and, if necessary, confirmed by loosening and reflecting the skin.

1. Anterior ends of maxillae well separated (fig. 2, upper) 2
- Anterior ends of maxillae in sutural contact or closely (but loosely) approximated (fig. 2, lower) 3
2. Fingers long, with prominent subarticular tubercles and small discs (fig. 10C); eyes larger, Eye/S-V, 0.11 or greater. *Hylophorbus*
- Fingers short, without subarticular tubercles, or terminal discs, bluntly pointed (fig. 11); eyes smaller, Eye/S-V, 0.09 or smaller . . . *Barygenys*

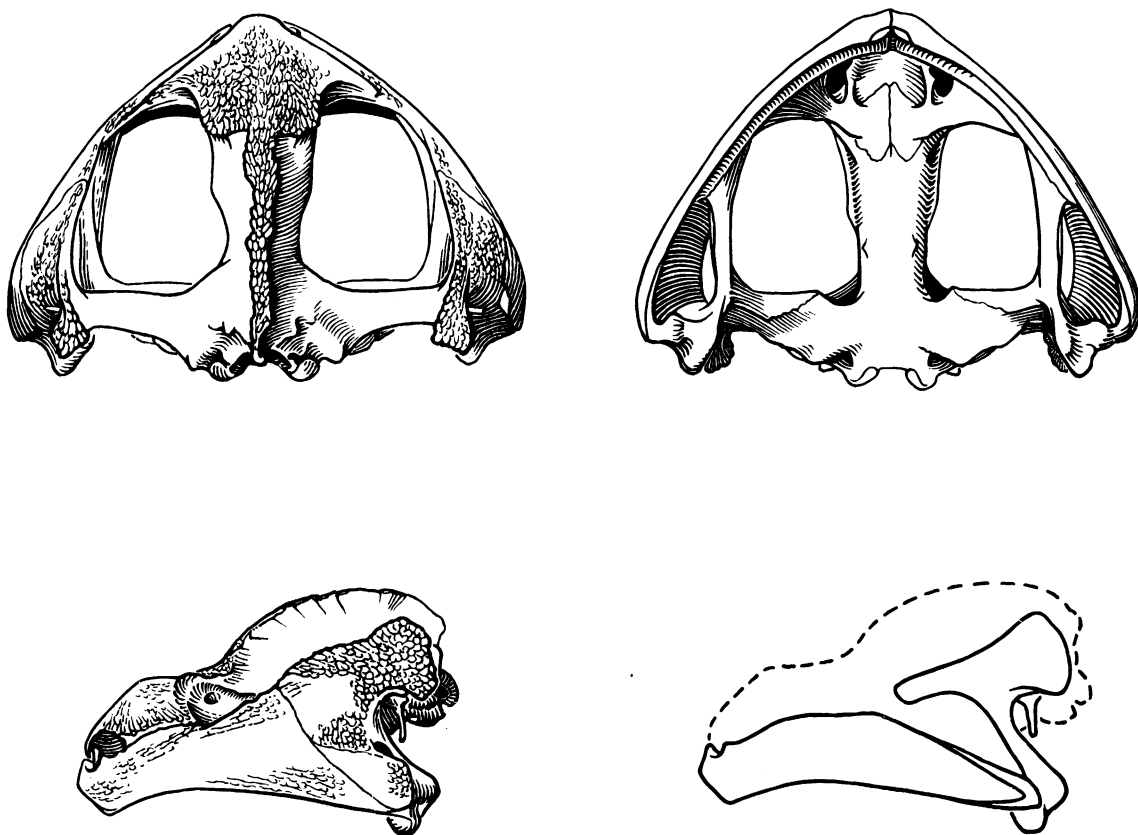


FIG. 8. Skull of *Asterophrys turpicula* (AMNH 78099) in dorsal (upper left), ventral (upper right), and lateral (lower left) views. Figure at lower right indicates condition seen in other skulls, without connection anteriorly between squamosal and maxilla. $\times 2.5$.

3. One or two prominent spikes on each vomer (fig. 3I) *Xenobatrachus*
Vomers without spikes, although small odontoids may be present 4
4. Head extremely broad, HW/S-V averaging about 0.50, rarely as low as 0.46; usually with one or more cutaneous projections on upper eyelid *Asterophrys*
Head narrower, HW/S-V rarely as great as 0.45; no cutaneous projection on upper eyelid 5
5. Area behind eye (between squamosal and maxilla) occupied by a broad subdermal sheet of bone *Pherohapsis*
No sheet of bone between squamosal and maxilla immediately behind eye 6
6. Eyes relatively small, Eye/S-V mean 0.09 or less, maximum observed in all species 0.097
Eyes relatively large, Eye/S-V mean 0.10 or greater, minimum observed in all species 0.083 *Phrynomantis*

GENUS *ASTEROPHRYS* TSCHUDI

Asterophrys TSCHUDI, 1838, p. 82 (type-species by monotypy, *Ceratophrys turpicula* Schlegel [1837-1844]).

DIAGNOSIS: *Asterophrys* is characterized by the following features of the skull: nasal bones rugose and fused, with no suture visible; frontoparietal bones compressed dorsally into a high thin crest with narrow, rugose dorsal edge; squamosals heavy and rugose, occasionally broadly joined to the maxillae anteriorly but not meeting the frontoparietals.

No other genus of the Asterophryinae has the frontoparietal crest that is so conspicuous in *Asterophrys*. Rugosity of the roofing bones, fusion of the nasals, and extensive lateral development of the squamosal are shared by *Asterophrys* and *Pherohapsis*, but the latter lacks the frontoparietal crest (the area is rugose and slightly concave)

and has a bony arcade connecting the squamosal and frontoparietal on each side.

CONTENT: *Asterophrys turpicula* is the only known species.

DESCRIPTION: The nasal bones are fused, with no trace of a suture visible dorsally, and with their common surface rugose in a vermiculate pattern. The frontoparietals are compressed into a dorsal crest, the narrow edge of which is rugose in the manner of the nasals. The maxillae form a firm, broad anterior suture. In one specimen, the squamosals and maxillae are joined anteriorly by a broad sheet of bone (fig. 8), whereas in six others there is the more typical dorsal, anterior projection of the squamosal, with a gap between the anterior edge of the squamosal and the dorsal edges of the maxilla and quadratojugal. In all instances, however, the squamosal is broad and both it and the maxilla have rugose surfaces. The vomers flare along their midline contact, with slightly more anterior than posterior projection (fig. 3F). A thin, anterior vomerine process is present mesial to the internal naris; the area between the processes is heavily calcified cartilage. The braincase has a notable posterior taper. Anteriorly, the parasphenoid is about 65 per cent of the width of the frontoparietals. The dentaries form a median suture and are fused with the mento-meckelian bones.

Brongersma (1953, pp. 573–575) has given a detailed description of the skeleton and soft parts, from which I quote: “The vertebral column is diplasiocoelous: the anterior seven vertebrae are procoelous, the eighth vertebra is biconcave, the sacral vertebra is biconvex with two condyles for the coccyx. The sacral diapophyses are moderately dilated. Procoracoid, clavicles, and omosternum are absent. Terminal phalanges T-shaped. . . .

“There are two palatal ridges. The anterior is poorly developed; it is very short, and shows faint traces of being divided into a few globose tubercles; on either side of this ridge one or two feebly developed tubercles may be present. . . . The posterior palatal ridge is denticulated; it shows from 9 to 11 pointed denticles.

“The tongue is adherent; it shows a more or less marked median groove, ending posteriorly in a pouch. In the fresh specimens two parts of the tongue may be distinguished; a horseshoe-shaped part forming the anterior and anterolateral borders, distinguished by a bluish color; the central and posterior parts of the tongue are

whitish. . . .” Brongersma (*loc. cit.*) illustrated the vomers, terminal phalange, and tongue.

See the following species account for external characteristics.

DISTRIBUTION: See species account.

Asterophrys turpicula (Schlegel)

Figure 9

C[erato]phrys. turpicula SCHLEGEL, 1837 (1837–1844), p. 30 (type locality, “west coast of New Guinea,” defined by Brongersma [1953, p. 573] as “Lobo district, Triton Bay, Dutch New Guinea”; syntypes [2], RMNH 2153, collected by S. Müller in August, 1828).

Asterophrys turpicula: TSCHUDI, 1838, p. 82 (new genus proposed, with *turpicula* the type species).

Cerato]phrys turpicula: S. MÜLLER, 1840, p. 24.

Cerato]phryne turpicula: SCHLEGEL, 1858, p. 57.

Asterophrys turpicula: LEUNIS, 1883, p. 614.

Asterophrys leopoldi WITTE, 1930a, p. 131 (type locality Arfak Mountains, Vogelkop Peninsula, West Irian, elevation 1000 m.; holotype IRSNB 1018, collected by Prince Leopold of Belgium on March 8, 1929).

Asterophrys steini AHL, 1932, p. 894 (type locality, Jobi Island, West Irian; holotype, ZMB 34107, collected on March 7, 1931, by G. H. W. Stein).

DIAGNOSIS: This is a moderately large asterophryine (S–V up to 65 mm.) with an extremely broad head (about 50 per cent of snout-vent length), internarial distance less than distance from eye to naris, and usually with prominent cutaneous appendages on the eyelids. No other asterophryine normally has so broad a head. The only Papuan microhylid likely to be confused with *A. turpicula* is *Genyophryne thomsoni*, a member of the Sphenophryninae, which is distinguished by its smaller size (maximum recorded S–V length 38 mm.), smaller eyes, more widely spaced nostrils (E–N/IN typically is less than 1.0), and lack of finger discs.

DESCRIPTION: This is a heavy-set, broad-headed, short-legged species of frog. The head width is typically half the body length and is equal to or slightly less than the greatest width of the body. The largest specimen I examined measured 62 mm. from snout to vent; Parker (1934, p. 67) recorded a length of 65 mm., presumably based on a specimen (Dresden Museum, from the Torricelli Mountains) that I did not examine. The eyes are moderately large and the internarial distance invariably less than the distance from eye to naris. The tympanum

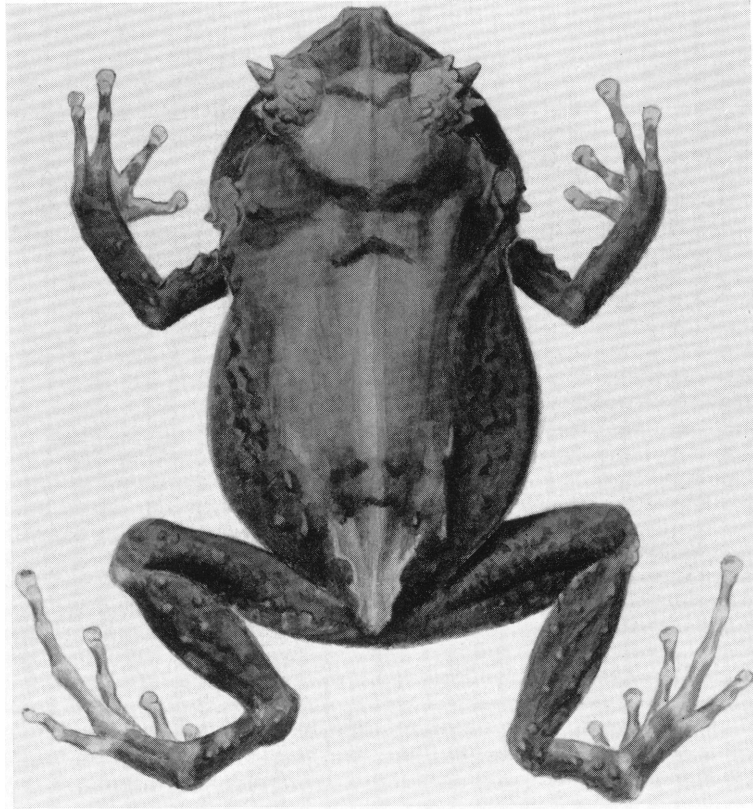


FIG. 9. *Asterophrys turpicula* (SW 139) in dorsal aspect. $\times 1.5$.

is distinct, its horizontal diameter about one-half to two-thirds that of the eye. The canthus rostralis is angular but not sharp, the loreal region nearly vertical and slightly concave, the snout truncate.

The skin of the middorsal area is relatively smooth, but other surfaces are warty. Wartiness is especially evident on the sides of the body and upper surfaces of the limbs. Two warts are prominent near the mental symphysis. The chin and other ventral surfaces are smoother than the sides of the body but definitely wartier than the middorsal region. All individuals show some warts on the upper eyelids, and in some there are elongate cutaneous projections that extend well beyond the edge of the eyelid. A slight fold of skin passes diagonally from the posterior corner of the eye above and behind the tympanum.

The relative lengths of the fingers are $3 > 4 > 2 > 1$ (or $4=2$) (fig. 10A). The tips of the fingers and toes are slightly broadened, those of the toes a bit larger than those of the fingers. The en-

largement in each case is no more than one and one-half times the width of the narrowest part of the penultimate phalange. I can find no terminal groove in the finger discs, although a slight groove is present on the toes. Rounded, relatively prominent subarticular tubercles are present on toes and fingers. The only other tubercles are low, rounded inner metacarpal and inner metatarsal tubercles.

Preserved specimens are dark gray-brown dorsally, often with the middorsal area from eye level to cloacal opening paler but incorporating dark brown markings. The chin is dark brown, but this color gives way to a gray-brown mottling posteriorly on the abdomen and under surfaces of the hind legs. Brongersma (1953, pp. 576-578) gave detailed color notes on specimens from the Vogelkop Peninsula, and reported that the color pattern of one in life "was made up of different shades of brown, of black, and of cream colour."

VARIATION IN PROPORTIONS: Means are ac-

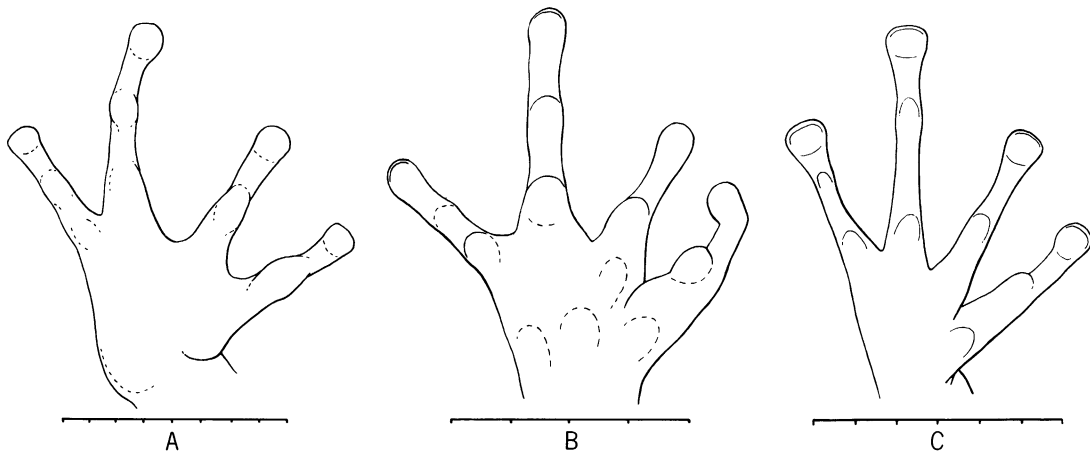


FIG. 10. Hands in palmar view. A. *Asterophrys turpicula*. B. *Pherohapsis menziesi*. C. *Hylophorbus rufescens*. Scale lines subdivided in millimeters.

accompanied by their standard errors; ranges are given in parentheses. In all instances except E-N/IN (where $N=13$), the data were taken from 14 specimens: TL/S-V, 0.367 ± 0.006 (0.33–0.41); HW/S-V, 0.498 ± 0.006 (0.46–0.52); Eye/S-V, 0.111 ± 0.002 (0.097–0.124); E-N/IN, 1.27 ± 0.033 (1.12–1.45).

TAXONOMIC NOTES: Brongersma (1953) compiled a detailed synonymy for this species. He considered Schlegel rather than “Müller in Schlegel” (Parker, 1934, p. 66) the author and noted that *turpicula*, the spelling used by both Schlegel and Müller in subsequent publications, should be used in place of the erroneous *turpicola*.

Both Parker (1934, p. 66) and Brongersma (1953, pp. 572, 578, 579) treated *Asterophrys steini* Ahl, with question, as a synonym of *turpicula*. Brongersma has presented a good case for the synonymizing of *steini* in disposing of all but one supposed difference between the species. The remaining difference—16 denticles in the posterior palatal ridge compared with nine to 13—scarcely justifies giving specific status to *steini*. I have not examined the type specimen of *steini*, but the illustrations (Ahl, 1932, p. 895) show a frog virtually identical with *turpicula* I have examined.

That *Asterophrys leopoldi* is a synonym of *turpicula* was questioned by neither Parker nor Brongersma. I have examined the holotype of *leopoldi* and concur with its synonymization.

ECOLOGICAL NOTES: Brongersma (1953, p. 578) recorded a lizard (*Carlia fusca*), lizard eggs,

and insect remains in the stomachs of specimens from the Vogelkop. Fred Parker reported (*in litt.*) that *turpicula* “is a strange animal—calls like a kitten’s miaow, and bites and attacks hands quite viciously.” It is curious that similar behavior and similar bizarre appearance are found in such distantly related forms as *Asterophrys*, a hyloid frog, *Hemiphractus panamensis* (Myers, 1966), and leptodactylids such as *Ceratophrys* (Gadow, 1901, p. 218; Cochran, 1961, p. 64).

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 23): The few specimens of this species in collections come from widely scattered localities, suggesting that the species is broadly distributed throughout the lowland rain forest of New Guinea. A record for the Northern District of Papua (Burt and Burt, 1932, p. 483) was based on a specimen of *Genyophryne thomsoni* (Zweifel, 1956, p. 3).

West Irian: Triton Bay, Lobo District (RMNH 2153, 2 syntypes); Ajamaroe, Vogelkop Peninsula (RMNH 9830); Erokwer, Vogelkop Peninsula (RMNH 9831, 2 specimens); Komara, Vogelkop Peninsula (Brongersma, 1953, p. 573); Aifat, Vogelkop Peninsula (RMNH 16655); Waren, Vogelkop Peninsula (RMNH 16656); Jobi Island (Ahl, 1932; *Asterophrys steini*); Arfak Mountains at 1000 m. (3280 ft.) (IRSNB 1018, holotype of *Asterophrys leopoldi*); Tanah Merah (RMNH 16653).

Territory of New Guinea, West Sepik District: Torricelli Mountains (Wandolleck, 1911, p. 14); Mt. Nibo, Torricelli Mountains, 12 mi.

NE Lumi (AMNH 78098); Mt. Menawa, Bewani Mountains, 10 mi. NE Uta (AMNH 78099).

Territory of Papua, Western District: Olsobip (UPNG 1548); Didessa, north side of Mt. Bosavi (SW 139). Gulf District: Omati (MCZ 28200; locality given by Loveridge [1955, p. 1] as "Omati, near Port Moresby"; Omati is 20 mi. W Kikori, about 250 mi. NE Port Moresby.)

GENUS *BARYGENYS* PARKER

Barygenys PARKER, 1936, p. 73 (type-species by original designation, *B. cheesmanae* Parker).

DIAGNOSIS: *Barygenys* is the only genus of the Asterophryinae in which the maxillae do not meet in front of the premaxillae, and the dentaries form a median suture and fuse with the mento-meckelian bones. *Hylophorbus* shares the eleutherognathine condition of the upper jaw with *Barygenys* but has the same free condition in the lower jaw. Externally, the two genera are easily distinguished by eye size (Eye/S-V, 0.09 or less in *Barygenys*, 0.11 or greater in *Hylophorbus*) and the absence of terminal discs on the fingers of *Barygenys*. There is superficial similarity between *Barygenys* on the one hand and *Xenobatrachus* and *Xenorhina* on the other. The three vertical ridges on the snout of most *Barygenys* will usually distinguish it from the other genera, but the condition of the upper jaw (symphygnathine in the other genera) must be determined for positive identification.

CONTENT: Parker (1936) erected the genus

Barygenys to accommodate *Xenorhina atra* Günther (*Metopostira atra*: Parker, 1934) and *Barygenys cheesmanae*, the latter described as a new species. Zweifel (1963) described *B. exsul*, and two new species are described herein, giving a total of five.

DESCRIPTION: The species of *Barygenys* are frogs of small to moderate size (26 to 41 mm. S-V) with squat body, narrow head, and tiny eyes. The snout in four of the five species bears three vertical ridges, and traces of these ridges can be detected in the fifth species. These ridges are unique among the genera of Asterophryinae and are the external manifestation of slight protuberances at the contacts between the premaxillary bones on the midline and the premaxillary and maxillary bones laterally. The only other distinguishing character in external morphology is the shape of the fingers. They are unusually short and taper to rather sharply rounded tips (fig. 11). Other forms with fingers of similar relative length have less tapered fingers with blunter tips.

Members of this genus have the following characteristics, in addition to those mentioned above in the diagnosis: skull relatively deep; nasals large, in contact along midline and with frontoparietals, excluding ethmoid from dorsal surface of skull; anterior arm of squamosal short, not approaching maxilla; parasphenoid more than half as broad as frontoparietals; no arch of bone in prootic region; vomers large, undivided, expanded and in contact mesially, with their postchoanal portions overlying the

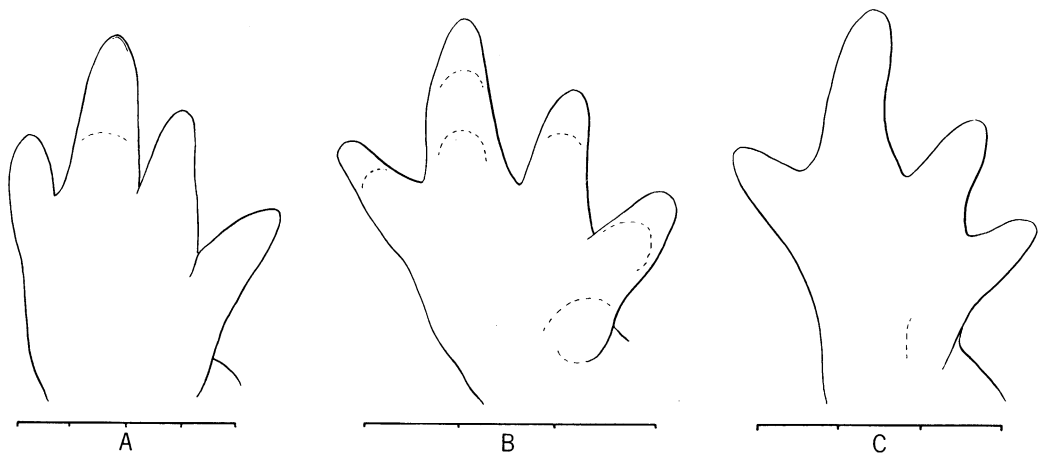


FIG. 11. Hands of *Barygenys* in palmar view. A. *B. atra*. B. *B. nana*. C. *B. flavigularis*. Scale lines subdivided in millimeters.

TABLE 4
BODY PROPORTIONS IN SIX SAMPLES OF THE GENUS *Barygenys*

| Sample | N | TL/S-V | | HW/S-V | | Eye/S-V | | E-N/IN | |
|------------------------|----|-------------------|------------------------|-------------------|------------------------|-------------------|------------------------|-------------------|------------------------|
| | | Mean | Range $\pm\sigma_m$ | Mean | Range $\pm\sigma_m$ | Mean | Range $\pm\sigma_m$ | Mean | Range $\pm\sigma_m$ |
| <i>B. atra</i> | 3 | 0.397 | — (0.38–0.41) | 0.307 | — (0.30–0.31) | 0.044 | — (0.039–0.049) | 0.703 | — (0.66–0.78) |
| <i>B. cheesmanae</i> | 3 | 0.233 | — (0.23–0.24) | 0.337 | — (0.32–0.36) | 0.057 | — (0.055–0.061) | 0.543 | — (0.52–0.57) |
| <i>B. exsul</i> | 2 | 0.34 | — (0.34) | 0.330 | — (0.32–0.34) | 0.053 | — (0.052–0.055) | 0.555 | — (0.50–0.61) |
| <i>B. flavigularis</i> | 3 | 0.261 | — (0.26–0.27) | 0.367 | — (0.35–0.39) | 0.084 | — (0.077–0.089) | 0.745 | — (0.67–0.79) |
| <i>B. nana</i> | | | | | | | | | |
| Eastern Highlands | 8 | 0.240 \pm 0.007 | (0.22–0.27) | 0.342 \pm 0.007 | (0.30–0.36) | 0.082 \pm 0.002 | (0.075–0.087) | 0.622 \pm 0.022 | (0.53–0.73) |
| Western Highlands | 16 | 0.262 \pm 0.004 | (0.23–0.29) | 0.343 \pm 0.006 | (0.31–0.38) | 0.077 \pm 0.001 | (0.070–0.085) | 0.691 \pm 0.010 | (0.61–0.76) |

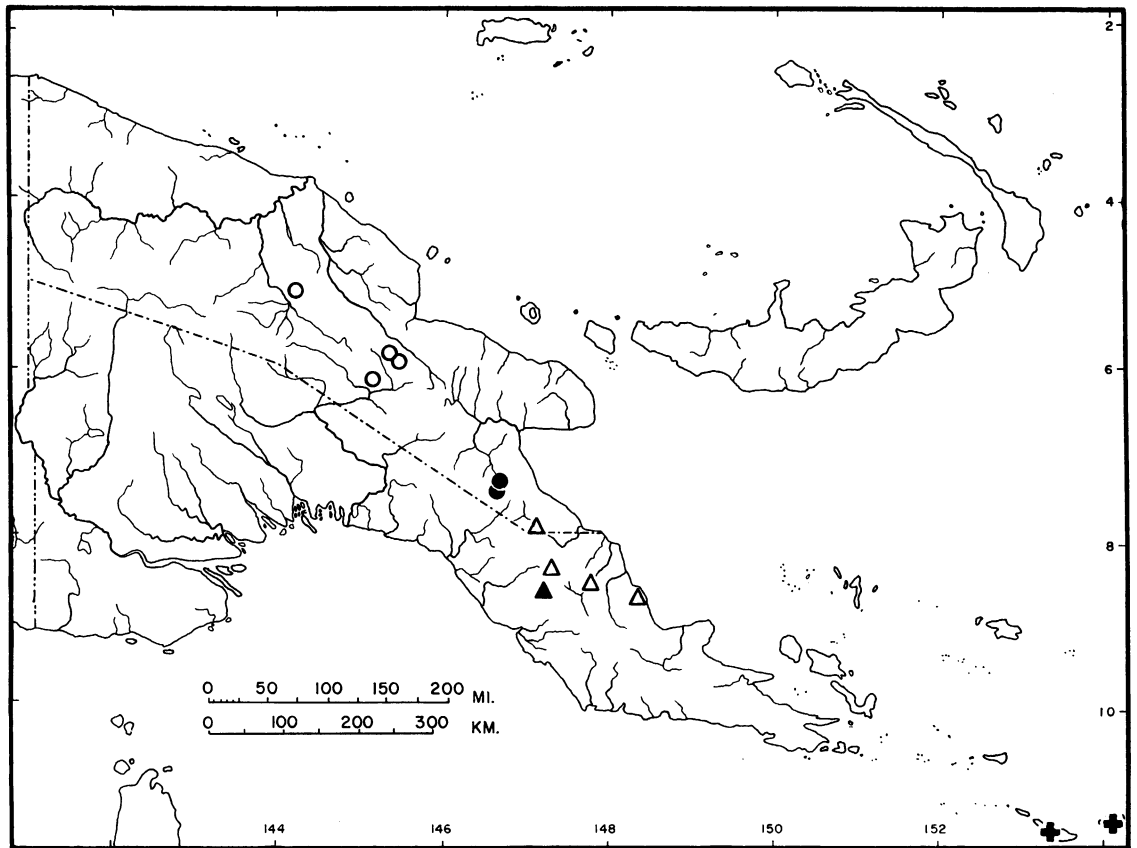


FIG. 12. Distribution of species of *Barygenys*. Open circles, *B. nana*; closed circles, *B. flavicularis*; open triangles, *B. atra*; closed triangles, *B. cheesmanae*; crosses, *B. exsul*.

palatine region; clavicles and omosternum absent; sternum cartilaginous; terminal phalanges T-shaped; pupil horizontal; tongue large, subcircular, almost entirely adherent behind, and with a medial longitudinal furrow; a denticulated dermal ridge across the palate in front of the pharynx, preceded by a shorter one (partly from Parker, 1936, pp. 73-74).

DISTRIBUTION: The genus *Barygenys* is known from only a few localities scattered from the high mountains of the Western Highlands of the Territory of New Guinea to the outermost islands of the Louisiade Archipelago 700 mi. to the southeast (fig. 12). There are no known instances of sympatry between species of *Barygenys*.

KEY TO THE SPECIES OF *Barygenys*

1. Toes with distinct discs bearing terminal grooves 2
- Toes without discs 3

2. Snout lacking distinct vertical ridges *atra*
- Snout bearing three low but distinct vertical ridges *exsul*
3. Maximum snout-vent length about 26 mm., Eye/S-V equal to 0.070 or greater 4
- Maximum snout-vent length about 40 mm., Eye/S-V, 0.061 or less *cheesmanae*
4. Throat yellow, abruptly differentiated from gray of chest; snout ridges weak *flavicularis*
- Throat not sharply differentiated in color and pattern from rest of ventral surfaces; snout ridges strong *nana*

Barygenys atra (Günther)

Figure 13

Xenorhina atra GÜNTHER, 1896, p. 184 (type locality: "A single specimen was obtained by Mr. W. Day of the unfortunate Clarke Expedition on the Clyde River, within a few miles of the frontier between British and German New Guinea." The Clyde River is now known as the Mambare River. It is

entirely within the Territory of Papua, draining the northeastern flank of the Wharton Range from Mt. Albert Edward to Mt. Bellamy and emptying into the southern edge of Huon Gulf. The type-specimen probably was found within 60 miles [on the river] of the coast; see comments that follow under distribution; holotype, BMNH 1947.2.10.78 [formerly 96.7.7.3], obtained by W. Day in 1895, probably in July or August).

Xenorhina oxycephala: VAN KAMPEN, 1923, p. 132 (in part).

Metopostira atra: PARKER, 1934, p. 70.

B[arygenys]. *atra*: PARKER, 1936, p. 76.

DIAGNOSIS: *Barygenys atra* differs from the other three species of *Barygenys* in lacking distinct vertical ridges on the snout and in having relatively longer legs (minimum known TL/S-V=0.38) and relatively smaller eyes (maximum known Eye/S-V=0.049). It differs additionally from *B. nana* and *B. flavigularis* in greater maximum size, 41 mm. snout-to-vent contrasted with 26 to 27 mm., and from *flavigularis*, *nana*, and *cheesmanae* in possessing toe discs with terminal grooves.

DESCRIPTION: The following description is composite, being based on the descriptions published by Günther (1896), Parker (1934), and my examination of the type-specimen and two other individuals. The proportions specified are those of the holotype.

Barygenys atra is a heavy-bodied frog with a small head (HW/S-V, 0.31), moderately long hind limbs (TL/S-V, 0.41), and pointed nose. Parker (1934, p. 70) gave the maximum length as 42 mm. The snout bears only the faintest trace of the three vertical ridges prominent in the other species of *Barygenys*. The external nares are

widely spaced (E-N/IN, 0.78) and the eyes are extremely small (Eye/S-V, 0.039). The loreal region is oblique and very shallowly concave, with no canthal angle. The outline of the tympanum is scarcely visible; the horizontal diameter of the tympanum is approximately the same as the length of the orbit.

There is a slight fold of skin behind the tympanum, but elsewhere the skin is smooth.

The fingers (fig. 11A) are short and broad at the base, tapering to narrowly rounded tips. Only the third finger bears a faint terminal groove. There are no subarticular tubercles, and the inner metacarpal tubercle is a low, rounded elevation. The relative lengths of the fingers are $3 > 4 = 2 > 1$. The tips of the toes are broadened into small discs all with terminal grooves. The toes are unwebbed. Subarticular tubercles and the inner metatarsal tubercle are represented only by low, smooth elevations. The relative lengths of the toes are $4 > 3 > 5 > 2 > 1$.

The anterior ends of the maxillary bones are well separated, but the dentaries meet on the midline.

The dorsal color (in preservative) is dark purplish brown, with the snout region slightly lighter. An irregular dark band begins behind the eye, is interrupted above the front leg, and continues to the groin. The band is faintly edged above with white but is not clearly distinguished from the ventral color. A thin, indistinct, light vertebral line is present and a similar line extends along the dorsal surface of the thigh. A series of dark spots runs from a point above the groin to near the cloacal opening. The dorsal surface of the body is faintly speckled with light pigment, especially laterally. The legs are similarly marked, with the light color tending to be arranged in short lines. The ventral surfaces of body and legs are similar in color to the dorsal, but are slightly paler and more mottled. The palms are distinctly paler than other ventral surfaces. This description of color pattern is based on SAM 6001, but does not differ importantly from descriptions given by Günther (1896) or Parker (1934).

A living individual from Garaina (fig. 13) had the following features of color and pattern: dorsal color of body and limbs reddish brown; black spots with brown centers on posterior part of back; grayish crossbanding on lower hind limbs; a black "seat" patch; snout ridges gray, upper surface of snout rugose and much grayer

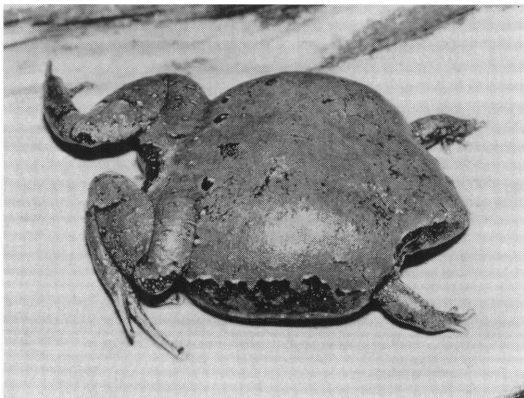


FIG. 13. *Barygenys atra* (AMNH 82902).

than brown of head; side of face anterior to eye same gray as snout; sides of body very dark gray, almost black, spotted with same brown as dorsum; chin, chest, abdomen, and undersides of legs and feet dark gray with light gray mottling; iris reddish brown, similar to dorsal color.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 41; HW, 12.8; TL, 16.8; Eye, 1.6; E-N, 2.5; IN, 3.2.

COMPARISON WITH OTHER SPECIES: *Barygenys atra* is distinct from the other three species of *Barygenys* and cannot easily be confused with them. *Barygenys cheesmanae*, *B. flavigularis*, and *B. nana* have prominent ridges on the snout and lack discs on the toes, whereas *B. atra* lacks distinct snout ridges and has toe discs. The relationship of *atra* to *exsul* evidently is much closer. The snout ridges of *exsul* are less well developed than those of *cheesmanae* or *nana*, and the toe discs are the same as in *atra*. *Barygenys atra* and *B. exsul* share a similar dark gray to purplish brown ground color in preservative, but details of color pattern differ. *Barygenys exsul* stands between *atra* and the other two species in relative length of hind legs.

Despite the similarity of *Barygenys atra* and *B. exsul*, I think that the relationship is specific rather than subspecific. The differences in proportions (leg length and eye size) and color pattern together with the isolation of *exsul* in the Louisiade Archipelago 400 miles from the known range of *atra* recommend treating the forms as different species.

DISTRIBUTION AND SPECIMENS EXAMINED: So far as is known, *B. atra* is confined to the northern watershed of the eastern "tail" of New Guinea, from Garaina to Popondetta (fig. 12). Territory of Papua, Northern District: Mambare River, presumably within 60 mi. of the mouth (BMNH 1947.2.10.78, holotype); Martyr's Memorial School, Popondetta (SAM 6001) Albert Edward Ranges, 6000 ft. (1830 m.) (Parker, 1934, p. 70).

Territory of New Guinea, Morobe District: Garaina, 2300 ft. (700 m.) (AMNH 82902).

The type locality cannot precisely be fixed. According to Murray (1912, pp. 326-327), Clarke and his party (including Day) had progressed 45 miles up the Mambare River when natives attacked, killing Clarke and forcing the rest to return downriver without their equipment or supplies. Another group composed in

part of survivors of the Clarke Expedition (possibly including Day) soon organized and penetrated upriver to a point 15 mi. above the point of the attack before returning. The type-specimen may have been obtained on this foray rather than on the original expedition. The elevation at which the type was obtained certainly was below 1000 ft. (300 m.). Also in the same collection were lizards and a frog typically found in lowland rain forest: *Emoia caeruleocauda*, *Sphenomorphus jobiensis*, *Cyrtodactylus louisiadensis*, and *Litoria infrafronata* (Günther, 1896, p. 185).

Barygenys cheesmanae Parker

Barygenys cheesmanae PARKER, 1936, p. 74 (type locality, "Mt. Tafa [8500 ft.], [Central District] Papua" holotype, BMNH 1947.2.10.84 [formerly 1935.3.9.125], a male obtained by L. E. Cheesman in February, 1934).

Baragenys cheesmanae: ZWEIFEL, 1956, p. 9, fig. 4 (misspelled generic name).

DIAGNOSIS: The characters that in combination distinguish *Barygenys cheesmanae* from its congeners are the presence of three vertical ridges on the snout, absence of discs on the toes, extremely small eyes (Eye/S-V mean 0.057), large body size (S-V to 40 mm.) and short hind limbs (TL/S-V mean 0.23).

Barygenys nana and *B. flavigularis* are much smaller than *B. cheesmanae* (maximum snout-vent length, 26-27 mm.) and have relatively larger eyes (Eye/S-V mean 0.08). Both *B. atra* and *B. exsul* have toe discs and longer hind limbs (TL/S-V minimum is 0.38 in *atra*, 0.34 in *exsul*), and *atra* differs in addition in lacking distinct ridges on the snout.

DESCRIPTION: The following description is based on that of the holotype and paratypes published by Parker (1936, pp. 74-75), supplemented by my examination of the holotype and two topotypic specimens. Proportions and measurements given are those of the holotype.

The body is globose with narrow head (HW/S-V=0.32), very short hind limbs (TL/S-V=0.24) and pointed snout. There are three conspicuous vertical ridges on the snout. The central ridge extends from near the margin of the lip to the level of the nostrils, whereas the two lateral ridges terminate slightly below and mesial to the nostrils. The nostrils are widely spaced (E-N/IN=0.52). The loreal region is oblique and the

canthal area rounded, without trace of a canthal ridge. Parker (1936, p. 74) stated that the loreal region is convex. I did not make note of this feature of the type-specimen, but the region is shallowly concave in a topotypic specimen. The tympanum is too indistinct externally to be measured.

The skin is largely "smooth above, with a few small scattered pustules" (Parker, 1936, p. 75). In a topotype the pustules are most prominent between the eyes and in the postsacral region. There is a "slight fold from the eye above the tympanic region" (Parker, *loc. cit.*), that in a topotype extends behind the eye at a right angle to the axis of the body.

The fingers are short and broad at the base, tapering to rounded tips that are more nearly pointed on the first and second fingers, blunter on the third and fourth. The relative lengths of the fingers are $3 > 2 > 4 > 1$; there are no terminal grooves. The toes are unwebbed and have rounded tips without terminal gooves or dilations. The relative lengths of the toes are $4 > 3 > 5 > 2 > 1$. No subarticular tubercles are present on hands or feet, and the inner metacarpal and inner metatarsal tubercles are scarcely indicated as low elevations.

The holotype is "Pale brown above, with a few irregularly scattered dark spots. Hind limbs darker and the thickened skin of the snout with a grey tinge. Lower surfaces dirty brown with some minute white dots." Among the 13 paratypes (topotypes), the "groundcolour varies from a brownish yellow to a deep red-brown, with more or less black spots irregularly scattered on it. Some pink spots may also be present and a reddish colour may be present on the hind limbs. The lower surfaces vary from dirty yellow to brown" (Parker, 1936, p. 75).

MEASUREMENTS: S-V, 38; HW, 12.2; TL, 9.1; Eye, 2.1; E-N, 1.6; IN, 3.1. Parker (1936, p. 75) gave the maximum length in his series of 14 specimens as 40 mm.

COMPARISON WITH OTHER SPECIES: The absence of toe discs, presence of prominent snout ridges, and short limbs are features common to *Barygenys cheesmanae*, *B. flavigularis*, and *B. nana* and set these species apart from *B. atra* and *B. exsul*. The larger body size of *cheesmanae* (to 40 mm., S-V) is its most obvious difference from *nana* and *flavigularis* (26-27 mm.). A marked difference in relative size of the eyes also distinguishes these two from *cheesmanae*, so

they cannot be regarded as merely dwarfed races of *cheesmanae*. That these three species occupy habitats at high elevations also allies and distinguishes them from the other two species.

ECOLOGICAL NOTES: Parker (1936, p. 76) reported that the "species lives in holes in the ground on Mt. Tafa, and the call of the male, heard throughout the day, was a peculiar drumming. The native name is 'Tunbera.'"

Archbold and Rand (1935, pp. 562-563) described the habitat at 2070 m. (ca. 6800 ft.) on the east slope of Mt. Tafa where a specimen was captured on June 2, 1933: "The country was rough with steep slopes of several hundred meters and more. Streams were numerous but small and there were no swampy areas. The forest from 2000 to 2200 meters was of trees surprisingly large for this altitude. . . . There were large trees, 35-45 meters tall . . . with of course many smaller trees between." The American Museum specimen was found by A. L. Rand on the ground in a clearing made in the forest (field notes).

DISTRIBUTION AND SPECIMENS EXAMINED: *Barygenys cheesmanae* is known only from elevations of 6800 to 8500 ft. (2070-2590 m.) on Mt. Tafa (fig. 12). The mountain, which has a maximum elevation of 2725 meters (8940 ft., Archbold and Rand, 1936, p. 559), is part of a spur that extends to the west of the main central mountainous ridge some 60 mi. N Port Moresby. Territory of Papua, Central District: Mt. Tafa, 8500 ft. (2590 m.) (BMNH 1947.2.10.84, holotype; MCZ 19921, paratype); Mt. Tafa, east slope, 2070 m. (6800 ft.) (AMNH 58008).

Barygenys exsul Zweifel

Figure 14

Baragenys exsul ZWEIFEL, 1963, p. 3 (generic name misspelled, type locality, "Abaleti, Rossel Island, Louisiade Archipelago [Milne Bay District], Territory of Papua, New Guinea, at an elevation between sea level and 50 meters"; holotype, AMNH 60103, obtained by Russell F. Peterson between September 26 and October 10, 1956).

DIAGNOSIS: *Barygenys exsul* differs from *B. cheesmanae*, *B. flavigularis*, and *B. nana* in possessing discs on the toes (absent from *cheesmanae*, *flavigularis*, and *nana*), and in having relatively longer hind legs (TL/S-V averages 0.23 to 0.26 in *cheesmanae*, *flavigularis*, and *nana*, is 0.34 in two *exsul*). *Barygenys atra* has longer hind limbs than

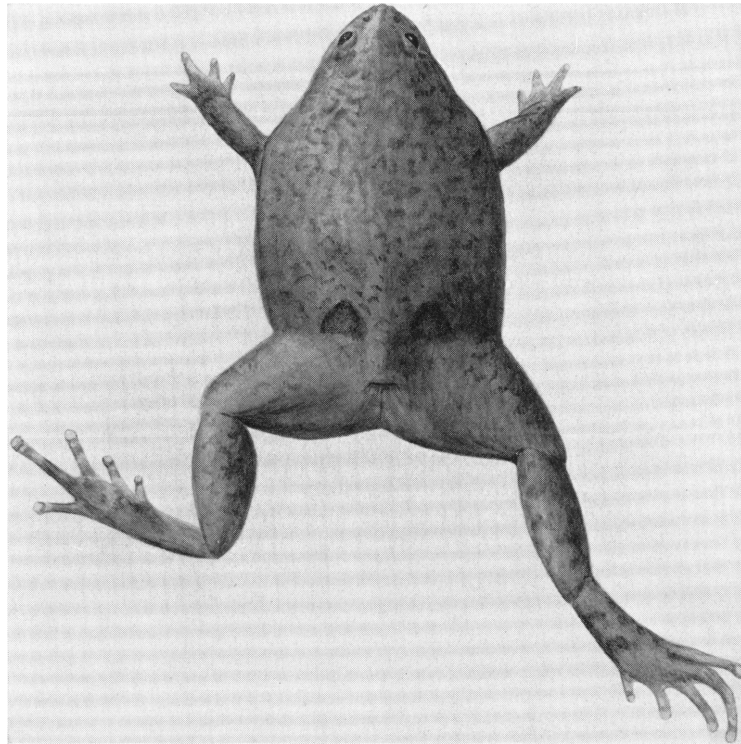


FIG. 14. *Barygenys exsul* (AMNH 60103, holotype), dorsal view. $\times 1.5$.

B. exsul ($TL/S-V=0.38-0.41$) and lacks the three vertical ridges on the snout seen in *exsul* and the other species.

DESCRIPTION: This composite description is based on the only two specimens of the species. Where measurements and ratios are given, the first pertains to the holotype.

Barygenys exsul has a heavy set body with narrow head ($HW/S-V=0.34, 0.32$) and limbs of moderate length ($TL/S-V=0.34, 0.34$). The snout is bluntly pointed and bears three indistinct vertical ridges. The nostrils are widely spaced ($E-N/IN=0.61, 0.50$), the loreal region gently sloping and shallowly concave with no canthal angle, and the eyes small ($Eye/S-V=0.052, 0.055$). The outline of the tympanum can scarcely be seen.

A fold of skin is faintly visible above the tympanum of the paratype, but none can be seen in the holotype. The skin elsewhere is smooth except for small, indistinct tubercles present dorsally on the lower hind legs of the holotype and for similarly indistinct ridges in the same region of the paratype.

The fingers are short and broad, with the tips of the third and fourth rounded, the first and second more pointed; there are no terminal grooves. There is scarcely any indication of sub-articular or metacarpal tubercles. The relative lengths are $3 > 4 = 2 > 1$. The toes are unwebbed, and the tips bear small but distinct discs, all with terminal grooves. Distinct subarticular, plantar, and metatarsal tubercles are lacking, although the position of the inner metatarsal tubercle is indicated by a slight elevation further distinguished by a lack of dark pigment. The relative lengths of the toes are $4 > 3 > 5 > 2 > 1$.

The dorsal ground color (in preservative) of the holotype is gray-brown. There is slightly darker vermiculation on the head and body, and indistinct, irregular dark bands cross the tibia. The chin, chest, abdomen, and lower surfaces of the limbs have a fine network of melanophores broken infrequently by light spots. These light spots are more numerous on the anterior part of the chin. The dorsal and ventral patterns grade smoothly into each other without a sharp line of demarcation. A dark spot is present on each side

of the lumbar region above the groin. The paratype differs in that the dorsal color is dark lead-gray, with little trace of pattern distinguishable. The pattern of the ventral surfaces is like that of the type, differing only in being darker.

MEASUREMENTS: S-V, 39, 36; HW, 13.0, 11.7; TL, 13.0, 12.5; Eye, 2.0, 2.0; E-N, 1.7, 1.5; IN, 2.8, 3.0; disc of 4th toe, 1.3, 1.8; penultimate phalange of fourth toe, 0.9, 1.2.

COMPARISON WITH OTHER SPECIES: Possession of toe discs and the relatively poor development of ridges on the snout ally *Barygenys exsul* with *B. atra* rather than with *B. cheesmanae*, *B. flavigularis*, or *B. nana*. The snout ridges are prominent in the last three species, but although distinctly present in *exsul*, are lower and less evident. One without prior knowledge of the ridges in the other three species would almost certainly overlook the faint trace of them present in *B. atra*. For other comparisons see the accounts of the other species.

ECOLOGICAL NOTES: No specific notes accompanied the type and paratype. Brass (1959, p. 55) characterized the type locality (Abaleti) as a region where "precipitation is very heavy, conceivably in excess of 200 inches a year." Collecting was carried on in both second-growth and primary rain forest. The habitat where the paratype was obtained on Sudest Island evidently was similar: "At camp level we were at about the middle altitudes and probably the climatic optimum of the great, continuous rain forest that covers most of the island. . . . Almost everywhere only a very shallow layer of litter and humus covered a stiff, yellow clay. . . . The forest . . . was very poor in undergrowth species, lianes and epiphytes" (Brass, 1959, p. 53).

DISTRIBUTION AND SPECIMENS EXAMINED: This species is known from only two specimens from the easternmost islands of the Louisiade Archipelago (fig. 12). Territory of Papua: Abaleti, Rossel Island, between sea level and 50 m. (160 ft.) (AMNH 60103, holotype); west slope of Mt. Riu, Sudest (Tagula) Island, between 250 and 350 m. (820-1150 ft.) (AMNH 60069, paratype).

Barygenys flavigularis, new species

Figure 15

HOLOTYPE: AMNH 82903, collected on Mt. Kaindi, Morobe District, Territory of New Guinea, at an elevation of about 7500 ft.

(2280 m.) on September 7, 1969 by R. G. Zweifel.

PARATYPES: BBM 3685 from the type locality, collected by Philip Colman, and BBM 3684 from the Bulldog Road, south-southeast of Wau, 2100-2700 m. (6890-8860 ft.), Morobe District, Territory of New Guinea, collected by J. Sedlacek.

DIAGNOSIS: *Barygenys flavigularis* differs from *B. atra*, *B. cheesmanae*, and *B. exsul* in its smaller size and relatively larger eyes. The largest of three adult specimens of *flavigularis* has a length from snout to vent of 27 mm., whereas adults of the other species reach at least 38 mm. The maximum ratio Eye/S-V in *cheesmanae* is 0.06, compared with a minimum of 0.08 in *flavigularis*, and the maximum is even lower in the other two species. Other differences include lower E-N/IN ratios in *cheesmanae* and *exsul* and longer legs in *atra*.

Barygenys flavigularis is most similar to *B. nana*, which it resembles in body size, leg length, and eye size. The nostrils are more widely spaced in *flavigularis* (E-N/IN mean 0.74, compared with 0.62 and 0.69 in two samples of *nana*), but the ranges of variation in the ratio E-N/IN overlap. The subjective impression that *nana* has a narrower and more pointed head is to some extent borne out by its lower HW/S-V ratio: mean for *nana* 0.34; for *flavigularis* 0.37. The snout ridges of *nana* are much more prominent, almost knifelike, compared with the low ridges of *flavigularis*. The contrast between yellow chin and gray abdomen so evident in *flavigularis* is not seen in *nana*, in which the chin is little if any paler than the chest and abdomen.

DESCRIPTION OF TYPE-SPECIMEN: The general form of this frog is rather chunky, with short legs (TL/S-V, 0.26), and the head distinctly narrower than the body (HW/S-V, 0.36). The nostrils are widely spaced (E-N/IN, 0.78), and the loreal region is an oblique plane with a rounded canthus. The snout bears three low, parallel vertical ridges. The eyes are small (Eye/S-V, 0.09), shorter than the snout, with upper lids each less than 40 per cent as wide as the interorbital space. The tympanum is scarcely visible and is about 62 per cent of the horizontal diameter of the eye. There is no fold of skin associated with the tympanum. The body is smooth above and below, with only slight pustulosity on the dorsal surfaces of the hind limbs.

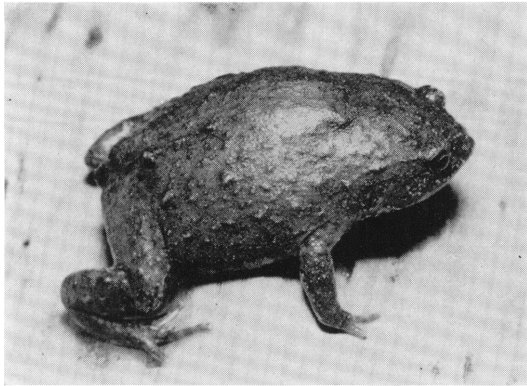


FIG. 15. *Barygenys flavigularis*
(AMNH 82903, holotype).

The fingers are short, broad, and pointed and lack both terminal grooves and subarticular tubercles (fig. 11C). There is a slight inner metacarpal elevation. The relative lengths of the fingers are $3 > 2 > 4 > 1$, of the toes $4 > 3 > 5 > 2 > 1$. The toes have more rounded tips than the fingers and are grooved, but lack terminal expansions. There are no subarticular tubercles, but a low inner metatarsal tubercle is present.

The pupil is a horizontally oriented oval.

The dorsal surfaces of the body and limbs were (in life) dark brown with indistinct reddish brown blotches. The three ridges on the snout were light gray. The inner three fingers, lower surfaces of front legs and throat were bright yellow with gray flecks. On the chest the yellow ground color was abruptly replaced by dark gray with lighter flecks, and this pattern persisted over the abdomen and undersides of the thighs; the lower legs were yellow and gray beneath. The iris was reddish brown.

MEASUREMENTS OF HOLOTYPE: S-V, 24.5; TL, 6.3; HW, 8.9; Eye, 2.1; E-N, 1.4; IN, 1.8; tympanum (horizontal), 1.3.

The holotype is a male, presumably adult.

VARIATION: Proportional variation is summarized in table 4. One of the paratypes measures 27.1 mm. snout to vent, the other 23.7. No marked variation in color pattern is evident in this small series. The collector of the topotype, Philip Colman, noted "yellow under throat, under forelimbs, and fore and hind digits," so this specimen evidently resembled the holotype closely in life. The other paratype has the same

ventral pattern and a trace of yellow remains on the throat.

COMPARISON WITH OTHER SPECIES: *Barygenys nana* is the only form that merits extended comparison with this new species, and nothing can be added to the material in the diagnosis. Certainly these two species are more closely related to each other than to other species in the genus. Insofar as material presently available indicates, the ventral color pattern and different development of the snout ridges are sufficient to distinguish *flavigularis* from *nana*. Several high ranges lie in the 130-mile gap between the closest localities for the two species, and it is quite possible that morphologically intermediate populations remain to be discovered in this little-known region. On the basis of present evidence, however, specific recognition is indicated.

ECOLOGICAL NOTES: I found the holotype in the daytime beneath a chunk of wood beside a trail through heavily mossed forest, and P. H. Colman, the collector of the topotype, noted similarly, "under rotting wood in Moss Forest." For a description of habitat conditions on Mt. Kaindi, see Brass (1964, pp. 182-185).

DISTRIBUTION AND SPECIMENS EXAMINED: The holotype and paratypes are the only specimens known (fig. 12). The type locality is about 3 mi. W Wau, Morobe District, and the locality on the Bulldog Road may be about 10 to 15 mi. SSE Wau (exact locality not given). Presumably the species is limited to high elevations; it should be looked for in disjunct montane habitats to the northeast (Mt. Missim), as well as in the Kratke Mountains to the northwest and south into Papua.

ETYMOLOGY: The specific name is derived from the Latin *flavus* (golden-yellow) and *gula* (throat).

Barygenys nana, new species

Figures 16, 17

HOLOTYPE: AMNH 76471, obtained by Fred Parker at Daulo Pass, Eastern Highlands District, Territory of New Guinea on October 3, 1965.

PARATYPES: MCZ 53100, 53101, Daulo Pass; MCZ 53096, Mt. Otto, 11,600 ft. (3540 m.); MCZ 81667, Kotuni, Mt. Otto, 6000 ft. (1830 m.); MCZ 53102, 53103, AMNH 84438, Mt. Elimbari; all from Eastern Highlands District,

Territory of New Guinea, collected by Fred Parker. AM 22780, 22782, 22784, 22786, 22788, 22793, 22797, 22800–22802, 22804, 22808, 22809, 22811, 22813, Fungoi, Kaironk Valley, Schrader Mountains, Western Highlands District, Territory of New Guinea, collected by Harold Cogger.

DIAGNOSIS: *Barygenys nana* differs from three of the other four species of its genus in its small size and relatively larger eyes. *Barygenys atra*, *B. cheesmanae*, and *B. exsul* reach lengths from snout to vent of approximately 38 to 42 mm., whereas the largest of 24 specimens of *nana* is an adult female with a snout-vent length of 26 mm.

The ratio of eye size to snout-vent length in *B. nana* averages about 0.08, whereas the largest ratio observed in *atra*, *cheesmanae*, or *exsul* is 0.06. *Barygenys nana*, at a snout-vent length of 23 to 24 mm., has eyes as large as or larger than (in an absolute as well as a relative sense) individuals of these species 10 to 15 mm. longer.

Barygenys nana most closely resembles *B. flavigularis*, but differs from that species in having less widely spaced nostrils and narrower head with a more pointed snout with more prominent ridges. The sharp contrast between yellow throat and gray abdomen so evident in *flavigularis* is not seen in *nana*.

DESCRIPTION OF TYPE-SPECIMEN: A small, squat-bodied frog with short limbs ($TL/S-V = 0.24$), a relatively narrow head ($HW/S-V = 0.36$) and a pointed nose. The eyes are small ($Eye/S-V = 0.08$) and the external nares widely spaced ($E-N/IN = 0.61$). There are three prominent vertical ridges on the snout. The central one, which is the longest, extends from the margin of the lip to the level of a line connecting the nares; the other two are slightly shorter. The loreal region is a flat, gentle slope marked dorsally by a slight canthal angle. The tympanum is only faintly visible externally; its horizontal diameter is about 65 per cent of the length of the small eye.

Except for the ridges on the snout, there are no prominent skin folds. A post-tympanic fold is only faintly indicated. The skin of the dorsal surfaces of the body is smooth anteriorly but becomes pustulose in the post-sacral region. The hind legs, including the tarsal regions, are especially pustulose. The ventral surface is smooth.

The fingers are short and broad at the base, but taper to narrow, rounded tips (fig. 11B).

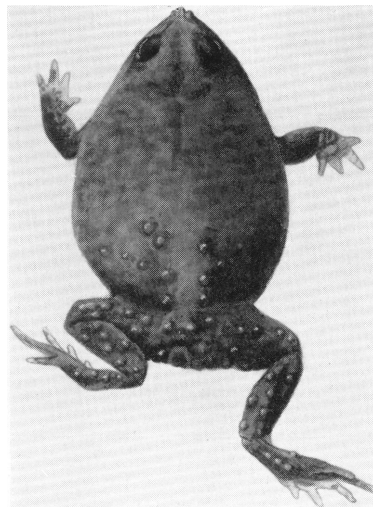


FIG. 16. *Barygenys nana* (AMNH 76471, holotype), dorsal view. $\times 2$.

There is a faint terminal groove on the third finger. There is a rounded inner metacarpal tubercle, but no subarticular tubercles are evident. The relative lengths of the fingers are $3 > 2 > 4 > 1$. The toes are unwebbed. There is no development of discs, but the fourth toe shows a faint terminal groove. The low, rounded inner metatarsal tubercle is about as long as the rather short first toe. There are no other tubercles. The relative lengths of the toes are $4 > 3 > 5 > 2 > 1$.

The anterior ends of the maxillary bones are widely separated, but the dentaries make a loose contact. The coracoids and cartilaginous sternal plate are the only ventral elements in the pectoral girdle.

The dorsal surface of the body (in preservative) is light brown with a darker infuscation in no clear pattern. The ventral surface is light brown with fine, darker mottling; the chin is slightly lighter than the chest and abdomen. The palms and fingers (lower surfaces only) are pale, with little melanistic pigment. The soles, however, are almost as dark as the upper surface of the foot.

MEASUREMENTS OF HOLOTYPE: S-V, 20.7; TL 4.9; HW, 7.5; Eye, 1.7; E-N, 1.1; IN, 1.6; tympanum horizontal, 1.1, vertical, 1.4.

The type-specimen is a male and from its size (in comparison to the size of obviously adult females) is assumed to be adult.

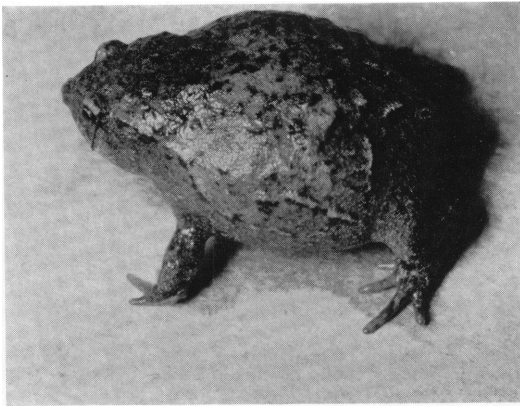


FIG. 17. *Barygenys nana* (MCZ 53104).
Photo by Fred Parker.

VARIATION: Variation in proportions is set forth in table 4. The largest specimen from the Eastern Highlands is a gravid female 23.9 mm. in length from snout to vent containing ova approximately 3 mm. in diameter. Other females from this region measuring 22.7 and 23.1 mm. in length also are gravid. The largest specimen in the series from the Western Highlands is a female 25.7 mm. in length.

None of the paratypes differs markedly from the holotype specimen in color pattern, although there is some variation in intensity. The palms are not so conspicuously pale in all as they are in the holotype, and the dark markings of the dorsal surfaces are more distinct in some specimens. The ventral surfaces of the individuals from the Schrader Mountains are brown with irregular light flecks, and thus these frogs are darker than the holotype. Some frogs from the Eastern Highlands equal those from the Schrader Mountains in ventral darkness, but others are even paler than the holotype specimen. The two frogs from Mt. Otto differ in being pale gray rather than gray-brown dorsally, and have what may in life have been rust-colored patches. One has a narrow dark streak along the canthal angle that continues for a brief distance posterior to the eye and extends in much fragmented fashion along the flank. This mark is only slightly indicated in the other frog from Mt. Otto.

The degree of dorsal rugosity varies greatly. Among the frogs from the Schrader Mountains, there are some that are entirely smooth and others that are conspicuously rugose.

COMPARISON WITH OTHER SPECIES: *Barygenys nana* is sufficiently distinct from *B. atra*, *B. cheesmanae*, and *B. exsul* in its smaller maximum body size and larger eyes not to be easily confused with them. All individuals in the small samples of the other three species are much larger than any *nana*, including gravid females of the latter. There is no overlap in ranges of the ratio Eye/S-V of *nana* and the other three species.

Barygenys nana is most similar to *B. flavigularis*; see the account of the latter for comparisons.

Barygenys nana, *B. flavigularis*, and *B. cheesmanae* are similar in that the tips of the toes are not widened and lack terminal grooves or have grooves poorly developed, whereas both *B. atra* and *B. exsul* have toes with well-defined discs, all of which have terminal grooves. The fingers are much the same in all species. The ridges on the snout are best developed in *cheesmanae*, *flavigularis*, and *nana*, weakly developed in *exsul*, and only faintly indicated as indistinct elevations in *atra*.

DISTRIBUTION AND SPECIMENS EXAMINED: The species is known only from moderate to high elevations, about 6000 to 11,600 ft., in mountains of the Eastern and Western Highlands districts (fig. 12). One specimen from Mt. Otto came from near the summit, the elevation of which is 11,613 ft. (3540 m.), the other from 6000 ft. (1830 m.). Fungoi is situated at 5500 ft. (1680 m.), but the surrounding mountains rise to over 7000 ft., and the specimens may not have come from the village itself (Cogger, 1964).

The specimens examined are listed under Holotype and Paratypes. The discovery of this new species independently by Parker and by Cogger extends the known range of the genus almost 300 miles northwest of the earlier records in the mountains and lowlands of Papua.

ETYMOLOGY: The specific name is from the Latin *nanus* (dwarf).

GENUS *HYLOPHORBUS* MACLEAY

Hylophorbus MACLEAY, 1878, p. 136 (type-species by monotypy, *H. rufescens* Macleay).

Mantophryne BOULENGER, 1897, p. 12 (type-species by monotypy, *M. lateralis* Boulenger; *Mantophryne* = *Hylophorbus* only in part, as the type series of *M. lateralis* includes individuals belonging to three genera; see below and account of *Phrynomantis lateralis*).

Metopostira MÉHELÏ, 1901, p. 239 (type-species by monotypy, *M. ocellata*).

DIAGNOSIS: *Hylophorbus* differs from all other genera of the Asterophryinae in that both the maxillae and the dentaries fail to form anterior sutures, and the dentaries are not fused with the mento-meckelian bones. Only one other asterophryine genus, *Barygenys*, has the eleuthero-gnathine condition of the maxillae, but in that genus the dentaries are symphygnathine and are fused with the mento-meckelian bones.

CONTENT: The genus includes only one species, *H. rufescens*, with three geographic races. (See Taxonomic Notes below.)

DESCRIPTION: The skull is relatively simple compared with that of other asterophryine genera (see Méhelý, 1901, pl. 7). The nasals are large and form a median suture, but the sphenethmoid is exposed dorsally between the nasals and the frontoparietals. The maxillae broadly overlap the premaxillae but are not sutured or closely approximated. The dentaries do not meet and are not fused with the mento-meckelian bones. The vomers show scarcely any expansion along their midline contact, but there is a strong anterior process that passes mesially and then slightly anteriorly to the internal naris. The parasphenoid is quite narrow anteriorly, less than one-half the width of the frontoparietals. The skull bones are smooth, showing none of the rugosity seen in some other genera.

Clavicles, procoracoids, and omosternum are absent. The vertebral column is diplasiocoelous. The terminal phalanges are T-shaped.

The tongue is adherent, without a significantly free posterior margin.

See the following species account for external characteristics.

TAXONOMIC NOTES: Macleay (1878, p. 136) based his description of the new genus and species, *Hylophorbus rufescens*, on one specimen. The description omitted mention of features of skeletal morphology later found to be significant in characterizing genera and species of microhylid frogs. The new species received no critical attention in the literature until Fry (1913) published the results of his re-examination of Macleay's type specimens of frogs from Australia and New Guinea. He noted that *Hylophorbus rufescens* resembled *Mantophryne lateralis* Boulenger, 1897 "in every detail except that the form is slightly more slender, while the two warts on the chin of Boulenger's specimen are not discernible," and proposed that *M. lateralis* be placed in the synonymy of *H. rufescens*. The

conspecificity of the two forms has not been questioned subsequently, though Parker (1934, p. 62) referred *rufescens* to the genus *Asterophrys*.

I was privileged to examine the type specimen of *Hylophorbus rufescens*, MM 144. The maxillary bones in *H. rufescens* overlap the premaxillae but fall well short of meeting, so are eleuthero-gnathine. Therefore, *Hylophorbus rufescens* is clearly not an *Asterophrys* (in the broad sense of Parker, 1934) and is not conspecific with *Mantophryne lateralis* (as the name was restricted by Parker, 1934, p. 62), which is symphygnathine.

In addition to differing in the critical character of the maxillary bones, the type of *Hylophorbus rufescens* differs slightly from *Mantophryne lateralis* in some proportions. The eye of *rufescens* is distinctly larger and the eye-naris distance relatively shorter. There appears to be little difference between the two in relative internarial distance, and the tibia of *rufescens* is scarcely if at all longer than that of *lateralis*. Fry (1913) commented on the absence in *rufescens* of the paired chin tubercles (projections of the mento-meckelian bones) described by Boulenger for *lateralis*.

The type-specimen of *Hylophorbus rufescens* was "quite bleached" more than 50 years ago (Fry, *loc. cit.*), but the original description is reasonably complete with regard to color pattern. The characteristic feature of the color pattern of *Mantophryne lateralis* is a broad, dark brown lateral band on the body. The "broad somewhat interrupted curved brownish red line, occasionally varied with yellow" that Macleay (1878, p. 136) described for *rufescens* resembles more closely a marking seen in many *Metopostira ocellata* than it does the marking of *lateralis*.

The skeleton and external morphology of *H. rufescens* agree in detail with those of the species commonly referred to as *Metopostira ocellata* Méhelý.

The conclusion is unavoidable that *Hylophorbus rufescens* Macleay, 1878 is the correct name for the species known since 1901 as *Metopostira ocellata* or as *Hylophorbus ocellatus*. Replacement of both generic and specific names is necessary, for both were the type-species of new genera. Boulenger's name *lateralis* is restored in the combination *Phrynomantis lateralis* for the species known to Parker (1934) as *Asterophrys rufescens*.

Parker (1934) assigned three species to the genus *Metopostira*: *Metopostira ocellata* Méhelý, *Hylophorbus kopsteini* Mertens, and *Xenorhina atra*

TABLE 5
BODY PROPORTIONS IN SIX SAMPLES OF *Hylophorbus rufescens*

| Sample | N | TL/S-V | | HW/S-V | | Eye/S-V | | E-N/IN | |
|---------------------------|----|-------------------|-------------|-------------------|-------------|-------------------|---------------|-------------------|-------------|
| | | Mean | Range | Mean | Range | Mean | Range | Mean | Range |
| | | $\pm\sigma_m$ | | $\pm\sigma_m$ | | $\pm\sigma_m$ | | $\pm\sigma_m$ | |
| <i>H. r. rufescens</i> | | | | | | | | | |
| Huon Peninsula | 24 | 0.529 \pm 0.005 | (0.48-0.57) | 0.362 \pm 0.003 | (0.33-0.39) | 0.124 \pm 0.002 | (0.114-0.147) | 0.705 \pm 0.008 | (0.62-0.77) |
| Torricelli Mountains | 35 | 0.529 \pm 0.004 | (0.48-0.56) | 0.358 \pm 0.007 | (0.33-0.39) | 0.126 \pm 0.001 | (0.114-0.145) | — | — |
| Bomai | 38 | 0.523 \pm 0.004 | (0.48-0.56) | 0.342 \pm 0.002 | (0.33-0.37) | 0.125 \pm 0.001 | (0.112-0.144) | — | — |
| Fergusson I., Normanby I. | 10 | 0.493 \pm 0.006 | (0.46-0.52) | 0.360 \pm 0.004 | (0.34-0.38) | 0.126 \pm 0.001 | (0.115-0.133) | — | — |
| <i>H. r. myopicus</i> | 18 | 0.498 \pm 0.005 | (0.45-0.54) | 0.345 \pm 0.002 | (0.33-0.36) | 0.123 \pm 0.002 | (0.117-0.145) | 0.748 \pm 0.009 | (0.68-0.82) |
| <i>H. r. extimus</i> | 26 | 0.469 \pm 0.004 | (0.42-0.51) | 0.350 \pm 0.002 | (0.33-0.36) | 0.125 \pm 0.001 | (0.113-0.156) | 0.745 \pm 0.010 | (0.66-0.85) |

Günther. Shortly thereafter (1936) he established the new genus *Barygenys* and reassigned *atra* to it. Parker did not examine specimens of *kopsteini*, and the original description (Mertens, 1930) made no mention of the diagnostic skeletal features. I examined the syntypes and found the maxillae to be only very narrowly separated; hence, I regard *kopsteini* as a member of the genus *Phrynomantis* (as redefined herein), and only the one species *rufescens* remains in the genus *Hylophorbus*.

DISTRIBUTION: *Hylophorbus* is the most widely distributed genus (and species) of microhylid in the New Guinea region and possibly the most widely distributed of all Papuan frogs (fig. 20). It occurs in all major physiographic regions of New Guinea, and ranges from virtually sea level to as high as 11,700 ft. (3570 m.) on Mt. Wilhelm, although evidently is rare at high elevations. It also occurs on Batanta Island at the western tip of New Guinea and on several islands off the eastern end.

Hylophorbus rufescens rufescens Macleay

Figure 18

Hylophorbus rufescens MACLEAY, 1878, p. 136 (type locality, "Katow" [Katow River=Binituri River], near Daru, Western District, Territory of Papua; holotype MM 144, collected on the "Chevert" expedition in July, 1875; see Fletcher [1893] for the itinerary of the expedition).

Mantophryne lateralis BOULENGER, 1897, p. 12 (in part; type locality, "Mount Victoria, Owen Stanley Range," Territory of Papua; syntype BMNH 1947.2.11.25 [formerly 96.10.31.35], collected by A. S. Anthony. This specimen is *H. rufescens*; the other four syntypes belong to two other species [Parker, 1934, pp. 62, 69, 178]).

Metopostira ocellata MÉHELÿ, 1901, p. 239 (type locality, "Sattelberg," Morobe District, Territory of New Guinea; syntypes [collected by Lewis Biró] formerly in the Hungarian Natural History Museum were destroyed in 1956 [I. Szabo, *in litt.*]; however, three syntypes received on exchange from Budapest are in the Naturhistorisches Museum, Vienna [J. Menzies, *in litt.*]).

Metopostira macra VAN KAMPEN, 1906, p. 167 (type locality, "Am Moso und Tami," the Moso and Tami rivers, east of Djayapura [Hollandia], West Irian; holotype, RMNH 4631, collected in 1903 on the Dutch New Guinea Expedition).

Hylophorbus ocellatus: VAN KAMPEN, 1919, p. 54.

DIAGNOSIS: The characters given in the generic diagnosis may be used to distinguish

rufescens from other asterophryine species. This species somewhat resembles *Phrynomantis lateralis* and *P. infulata* in external morphology, but examination of the maxillae will confirm the determination.

In that *H. rufescens* has eleutherognathine maxillae and lacks procoracoids and clavicles, it could be mistaken for a *Cophixalus*. Most *Cophixalus* with digital discs have those of the fingers larger than those of the toes, whereas the opposite is true of *rufescens*. Three Papuan species of *Cophixalus* have toe discs broader than finger discs: *C. tagulensis* is distinguished by webbed toes; *C. oxyrhinus* has much less prominent sub-articular tubercles on both hands and feet; *C. shellyi* is a diminutive form, less than 20 mm. long, with a black face mask.

The mainland subspecies *H. r. rufescens* differs from the insular races described below in having relatively longer hind limbs (TL/S-V averages greater than 0.50), smaller maximum size (approximately 44 mm. S-V, but rarely as long as 40 mm.), inguinal ocellus usually distinct, and posterior surface of thigh with about equal amounts of light and dark mottling. See the accounts of the new forms for elaboration.

DESCRIPTION: *Hylophorbus rufescens rufescens* is, for an asterophryine, a moderately slender frog, with the head only slightly narrower than the body (HW/S-V mean about 0.36) and with long legs (TL/S-V mean about 0.52–0.53). The eyes are relatively large (Eye/S-V averages about 0.12 in adults), with the width of the eyelids equal to or wider than the interorbital space. The external nares are widely spaced relative to their distance from the eyes (E-N/IN average



FIG. 18. *Hylophorbus rufescens rufescens* (AMNH 83039).

0.70) and are directed laterally, so that the openings are not visible in dorsal aspect. The loreal region is vertical and slightly concave; the canthus rostralis is rounded. Only in occasional individuals is the tympanum distinct enough to measure; its horizontal diameter usually falls between 0.6 and 0.7 of the diameter of the orbit. There is a weak fold of skin above the tympanum; otherwise the skin is smooth both dorsally and ventrally. The male has a single, subgular vocal sac with slitlike openings in the floor of the mouth.

The relative lengths of the fingers are $3 > 4 > 2 > 1$ (the fourth is only slightly longer than the second), and of the toes are $4 > 3 > 5 > 2 > 1$. The fingers (fig. 10) bear small discs, whereas those of the toes are distinctly larger, approximately 2.5 to 3.0 times the width of the narrowest part of the penultimate phalange. There is an outer metatarsal tubercle, and subarticular tubercles are prominent on both hands and feet. Fingers and toes are unwebbed.

Among almost 300 specimens from the mainland of New Guinea, only 10 are 40 mm. or greater in snout-vent length. The largest female specimen measured 44.3 mm. snout to vent, the largest male, 37.8 mm.; both are from the Torricelli Mountains. The smallest gravid female from this locality measured 35.0 mm., which may be approximately the size at which sexual maturity is attained. The sample from the Torricelli Mountains comprised 62 specimens. Among 174 from the Sibil Valley region of West Irian the largest measures only 35 mm., and specimens of 26 mm. and 30 mm. are gravid. Thus, there appears to be geographic variation in size among mainland populations.

Frogs from the mainland of New Guinea usually have (in preservative) the following features of color and pattern: The dorsal ground color is brown with dark spots few or absent. A curved, dark marking obscure in some individuals or even absent is situated above the arm. In rare cases this mark may pass into a narrow, dark dorsolateral line. The lumbar region bears a dark ocellus with a light border that is not too clearly defined. The sides of the body are pale with dark spots of various sizes and shapes usually present. A dark bar on the upper lip below the eye is bordered anteriorly and posteriorly by lighter areas and may continue as a distinct mark onto the lower jaw. The chin and chest in most specimens are dark gray with tiny

light spots, although some individuals have heavy dark maculations on a pale background. The hind limbs are uniform brown above, usually without markings. The underside of the thigh is unmarked in most specimens but may be heavily infuscated. The anterior and posterior surfaces of the thigh are mottled. The tibia is pale beneath with dark markings laterally.

An adult specimen from the Huon Peninsula had the following color pattern in life: dorsum reddish brown, somewhat more red laterally and especially surrounding the lumbar "eyespot"; no distinctive pattern on back except for ocelli; chin brown with ill-defined white flecks; chest region dark reddish, mainly due to liver showing through; undersides of hind limbs and posterior half of abdomen yellow.

Some variation in color is evident. A specimen from Garaina had the pale margins of the lumbar ocelli light tan, chin and chest gray, and undersides of thighs a reddish tint. In an individual from near Baiyer River the abdomen and hind limbs had the yellow color described above for the Huon specimen, but one from near Port Moresby had the yellow confined to the inguinal region and the undersides of the limbs were gray, and one from Alexishafen had yellow and black mottling in the groin.

In the original description of *Metopostira ocellata*, Méhely (1901, p. 240) quoted the following notes on color in life, made by the collector: "Greenish-brown. On both sides of the back anterior to the groin there typically always appears to be a carmine red spot which, in half-moon shape, surrounds a black, round inner spot. The red color is sometimes narrowly surrounded with yellowish-white. In many individuals there are some indistinct red flecks on the posterior side of the thighs, under the forelimbs, on the back, behind the tympanum or between the eyes. The iris is red." Evidently the color of the iris varies, for I noted it as golden in one individual, black with gold flecks in another, and brown (same as the head) in another.

Tyler (1963, p. 17) provided the following description in life, based on material from 3 miles north of Nondugl in the Eastern Highlands: "The colour in life of dorsal and dorso-lateral surfaces pale brown. Side of head from external nares, below canthus rostralis and eye, dark brown to black. Similarly coloured spot behind forelimb and above groin, connected by dorso-lateral streak which is continuous in four speci-

mens and interrupted in remainder [six specimens].

"Throat grey, ventro-lateral body surfaces, thorax and upper abdomen pale red, profusely spotted with minute white spots. Lower abdomen and thighs a pale olive green; back of thighs variegated with very dark brown in five specimens."

Van Kampen (1914, p. 375) noted that in a living specimen from the south coast of Humboldt Bay, the dark groin spot was bordered anteriorly by brick red and posteriorly by yellow, which color also was present on the anterior surface of the thigh.

Preserved frogs from Normanby and Fergusson islands show a slightly greater tendency to dark dorsal spotting than do mainland frogs, but are otherwise similar, including the same degree of mottling on the thighs and well-developed lumbar ocelli.

One specimen from Batanta Island, West Irian, differs from others I have examined from the mainland of New Guinea and the southeastern islands in having a broad, dark band passing from the eye through the tympanum and terminating at the anterior light border of the inguinal ocellus. The band contrasts markedly with the pale, lightly spotted ground color of the lower sides but less so with the brown of the dorsum. The loreal area is dark also, but because the top of the snout is darker than the back, the effect of a band or stripe, as seen on the body, is lacking. A thin light line, indistinct on the snout, becomes more evident as it passes beneath the eye and through the lower part of the tympanum. The dark bar beneath the eye common to most mainland specimens is lacking in this individual.

Evidently this individual does not represent a distinctive insular population, for the only specimen from the Vogelkop Peninsula is quite similar in pattern (Brongersma, 1953, p. 579): "The border of the upper lip is dark; the space between this dark border and the eye greyish; there is no distinct bar below the eye. . . . A blackish brown band from the eye along the sides of the body; the ocellus in the groin is present."

VARIATION: Aspects of individual variation in color and pattern have been covered in the above descriptive material, as has apparent geographic variation in maximum size in mainland samples. Proportions vary remarkably little

among samples from different areas on the mainland, as is seen in the data presented in table 5.

The systematic status of populations in the D'Entrecasteaux Islands is uncertain. Specimens from Fergusson Island (eight) and Normanby Island (two) are relatively large (maximum snout-vent length 45 mm., six of 10 specimens greater than 40 mm.) and short-legged (TL/S-V mean 0.493), and so resemble the insular subspecies *extimus* and *myopicus* in these respects. In color pattern, however, they are closer to mainland *rufescens*, so far as I can judge from preserved specimens. For the present, I refer these insular populations to *H. r. rufescens*, although I recognize that a change of status may eventually prove warranted.

Only three immature specimens are available from Misima Island, which lies approximately between Woodlark and Sudest islands where *myopicus* and *extimus* occur. These are short-legged frogs (TL/S-V, 0.45, 0.48, and 0.51) with nothing strikingly distinctive in the color pattern. I think this population also is best placed in *H. r. rufescens* pending receipt of material adequate for a satisfactory analysis.

In the foregoing discussion of color pattern, I noted the distinctive color pattern of a frog from Batanta Island and the apparent similarity of one described by Brongersma from the Vogelkop Peninsula. Additional material may show the desirability of recognizing another subspecies from the Vogelkop Peninsula and adjacent islands, but the information presently available is inadequate for satisfactory analysis. Therefore, I refer these specimens to *H. r. rufescens*.

A specimen from the Huon Peninsula, MCZ 23558, collected at Boana by Fred Parker, is sufficiently different from all other mainland frogs to deserve special attention. It is pale reddish brown dorsally and virtually unmarked. There is no dark mark above the arm, the inguinal ocellus is so pale as to be almost indistinguishable, and the dark bar beneath the eye is lacking. It is a gravid female of near maximum size (S-V, 42.5 mm.), and has much shorter hind legs than any other mainland specimen measured (TL/S-V, 0.45, compared to a minimum of 0.48). More specimens from the same locality are needed so that the systematic position of the population may properly be assessed.

ECOLOGICAL NOTES: *Hylophorbus rufescens* is a terrestrial frog that is active at night on the forest floor. Most of my captures were of frogs in their daytime retreats—two under rotten logs in primary mid-montane rain forest, one dug out of a shallow hole in the ground, and one uncovered when leaf litter was dug up in an attempt to find a diurnally calling frog (probably not the *Hylophorbus*, which was a female). Both Tyler (1963, p. 17) and Loveridge (1948, p. 420) reported individuals found beneath stones. On several occasions I found individuals calling at night, partly or completely hidden in the leaf litter. Van Kampen (1909, p. 41) found "ants and other insects" in the stomachs of specimens of *rufescens*, and Tyler (1963, p. 18)

reported that an individual had eaten two earthworms.

A specimen from the Huon Peninsula held 10 eggs (presumably the complete complement), each approximately 4 mm. in diameter. Parker (1940, p. 259) reported that individuals 8.5 mm. in length had the intestine packed with yolk. These frogs had just metamorphosed (a tiny vestige of tail remained), and obviously had had no free feeding period.

MATING CALL: The call is a series of notes each about 0.1 second in length separated by intervals of about the same time or slightly greater (fig. 19). Usually the frog utters a group of four to six such notes (mean, 4.0, 4.1, and 4.4 in three individuals) and then pauses an average

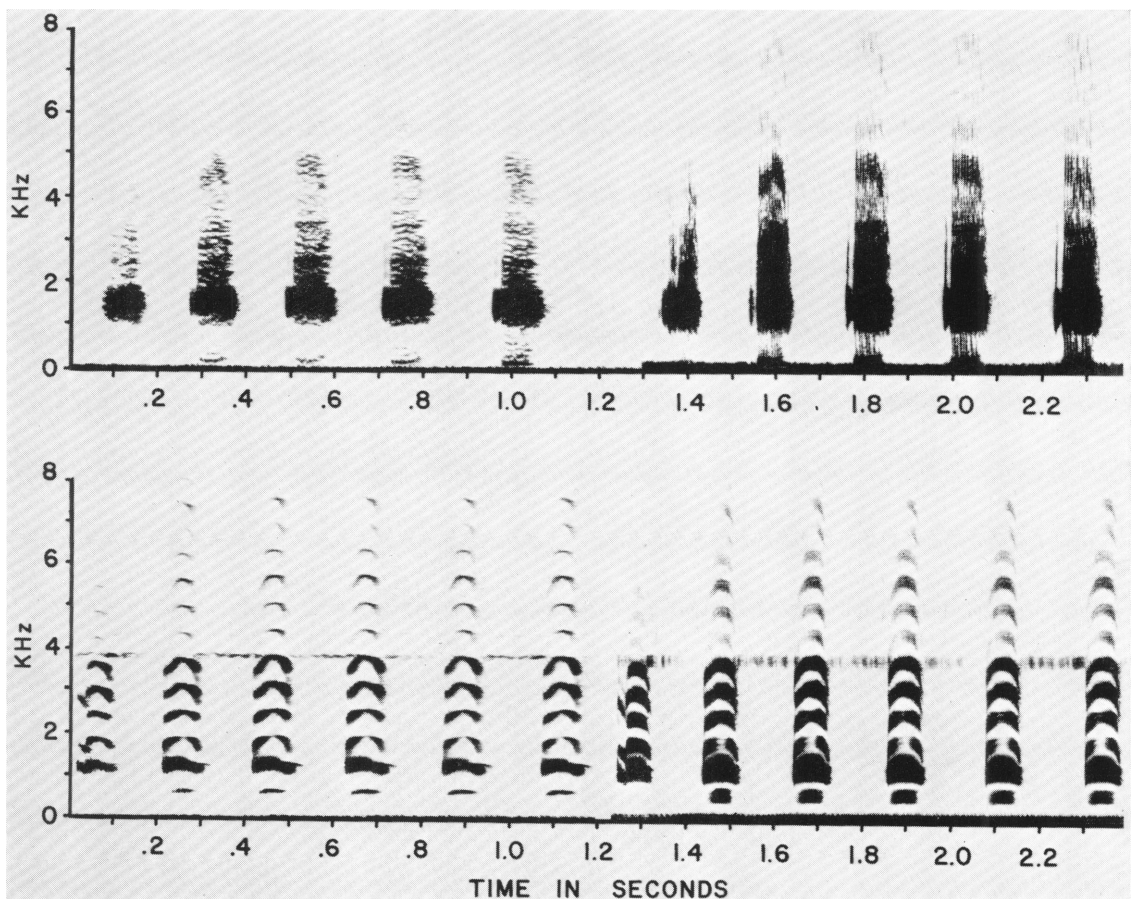


FIG. 19. Sound spectrograms of calls of *Hylophorbus rufescens rufescens*. *Upper:* Call of AMNH 81172 recorded at Garaina, Morobe District, June 26, 1968, air 21.8°C.; entire call of five notes shown on left using 45 Hz. filter and on right with 300 Hz. filter. *Lower:* Call of AMNH 81174 recorded at Hallstrom Park, Baiyer River, Western Highlands District, July 9, 1968, air 21.4°C.; same call shown twice, as above.

of 10 or 11 seconds (range six to 18 in three individuals) before calling again.

When I recorded this species at Garaina and at Ilolo Plantation near Port Moresby, the calls recorded and all others given by other individuals had a harsh quality that is reflected in the rather "muddy" audiospectrogram (fig. 19, upper). The peak energy lies in the region between 1000 and 2000 Hz. In marked contrast individuals heard near Baiyer River (one recorded) gave much more musical, rather whistling calls, without a strongly dominant frequency band (fig. 19, lower). No differences are evident between the two call-types in length of notes, numbers of notes per call, or rate of calling. Differences of the sort described may in some instances be attributable to the degree of inflation of the vocal sac, but here it seems to be a matter of entire local populations behaving consistently, not just individual variation. Information on the call of this species in other regions is needed to see if there is geographic consistency to the variation. I heard what I took to be the Baiyer River call-type near Alexishafen on the north coast, but was unable to record it or associate the call with a frog. Through the courtesy of James Menzies, I have examined an audiospectrogram of a call recorded at Alotau on Milne Bay that appears to be the same as those recorded at Garaina and Ilolo.

DISTRIBUTION AND SPECIMENS EXAMINED: This subspecies is found throughout the mainland of New Guinea as well as on islands near both the eastern and western tips of New Guinea (fig. 20). West Irian: Batanta Island, Mt. Besar above Wailebet, 1500 ft. (460 m.) (AMNH 74184); Kotjewer, Vogelkop Peninsula (Brongersma, 1953, p. 579); 4 km. SW Bernhard Camp, Idenberg River, 850 m. (2800 ft.) (AMNH 49564-49566, 49570); Lorentz River at Sabang (van Kampen, 1909, p. 40); Kloofbiwak, Lorentz River, 40 m. (130 ft.) (van Kampen, 1915, p. 40); Went Mountains, 800 m. (2600 ft.) and 1000-1630 m. (3300-5300 ft.) (van Kampen, 1913, p. 461; Mabilabol, Sibil Valley, 1260 m. (4130 ft.) (RMNH 16608, 16610 [3 specimens], 16611 [7 specimens], 16612 [4 specimens], 16615 [3 specimens], 16616 [24 specimens], 16617 [48 specimens], 16621 [5 specimens], 16624 [3 specimens], 16625, 16626, 16629 [14 specimens], 16632, 16646 [11 specimens], 16670 [6 specimens]; Nimdol, ca. 12 km. E, 3 km. N Mabilabol (RMNH 16633 [10

specimens]); Betabib, Sibil Valley, 1300 m. (4260 ft.) (RMNH 16627 [9 specimens]); Kigomendip, Sibil Valley (RMNH 16614 [13 specimens]); Kouh, Digul River (RMNH 16622); Tenmasigin, 6 km. N Mabilabol (RMNH 16618 [9 specimens]); Cyclops Range, 3000-4000 ft. (900-1220 m.) (Parker, 1940, p. 259); Doromena (FMNH 43351); Hollandia (van Kampen, 1914, p. 375); near south coast of Humboldt Bay (van Kampen, *loc. cit.*); Mosso River at Tami River (RMNH 4631, holotype of *Metopostira macra*); Kohari Mountains, ca. 600 m. (2000 ft.) (van Kampen, *loc. cit.*); lower Bewani River (van Kampen, *loc. cit.*); Zoutbron (van Kampen, *loc. cit.*); Mt. Nomo, 600 ft. (180 m.) (Parker, 1940, p. 259); Njau Limon (Parker, *loc. cit.*); Begowre River (van Kampen, 1923, p. 142).

Territory of New Guinea: West Sepik District: Mt. Nibo (AMNH 78119-78128+42 untagged); Mt. Somoro (AMNH 78129-78137); Lumi (AMNH 78138); Mt. Hunstein, 4000 ft. (1220 m.) (AMNH 77540, 77541); Telefomin (SAM, 1 specimen). East Sepik District: Matakau, Wakip River (MCZ 12958). Western Highlands District: Wahgi-Sepik Divide, 6300 ft. (1920 m.), 3 mi. N Nondugl (Tyler, 1963, p. 17); Hallstrom Park, Baiyer River, 3800 ft. (1160 m.) (AMNH 81174-81176); Tomba, 2450 m. (8040 ft.) (BBM 3010). Chimbu District: Bomai, 3500 ft. (1067 m.) (AMNH 76577-76579; MCZ 59834-59844, 59846-59868, X6567-X6586, X6662); Elamagale (MCZ 59872); Dege (MCZ 59871); Karimui (BBM 1013); Mt. Wilhelm, 11,700 ft. (3570 m.) (SAM, 1 specimen). Eastern Highlands District: Okapa (SAM 5242). Madang District: Nobonob, 1100 ft. (335 m.), 3 mi. W, 4 mi. N Madang (AMNH 83037); 5 mi. N Alexishafen (AMNH 83040). Morobe District: Finschhafen (SAM 4248 [5 specimens]); Sattelberg (Méhely, 1901, p. 239, type locality of *Metopostira ocellata*); Gang Creek, Mt. Rawlinson, 4400 ft. (AMNH 75023, 75024, 76012-76023); Tumnang, 4400 ft. (1340 m.) (AMNH 75018-75022; MCZ 28396); Tuwap, 1350 m. (4430 ft.) (BBM 1012); Pindiu, 2600 ft. (790 m.) (AMNH 76024); Joangeng, 4000 ft. (1220 m.) (MCZ 28405); Boana (MCZ 81671); Umi River, 1600 ft. (490 m.), Markham Valley (AMNH 66954, 66955); Aregenang (AMNH 81179-81194); Garaina, 2300 ft. (700 m.) (AMNH 81170-81173, 83038, 83039).

Territory of Papua: Western District: Katow (MM 144, holotype of *Hylophorbus rufescens*); Derongo (AMNH 82284); Imigibip, 4200 ft. (1280 m.) (AMNH 82253); Didessa, north side of Mt. Bosavi (SW [3 untagged specimens]); Wangbin, 4800 ft. (1460 m.) (AMNH 84528–84530). Gulf District: Omati (MCZ 28202); Soliabeda, 1800 ft. (550 m.) (AMNH 79969; MCZ 81669, 81670); Pio River, 1000 ft. (300 m.) (AMNH 79970). Central District: Mt. Victoria (BMNH 1947.2.11.25, syntype of *Mantophryne lateralis*); Ilo Plantation, 540 m. (1770 ft.), 5 mi. N, 17 mi. E Port Moresby (AMNH 81177, 81178); Mafulu (AMNH 58012–58014). Northern District: Kokoda, 1200 ft. (370 m.) (AMNH 75017); Albert Edward Ranges, 6000 ft. (1830 m.) (Parker, 1934, p. 69). Milne Bay District: Normanby Island, Mt. Pabinama (AMNH 60170, 60171); Fergusson Island, between Agamoia and Ailuluai (AMNH 59961–59968); Misima Island, Mt. Sisa (AMNH 59899–59901).

***Hylophorbus rufescens extimus*,**
new subspecies

HOLOTYPE: AMNH 60093, obtained by members of the Fifth Archbold Expedition on Mount

Riu, Sudest Island, Louisiade Archipelago, Milne Bay District, Territory of Papua, between August 23 and September 5, 1956.

PARATYPES: AMNH 60084–60092+17 untagged specimens, all bearing the same data as the holotype.

DIAGNOSIS: This insular subspecies is characterized by large size (snout-vent length up to 47 mm.; 11 of 26 specimens 40 mm. or greater in length), short hind legs (TL/S–V, 0.50 or greater in only two of 26 specimens), and light areas of posterior surfaces of thighs and of groin peach-colored (in freshly preserved specimens), with little or no heavy dark mottling.

Hylophorbus rufescens extimus differs from the other insular subspecies, *H. r. myopicus* of Woodlark Island in color pattern and to a lesser extent in leg length. The inguinal ocelli of *extimus* are usually distinct, whereas in the much darker *myopicus* these markings are indistinct or virtually absent. The posterior surfaces of the thighs of *myopicus* are more heavily mottled and lack the peach color of *extimus*. The mean ratio of tibia length to snout-vent length differs significantly in *extimus* and *myopicus* (0.469 ± 0.004 , and 0.498 ± 0.005 , respectively), but the ranges overlap too much to permit adequate segregation of samples on this basis alone.

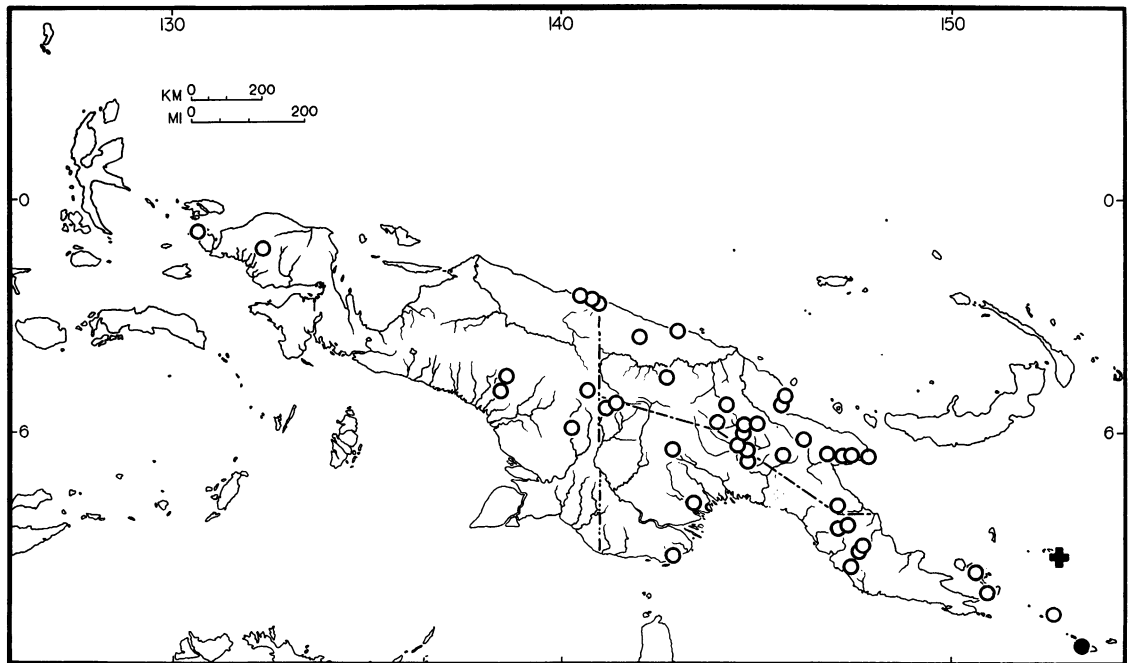


FIG. 20. Distribution of subspecies of *Hylophorbus rufescens*. Open circles, *H. r. rufescens*; closed circle, *H. r. extimus*; cross, *H. r. myopicus*.

The mainland subspecies of *H. r. rufescens*, is a smaller frog than *H. r. extimus* (rarely as large as 40 mm. snout to vent), with longer hind legs (TL/S-V averages greater than 0.50) and dark and light mottling on the posterior surfaces of the thighs.

DESCRIPTION OF TYPE-SPECIMEN: The holotype is an adult male with the following measurements: S-V, 39.7; TL, 18.5; HW, 13.7; E-N, 2.7; IN, 3.8; Eye, 4.7; tympanum, 2.8; disc of fourth toe, 1.6, width of penultimate phalange, 0.7; disc of third finger, 0.9, width of penultimate phalange, 0.6.

The snout protrudes slightly, is equal in length to the eye, and is blunt, almost truncate. The canthus rostralis is rounded, the loreal region is vertical and slightly concave. The nostrils are near the end of the snout and open laterally. The eyelids are slightly wider than the interorbital space. The skin of both dorsal and ventral surfaces is smooth except for a weak fold that passes from the posterior corner of the eye above and down behind the tympanum, which is not at all distinct externally. There are two palatal folds, the anterior smooth and the posterior serrate. A slitlike vocal sac opening is present on each side of the floor of the mouth. Both fingers and toes bear prominent, rounded subarticular tubercles. Outer and middle metacarpal tubercles are present, and there is one at the base of the first finger. There is a prominent, rounded inner metatarsal tubercle, but only a low, rounded elevation in the place of the outer tubercle. The relative lengths of the fingers are $3 > 4 = 2 > 1$, of the toes, $4 > 3 > 5 > 2 > 1$. The first finger is slightly shorter than the second. All fingers and toes bear discs with terminal grooves, the discs of the toes being larger.

The dorsal surface of the body is gray-brown without prominent markings; only slight mottling is visible under close examination. There is a dark inguinal spot, but its light border is not well developed. The deeper area of the groin is unmarked except for a few dark spots. The posterior surface of the thigh is lightly mottled over a peach ground color. The upper surfaces of the hind legs are the same color as the body and are without discrete markings. The ventral surfaces are pale except for light gray mottling on the chin and chest and darker gray markings on the lower surface of the tibia.

VARIATION IN THE PARATYPES: For a summary of variation in selected proportional character-

istics, see table 5. Most features of color pattern vary relatively slightly. The back is generally without discrete markings, although a few small, indistinct spots may be present. The inguinal ocellus is almost indistinguishable in a few individuals. Rarely, the posterior surface of the thigh may be heavily mottled. Typically, it is almost free of mottling and the peach tint is most distinct closer to the knee. The amount of dark pigmentation on the undersurfaces varies widely. The type is one of the lighter individuals; in others the chin may be largely dark, and dark spots may cover much of the chest and anterior part of the abdomen.

ECOLOGICAL NOTES: The type series was collected on the west slopes of Mt. Riu between 250 and 350 meters above sea level. See the account of *Barygenys exsul* for notes on the habitat.

DISTRIBUTION AND SPECIMENS EXAMINED: This subspecies is known only from the type series from Mt. Riu, Sudest Island (fig. 20). Considering the faunal similarities between Sudest and Rossel islands, it is somewhat surprising that members of the Fifth Archbold Expedition did not collect *Hylophorbus* on Rossel Island. Several other frogs are endemic to the two islands: *Phrynomantis lousiadensis*, *Barygenys exsul*, *Litoria lousiadensis*, and *Nyctimystes perimetri*.

ETYMOLOGY: The trivial name *extimus* is Latin (most remote), and alludes to geographic position of the subspecies.

***Hylophorbus rufescens myopicus*,
new subspecies**

HOLOTYPE: AMNH 59979, obtained at Kulumadau, Woodlark Island, Milne Bay District, Territory of Papua, by members of the Fifth Archbold Expedition between November 1 and 22, 1956.

PARATYPES: AMNH 59980-59988+8 untagged specimens, all with the same data as the holotype.

DIAGNOSIS: This subspecies differs from the other two races recognized in its large size (largest specimen 48.6 mm. snout-vent length; 10 of 18 specimens greater than 40 mm.), relatively short hind legs (TL/S-V mean = 0.498 ± 0.005), and dark brown coloration with inguinal eyespots indistinct.

Diagnostic comparison with *H. r. extimus* is made in the account of that subspecies. When

first received from the field, specimens of *extimus* and *myopicus* differed conspicuously in the presence of peach color in the groin and on the posterior surface of the thigh of *extimus*, whereas the comparable light areas of *myopicus* were gray or white. The specimens from the two islands were collected at about the same time and received similar treatment with respect to original preservation in formalin, so the differences seen in the preserved frogs undoubtedly reflect similar differences in the living animals. *Hylophorbus rufescens rufescens* of the mainland of New Guinea is a smaller frog (maximum length 44 mm., few reach 40 mm.), with longer hind legs (TL/S-V mean greater than 0.50) and lumbar eyespots usually distinct.

DESCRIPTION OF TYPE-SPECIMEN: The holotype is an adult female (ova 2.0 mm. in diameter) with the following measurements: S-V, 48.6; TL, 22.0; HW, 16.7; E-N, 3.6; IN, 4.8; Eye, 5.8; tympanum, 3.2; disc of fourth toe, 2.0, width of penultimate phalange, 0.7; disc of third finger, 1.4, width of penultimate phalange, 0.7.

The snout protrudes slightly and is slightly shorter than the length of the eye. In dorsal aspect the snout is blunt, almost truncate. The canthus rostralis is rounded, the loreal region vertical and slightly concave. The nostrils open laterally and are near the end of the snout. The upper eyelids are slightly wider than the interorbital space. The skin is smooth except for a weak fold from the posterior corner of the eye, over and down behind the tympanum. The tympanum is scarcely distinct externally. The fingers bear prominent, rounded subarticular tubercles and distinct discs, all with terminal grooves. There are rounded outer and middle metacarpal tubercles and a prominent tubercle at the base of the first finger. The first finger is long, almost as long as the second. The relative lengths of the fingers are $3 > 4 = 2 > 1$, of the toes, $4 > 3 > 5 > 2 > 1$. All toes bear grooved discs that are larger than those of the fingers. There are rounded, subarticular tubercles and a strong, rounded, inner metatarsal tubercle, but only a low elevation in the place of an outer tubercle.

The dorsal surfaces of body and limbs are dark gray-brown with darker spots and mottling faintly visible. The dark bar beneath the eye is poorly developed. There is no sharp line of demarcation between the dorsal color and the light, gray-spotted sides of the body. The chin is

gray with white spots, and the chest, anterior part of the abdomen, and underside of the thighs are white mottled extensively with gray. The dark inguinal mark is obscure and is not light-bordered; thus, it does not give the impression of an eyespot. The groin is white, heavily mottled with gray. The posterior surfaces of the thighs are largely but not uniformly dark.

VARIATION IN THE PARATYPES: Variation in selected proportional characteristics is summarized in table 5. The color pattern is much the same in all specimens—dark gray-brown with obscure spotting. Where dorsal markings are visible, they tend to appear as a row of spots along each side of the vertebral midline. The inguinal spot is indistinct or absent, and in none is there the distinct light border that produces the eyespot effect in other *Hylophorbus*. The chin is mottled gray-brown and white, or in darker individuals is gray-brown with white spots. Some mottling or gray spotting is present on the chest and anterior part of the abdomen of all individuals, and all possess some mottling on the under-surface of the thigh. Dark pigmentation on the underside of the thigh is rarely seen in other populations of *H. rufescens*.

ECOLOGICAL NOTES: The type-specimens were collected between sea level and an elevation of 100 meters. Brass (1959, p. 59) reported that Kulumadau has an annual average rainfall of 165 inches, "nearly evenly distributed throughout the year." He stated that "the whole area away from the settlement was entirely forested. This for the most part was second-growth rain forest, much of it tall and old."

DISTRIBUTION AND SPECIMENS EXAMINED: This subspecies is known only from the type series from the type locality Woodlark Island (fig. 20).

ETYMOLOGY: The trivial name *myopicus* is from the Greek *myops* (near-sighted), and alludes to the poorly developed lumbar eyespot.

***PHEROHAPSIS*, NEW GENUS**

TYPE-SPECIES: *Pherohapsis menziesi*, new species.

DIAGNOSIS: *Pherohapsis* differs from all other genera of Asterophryinae in having the squamosal and frontoparietal bones meet to form an arch over the prootic region. Additional peculiarities (uncommon although not unique features) include extensive rugosity of all dermal roofing

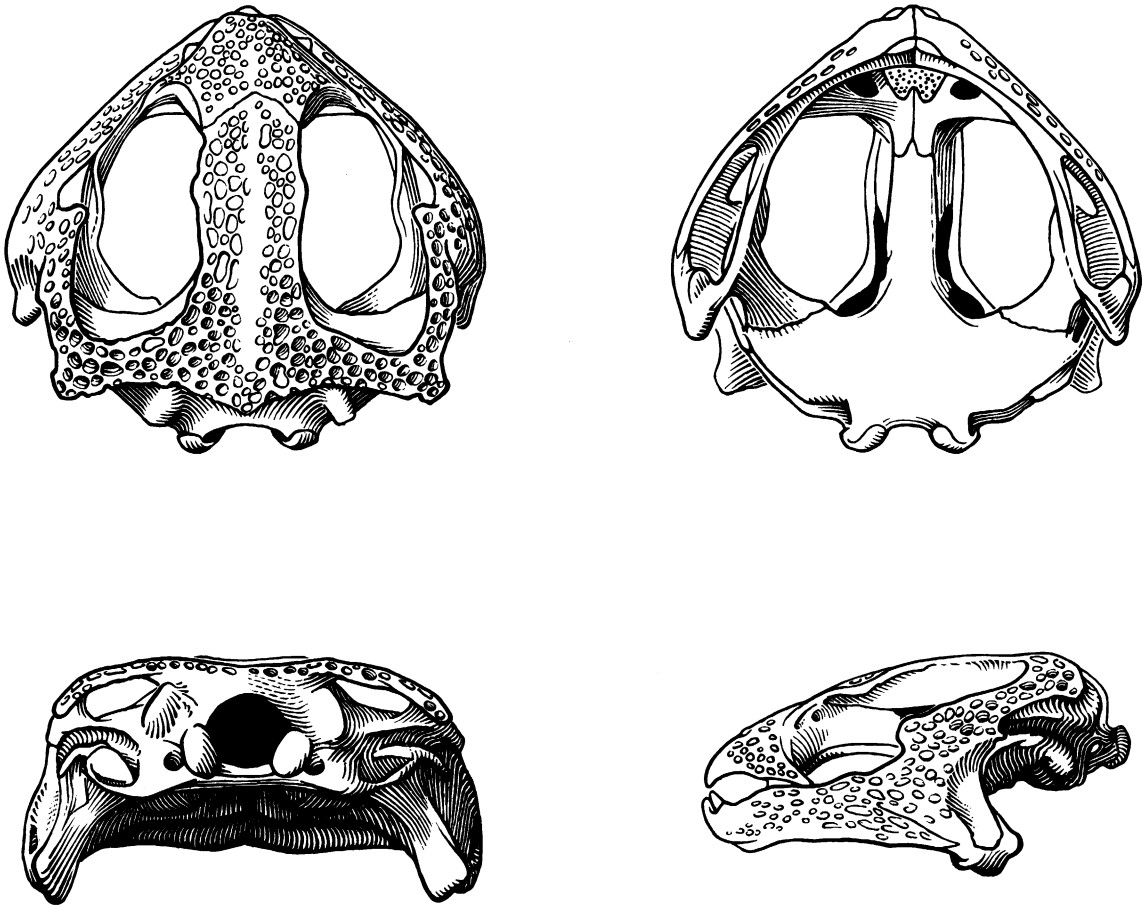


FIG. 21. Skull of *Pherohapsis menziesi* (AMNH 83842) in dorsal (upper left), ventral (upper right), posterior (lower left), and lateral (lower right) views. $\times 6.4$.

bones of the skull, fusion of the nasals to the extent that their common suture cannot clearly be seen, and the development of a broad sheet of bone continuous with the maxilla and the anterior part of the squamosal.

Pherohapsis resembles *Asterophrys* in rugosity of the roofing bones and in fusion of the nasals. Also, some (but not all) individuals of *Asterophrys* have a bony sheet between the squamosal and maxillae. The frontoparietals of *Asterophrys* are widely separated from the squamosals, not continuous with them, and the frontoparietals of *Pherohapsis* are flat to slightly concave, not compressed into a prominent crest.

CONTENT: *Pherohapsis menziesi* is the only species currently known in this genus.

DESCRIPTION: All roofing bones of the skull are pitted, giving the skull a very rugose appear-

ance (fig. 21). The nasal bones are fused, with the suture not identifiable. The ethmoid is not visible dorsally. The surface of the frontoparietals, which are scarcely separable, is slightly concave. At their posterior end, the frontoparietals flare laterally and are continuous with the squamosals. These projections are well separated from the underlying parts of the squamosals (and prootics), and so form arcades that are filled with muscle. No sutures can be seen, so it is uncertain to what extent the frontoparietals and squamosals contribute to the arcades. Anteriorly, the squamosals are broadly continuous with the maxillae, giving the frog a solid cheek region. The maxillae form a broad, firm anterior suture. The vomers broaden along their midline contact, with the projection being more pronounced posteriorly (fig. 3E). A slim

projection passes anteriorly from each vomer on the mesial side of the internal naris. The area between these projections is filled with a thin layer of calcified tissue. The parasphenoid is, at its anterior end, little more than one-quarter the width of the frontoparietals.

The vertebral column is diplasiocoelous. The sacral diapophyses are slightly expanded, and the sacrum articulates with the urostyle by a double condyle. The terminal phalanges are T-shaped, but not broadly so.

The tongue has scarcely any free margin, even posteriorly. There is a median furrow, best developed on the rear of the tongue. The usual posterior, denticulate palatal fold is present, but there is no anterior fold.

See the following species account for external characteristics.

DISTRIBUTION: See species account.

***Pherohapsis menziesi*, new species**

Figure 22

HOLOTYPE: AMNH 84452, collected by James Menzies and John Waldrop at Iarowari School, Sogeri, 1500 ft. (460 m.), 5 mi. N, 17 mi. E Port Moresby, Central District, Territory of Papua, on May 31, 1970.

PARATYPES: AMNH 83842, 84449–84451, and 84453, collected by Menzies and Waldrop at the type locality, and AMNH 84554, collected by Menzies at Brown River, Central District, Territory of Papua.

DIAGNOSIS: This species is readily distinguished from all other Papuan microhylids by the characters of the skull given in the generic diagnosis. There is nothing particularly distinctive in the external morphology. The relatively large size of the eye (Eye/S-V mean 0.103) serves to separate *Pherohapsis* from *Barygenys*, *Xenobatrachus*, and *Xenorhina*. *Asterophrys* is readily distinguished by its wider head (HW/S-V minimum 0.46, compared to a maximum of 0.37 in *Pherohapsis*). There is no way for one unfamiliar with the general appearance of the individual species to distinguish among *Hylomphorbus*, *Pherohapsis* and the small species of *Phrynomantis* that have small digital discs unless he makes a superficial examination of the skull. Such an examination is easily accomplished by making small incisions and reflecting the skin.

DESCRIPTION OF THE TYPE-SPECIMEN: The body is relatively slender, scarcely wider than the

head. The snout is truncate and projects well in front of the mouth opening. The loreal region is nearly vertical and is slightly concave. The nostrils are close to the tip of the snout, with the internarial distance equal to the distance from eye to naris. The eyes are relatively large, with the orbital length equal to the length of the snout. The interorbital width equals the width of an upper eyelid. The tympanum is indistinct and finely granular. It is oval in shape (long axis vertical), with a horizontal diameter slightly greater than one-half that of the eye.

There is only a faint supratympanic skin fold. The middorsal surface of the body is smooth, but the sides are slightly pustulose.

The relative lengths of the fingers are $3 > 2 \geq 4 > 1$, of the toes $4 > 3 > 5 > 2 > 1$. The finger tips are rounded and scarcely expanded (fig. 10B). No terminal grooves are present. The tips of the toes are slightly more expanded than those of the fingers, forming small discs, and have terminal grooves. Moderately well-developed, rounded subarticular tubercles are present on hands and feet.

The middorsal area is light gray-brown. The side of the head and body is a darker shade, but the darker pigment is not organized into a clearly distinct band or stripe. Darker markings are present on the top of the head, and there are light flecks in the dark area of the side of the head. There is an indistinct dark ocellar marking high in the groin region, but the deep groin is pale with slightly darker mottling. The upper



FIG. 22. *Pherohapsis menziesi* (topotype).
Photo by John Waldrop.

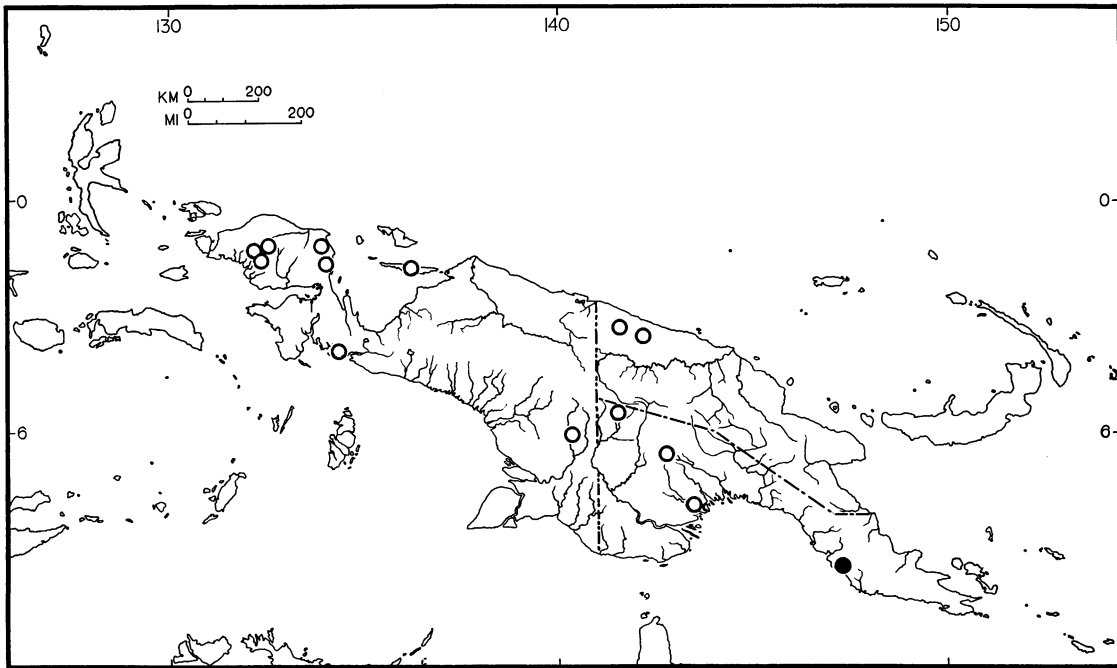


FIG. 23. Distribution of *Asterophrys turpicula* (open circles) and *Pterohapsis menziesi* (closed circle).

surfaces of the hind legs are light brown with indistinct darker markings. The anterior and posterior surfaces of the thighs are mottled with light and dark brown. The throat is dark gray-brown with lighter flecks. The chest is dark brown mottled with lighter brown. The amount of dark pigment reduces posteriorly, but there still is faint mottling at the posterior end of the abdomen.

The holotype is a male.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 28.5; TL, 9.5; HW, 10.3; Eye, 3.1; E-N, 2.2; IN, 2.2; EAR, 1.9. Proportions are as follows: TL/S-V, 0.333; HW/S-V, 0.361; Eye/S-V, 0.109; E-N/IN, 1.00.

VARIATION IN THE TYPE SERIES: Six of the seven specimens are adult males ranging in length from approximately 28 to 31 mm.; the seventh is a female (ova 2.0–2.5 mm.) of 31 mm. One individual dissected appears to have small, slightly puckered vocal slits lateral to the tongue that open into a single, subgular sac. There is no external sign of the vocal apparatus.

Proportions vary as follows (N=7): TL/S-V, 0.343 (0.33–0.36); HW/S-V, 0.360 (0.35–0.37); Eye/S-V, 0.103 (0.095–0.109); E-N/IN, 1.00

(0.92–1.09). In some specimens the fourth finger is slightly longer than the second.

Color pattern varies only slightly in the series, the chief variation being the presence of more dark pigment in the middorsal region of some specimens.

ECOLOGICAL NOTES: Menzies reports (personal commun.) that the frogs from Sogeri called from concealment within grass tussocks, probably at the mouths of holes, in a mowed, grassy area from which the forest had been cleared for about 10 years. The specimen from Brown River was in a teak plantation, but Menzies also heard the species calling in forest nearby.

MATING CALL: Through the courtesy of Mr. Menzies, I received a tape-recording of the mating calls of two individuals. The call (fig. 24) consists of a series of short, rather harsh notes about 0.2 second in length (mean length, 0.21 sec. in one sample, 0.18 in the other), separated by irregular intervals ranging from 0.22 to 0.91 second long (mean in one sample, 0.72 sec.; in the other, 0.31 sec.). Mr. Menzies reports that typically about 25 such notes comprise a call sequence. Most of the energy in the call is within the range from 1000 to 2000 Hz. The call

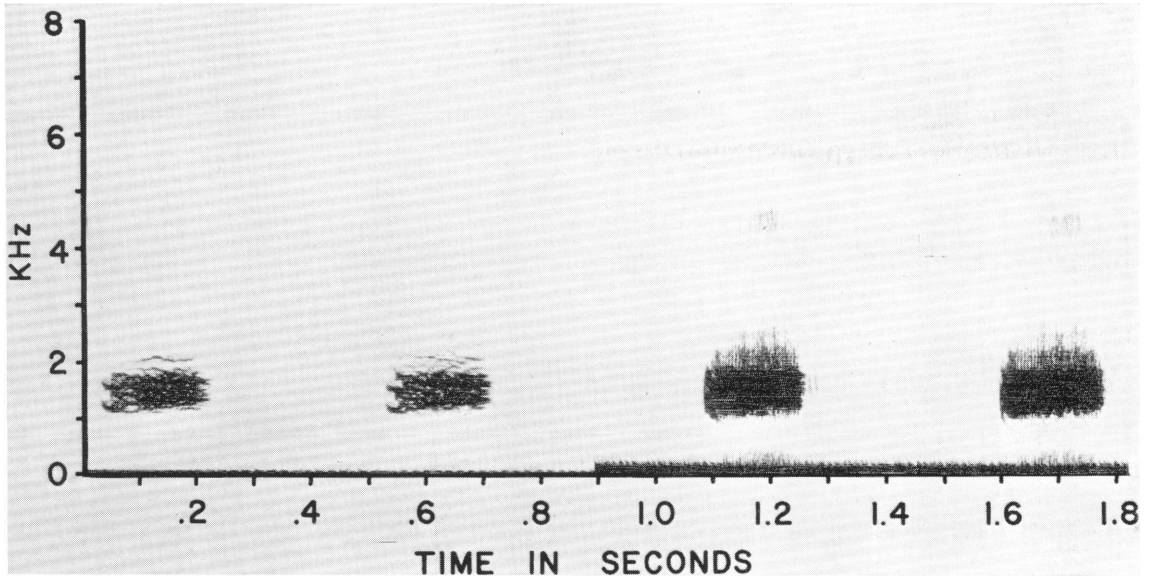


FIG. 24. Sound spectrogram of call of *Pherohapsis menziesi*, UPNG 1865, recorded by J. Menzies at Sogeri, Central District, on November 16, 1969 (temperature not noted). Four successive notes of a long sequence are shown, first two with 45 Hz. filter, last two with 300 Hz. filter.

is similar in quality to the "harsh" call of *Phrynomantis lateralis* or the typical call of *Hylophorbus rufescens* (see species accounts).

DISTRIBUTION AND SPECIMENS EXAMINED: The species is known only from Sogeri and Brown River (ca. 20 mi. N Port Moresby), Central District, Territory of Papua (fig. 23). Despite their proximity to Port Moresby, the southern slopes of the Owen Stanley Range have not been well explored herpetologically (e.g. the recent discovery of a striking new tree frog [Menzies, 1969]), and it is likely that *P. menziesi* ranges much more widely than the available information shows.

ETYMOLOGY: The species is named in honor of Mr. James Menzies, who first collected it and recognized its distinctness.

GENUS *PHRYNOMANTIS* PETERS

Phrynomantis PETERS, 1867, p. 35 (type-species by subsequent designation [Noble, 1926, p. 20], *Phrynomantis fusca* Peters, 1867).

Mantophryne BOULENGER, 1897, p. 12 (type-species by monotypy, *Mantophryne lateralis*).

Gnathophryne MÉHELÏ, 1901, p. 177 (type-species by subsequent designation [Parker, 1934, p. 58], *Mantophryne robusta* Boulenger, 1898b).

Pomatops BARBOUR, 1910, p. 89 (type-species by monotypy, *Pomatops valvifera*).

DIAGNOSIS: *Phrynomantis* is distinguished from other asterophryine genera by the following combination of characters: (1) maxillary bones in contact in front of the premaxillae; (2) dentary bones in contact in front of and fused with the mento-meckelian bones; (3) vomerine bones lack prominent spikes (although small odontoids may be present), and not greatly expanded along their median line of contact; (4) central arm of parasphenoid bone narrow, little more than half the width of the frontoparietals; (5) no arch of bone over the prootic region; (6) eyes relatively large, Eye/S-V ratio averages greater than 0.090 in all species; (7) nasal bones paired.

Hylophorbus resembles *Phrynomantis* in all respects except that the maxillary and dentary bones do not meet in front of (respectively) the premaxillae and mento-meckelian bones. *Xenorhina* and *Xenobatrachus* have broad parasphenoids, extensive mesial expansion of the vomers, and small eyes. *Xenobatrachus* differs in addition in having vomerine spikes. *Asterophrys* and *Pherohapsis* differ from *Phrynomantis* in having fused nasals and extensive sculpturing of the roofing bones of the skull. *Asterophrys* differs

TABLE 6
BODY PROPORTIONS IN TWENTY-FOUR SAMPLES OF THE GENUS *Phrynomantis*

| Sample | N | TL/S-V | | | HW/S-V | | | Eye/S-V | | | E-N/IN | | |
|-----------------------------|----------------|-------------|-------------|---------------|-------------|-------------|---------------|-------------|---------------|---------------|-------------|-------------|---------------|
| | | Mean | Range | $\pm\sigma_m$ | Mean | Range | $\pm\sigma_m$ | Mean | Range | $\pm\sigma_m$ | Mean | Range | $\pm\sigma_m$ |
| <i>P. boettgeri</i> | 1 | 0.52 | — | (0.52) | 0.37 | — | (0.37) | — | — | — | — | — | — |
| <i>P. dubia</i> | 1 | 0.48 | — | (0.48) | 0.39 | — | (0.39) | — | — | (0.109) | — | — | — |
| <i>P. eurydactyla</i> | 2 | 0.45 | — | (0.44–0.46) | 0.37 | — | (0.35–0.39) | — | — | (0.124–0.129) | 0.770 | — | (0.73–0.81) |
| <i>P. fusca^a</i> | 5 | 0.378 | — | (0.36–0.39) | 0.348 | — | (0.33–0.36) | — | — | (0.099–0.127) | 0.849 | — | (0.79–0.90) |
| <i>P. glandulosa</i> | 1 | 0.31 | — | (0.31) | 0.36 | — | (0.36) | — | — | (0.102) | 0.75 | — | (0.75) |
| <i>P. h. humicola</i> | 57 | 0.390±0.003 | (0.35–0.43) | | 0.388±0.004 | (0.33–0.45) | | 0.119±0.002 | (0.099–0.157) | | 0.796±0.007 | (0.63–0.89) | |
| Mount Otto | 45 | 0.381±0.004 | (0.32–0.43) | | 0.396±0.005 | (0.33–0.51) | | 0.120±0.002 | (0.104–0.176) | | 0.859±0.008 | (0.69–0.96) | |
| Daulo Pass | 11 | 0.390±0.010 | (0.31–0.42) | | 0.391±0.007 | (0.37–0.44) | | 0.119±0.003 | (0.106–0.138) | | 0.821±0.015 | (0.73–0.94) | |
| Dumun and Masul | | | | | | | | | | | | | |
| <i>P. h. compta</i> | 32 | 0.355±0.003 | (0.31–0.39) | | 0.375±0.003 | (0.33–0.41) | | 0.114±0.002 | (0.095–0.138) | | 0.855±0.010 | (0.75–0.96) | |
| Wahgi Dividing Range | 16 | 0.329±0.004 | (0.30–0.36) | | 0.365±0.006 | (0.33–0.43) | | 0.114±0.003 | (0.103–0.145) | | 0.857±0.010 | (0.81–0.92) | |
| Kaironk Valley | 20 | 0.493±0.004 | (0.46–0.53) | | 0.356±0.004 | (0.31–0.39) | | 0.117±0.001 | (0.110–0.141) | | 0.786±0.007 | (0.73–0.84) | |
| <i>P. infulata</i> | 3 | 0.372 | — | | 0.361 | — | (0.34–0.37) | 0.114 | (0.110–0.119) | | 0.747 | — | (0.70–0.79) |
| <i>P. kopsteini</i> | 30 | 0.431±0.006 | (0.37–0.48) | | 0.380±0.003 | (0.35–0.43) | | 0.109±0.001 | (0.083–0.121) | | 0.992±0.017 | (0.83–1.21) | |
| <i>P. lateralis</i> | | | | | | | | | | | | | |
| <i>P. louisianensis</i> | | | | | | | | | | | | | |
| Rossel Island | 37 | 0.479±0.004 | (0.43–0.52) | | 0.412±0.004 | (0.38–0.47) | | 0.119±0.002 | (0.097–0.149) | | 0.863±0.009 | (0.77–0.96) | |
| Sudest Island | 7 | 0.422±0.007 | (0.40–0.46) | | 0.369±0.005 | (0.34–0.38) | | 0.129±0.002 | (0.121–0.136) | | 0.888±0.019 | (0.81–0.94) | |
| <i>P. personata</i> | 11 | 0.355±0.004 | (0.34–0.38) | | 0.384±0.003 | (0.37–0.41) | | 0.116±0.002 | (0.106–0.128) | | 0.821±0.019 | (0.76–0.93) | |
| <i>P. robusta</i> | 38 | 0.364±0.006 | (0.29–0.44) | | 0.375±0.005 | (0.30–0.44) | | 0.122±0.003 | (0.090–0.159) | | 0.877±0.012 | (0.74–1.12) | |
| <i>P. slateri</i> | 4 | 0.394 | — | (0.37–0.42) | 0.394 | — | (0.37–0.42) | 0.102 | (0.093–0.113) | | 1.24 | — | (1.12–1.34) |
| <i>P. stictogaster</i> | 56 | 0.327±0.002 | (0.29–0.38) | | 0.376±0.002 | (0.33–0.42) | | 0.098±0.006 | (0.088–0.123) | | 0.815±0.005 | (0.75–0.92) | |
| <i>P. wilhelmana</i> | | | | | | | | | | | | | |
| Mt. Wilhelm | 49 | 0.326±0.003 | (0.26–0.38) | | 0.365±0.003 | (0.33–0.43) | | 0.101±0.001 | (0.088–0.128) | | 0.752±0.006 | (0.67–0.83) | |
| Daulo Pass | 11 | 0.315±0.006 | (0.27–0.34) | | 0.381±0.006 | (0.36–0.43) | | 0.102±0.002 | (0.093–0.118) | | 0.782±0.013 | (0.72–0.83) | |
| Mt. Otto | 16 | 0.311±0.005 | (0.26–0.34) | | 0.377±0.005 | (0.35–0.42) | | 0.105±0.002 | (0.090–0.119) | | 0.751±0.014 | (0.61–0.83) | |
| Sikuri Pass and Dumun | 27 | 0.315±0.003 | (0.28–0.35) | | 0.379±0.006 | (0.34–0.44) | | 0.109±0.002 | (0.093–0.133) | | 0.819±0.012 | (0.71–0.90) | |
| Kup | 9 ^b | 0.344±0.003 | (0.32–0.36) | | 0.360±0.003 | (0.34–0.37) | | 0.100±0.001 | (0.097–0.107) | | 0.803±0.018 | (0.73–0.88) | |

^aSpecimen from Batanta Island not included.

^bN = 16 for TL_j/S-V only.

additionally in having the frontoparietals compressed into a crest (flattened or slightly concave in *Phrynomantis*). *Pherohapsis* differs also in its possession of a bony arcade over the prootic region and a solid sheet of bone connecting the squamosal and maxilla immediately behind the orbit.

CONTENT: I assign 15 species, six of them new, to this genus: *P. boettgeri* (Méhely); *P. dubia* (Boettger); *P. eurydactyla*, new species; *P. fusca*, Peters; *P. glandulosa*, new species; *P. humicola*, new species; *P. infulata*, new species; *P. kopsteini* (Mertens); *P. lateralis* (Boulenger); *P. louisianensis* (Parker); *P. personata*, new species; *P. robusta* (Boulenger); *P. slateri* (Loveridge); *P. stictogaster*, new species; and *P. wilhelmana* (Loveridge). One of the species is considered to be polytypic: *P. h. humicola* and *P. h. compta*, new species and subspecies.

DESCRIPTION: Adults range in maximum snout-vent length from 24 mm. (*dubia*) to 82 mm. (*louisianensis*). The genus includes species with a variety of body forms—relatively long-legged animals with broad toe and finger discs as well as heavy set, short-legged forms with no digital discs. Relatively large eyes are common to all species. Subarticular tubercles exist only as low, rounded elevations in some species but in others are much more distinctive elevations.

I have examined skulls (cleaned, or cleared and stained) of six species (*humicola*, *infulata*, *lateralis*, *louisianensis*, *stictogaster*, and *wilhelmana*), Méhely (1901, pls. 4, 6) published illustrations of two (*lateralis* and *robusta*), and I have made superficial examinations (by reflection of skin, but without deep dissection) of five others (*eurydactyla*, *fusca*, *glandulosa*, *personata*, and *slateri*). Two rare species, *P. boettgeri* and *P. dubia*, are assigned to this genus largely on the basis of external appearance. The former is definitely symphygnathine and the latter probably so (see species accounts).

The following features seemingly are common to the skulls of the species of *Phrynomantis*: nasals large, broadly in contact with each other and with frontoparietals, excluding ethmoid from dorsal surface of skull or largely so; maxillae in contact, in some instances firmly sutured in front of premaxillae; dentaries fused with and in contact in front of mento-meckelian bones; vomerine bones not notably expanded along midline of contact anteriorly and slightly or not at all posteriorly; tiny vomerine odontoids

present or absent; large vomerine spikes absent; vomer with anterior arm partly surrounding internal naris; no projection from maxillary shelf to vomer; anterior arm of parasphenoid narrow, approximately one-half width of frontoparietal region; anterior end of squamosal with cartilaginous tip not contacting maxilla; dorsal surface of skull smooth or slightly pitted, lacking bony arcade in prootic region.

DISTRIBUTION: This genus ranges throughout the New Guinea region, from the Moluccas through New Guinea proper to the easternmost islands of the Louisiade Archipelago. It is the only genus of Asterophryinae known from the Moluccas. The range in elevation is from sea level to 3400 m. (11,100 ft.).

KEY TO THE SPECIES OF *Phrynomantis*

The species keyed out through couplet 9 should provide little difficulty in identification. The last five species (from couplet 10 on) differ in subtle ways or average proportions that are not readily expressed in a key. Hence, I have utilized a geographic breakdown.

1. Tips of fingers and toes without expanded, grooved discs 2
 Tips of fingers and toes, or toes alone, with expanded, grooved discs 4
2. A small tubercle between eye and nostril (fig. 57); size large, up to 80 mm. S-V; ventral surfaces dark with tiny light spots, or coarsely mottled, but never uniform . . . *stictogaster*
 No tubercle between eye and nostril; size moderate, up to 54 mm. S-V; ventral surfaces mottled or uniform in color 3
3. A conspicuous glandular fold above and behind tympanum; all ventral surfaces pale with darker mottling *glandulosa*
 Only a slight supra- and post-tympanic fold; ventral surface usually dark, rarely mottled and then only posteriorly *wilhelmana*
4. Finger discs large, equal to or broader than toe discs, that of third finger at least twice width of penultimate phalange 5
 Finger discs small or absent, equal to or smaller than toe discs, usually less than twice width of penultimate phalange 7
5. Disc on third finger essentially equal in width to that on fourth toe *eurydactyla*
 Disc on third finger distinctly broader than that on fourth toe 5
6. Hind legs longer, TL/S-V, 0.52 in the single specimen *boettgeri*
 Hind legs shorter, TL/S-V, 0.37-0.42 in four specimens *slateri*

7. Dorsal color pattern with a broad, dark dorso-lateral band, straight-edged or irregular, reaching from eye to groin 8
Dorsal color pattern not as described 9
8. Hind legs longer, TL/S-V, 0.46–0.53; maximum S-V, 39; internarial distance greater than eye-naris distance, E-N/IN maximum 0.84 *infulata*
Hind legs shorter, TL/S-V, 0.37–0.48; maximum S-V, 55; internarial distance approximately equal to eye-naris distance, E-N/IN minimum 0.83 *lateralis*
9. TL/S-V mean greater than 0.40 (range, 0.40–0.52) 10
TL/S-V mean less than 0.40 (range, 0.30–0.44) 11
10. Size large, up to 82 mm. S-V; fingers with prominent subarticular tubercles (Rossel and Sudest islands) *louisianensis*
Size small, single specimen 24 mm. S-V; fingers with low, rounded subarticular tubercles (Halmahera Island, Moluccas) *dubia*
11. Head black from snout to posterior corners of eyes and angles of mouth, sharply differentiated from paler body color *personata*
Head not markedly and abruptly different in color from body 12
12. Specimens from islands west of New Guinea 13
Specimens from New Guinea and islands to the southeast 14
13. E-N/IN mean 0.75, range 0.70–0.79 (Sulabesi Island) *kopsteini*
E-N/IN mean 0.85, range 0.79–0.80 (Amboina, Seram, and ?Batanta islands) *fusca*
14. Ventral coloration uniform; size larger, up to 73 mm. S-V *robusta*
Ventral coloration mottled; size smaller, up to 59 mm. S-V 15
15. A light (yellow or orange in life) stripe extending downward posteriorly from the eye *humicola compta*
Postocular stripe absent or faintly indicated only in juveniles *humicola humicola*

Phrynomantis boettgeri (Méhely),
new combination

Phrynixalus montanus: BOETTGER, 1900, p. 368 (part; specimen from Galela only).

Gnathophryne boettgeri MÉHELÝ, 1901, pp. 181, 229 (type locality, Galela, elevation 2200 ft., Halmahera, Moluccas Islands [Boettger, 1900, p. 368]; holotype, SMF 4200, collected by W. Kükenenthal in 1894).

Hylophorbus boettgeri: VAN KAMPEN, 1923, p. 140.

Asterophrys boettgeri: PARKER, 1934, p. 61.

DIAGNOSIS: Only *Phrynomantis boettgeri* and *P. slateri* among all known *Phrynomantis* have finger

discs conspicuously enlarged and broader than the toe discs. The only other species with large finger discs, *P. eurydactyla*, has those of the toes equally enlarged.

So far as present information reveals, *boettgeri* and *slateri* are best differentiated by relative leg length: TL/S-V is 0.52 in the only specimen of *boettgeri* and is 0.37–0.42 in the four specimens of *slateri*. For further discussion, see the accounts of *P. slateri* and *P. eurydactyla*.

DESCRIPTION OF TYPE-SPECIMEN: The following description is based on Méhely's description (1901, pp. 229–230) and my examination of the unique specimen. The body is thick-set with moderately broad head. Méhely stated: "Eyes large, very protuberant. Interorbital space as broad as an eyelid." The skull has been removed, so I could not make accurate measurements of the eyes. Méhely's description continues: "Snout short and high, somewhat shorter than the diameter of the eye, abruptly narrowed anteriorly and broadly rounded at the end; canthus rounded. The naris is much closer to the tip of the snout than to the eye [internarial distance scarcely greater than distance from eye to naris]. Tympanum rather distinct, the diameter equal to about half of the diameter of the eye; it lies a distance equal to its own diameter from the posterior corner of the eye . . ."

The skin is mainly smooth, but there are pustules on the eyelids, posterior part of the head, shoulder region and the sides of the body. A fold of skin passes from the posterior corner of the eye above and behind the tympanum.

The relative lengths of the fingers are $3 > 4 > 2 > 1$, and of the toes, $4 > 3 > 5 > 2 > 1$. Fingers and toes bear relatively large terminal discs. The width of the disc of the fourth toe is about 76 per cent of that of the disc of the third finger. Méhely stated that the discs of the fingers were four times as broad as the penultimate phalanges; by my measurement, the ratio is three to one for the third finger, but there may have been some shrinkage since Méhely studied the specimen. The fingers and toes are unwebbed. Subarticular tubercles and the inner metatarsal tubercle are present but are weakly developed. According to Méhely, the heel of the adpressed limb reaches almost to the nostril.

Méhely emphasized the symphygnathine nature of the maxillary bones. He noted that the tongue was scarcely free behind and provided with a median groove passing posteriorly into a

pit. The pharyngeal region has the usual two folds, the anterior smooth and the posterior serrate.

The ground color is brown, and there is a yellowish-white stripe from snout to cloacal opening. Dark markings on the back include a W-shaped mark in the scapular region and dark flecks on each side of the central light stripe. There are large, rounded reddish-brown markings on the sides of the head and body that run together. The ventral surfaces are light brown, with chestnut-brown spots on the chin, throat, chest, and undersides of limbs.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 38.3; TL, 19.8, HW, 14.2, IN, 3.3; E-N, 3.2; width of disc of third finger, 2.1 (penultimate phalange, 0.7); width of disc of fourth toe, 1.6 (penultimate phalange, 0.6). Because the skull has been removed, measurements on the head were made on loose skin and therefore are not of a high degree of accuracy; eye size was not measured.

ECOLOGICAL NOTES: Boettger (1900, p. 368) reported that the specimen (later designated as the type of *A. boettgeri*) was found under moss at the foot of a tree at an elevation of 2200 feet.

DISTRIBUTION AND SPECIMENS EXAMINED: The species is known only from the holotype, SMF 4200, from Galela, Halmahera, Moluccas Islands, Indonesia (fig. 25).

Phrynomantis dubia (Boettger),
new combination

Xenorhina dubia BOETTGER, 1895, p. 134 (type locality, "North Halmahera, up to 2200' in elevation," Moluccas, Indonesia; lectotype, SMF 4201, collected in 1894 by W. Kükenthal. Originally there were two syntypes [Boettger, 1895], but Mertens [1967, p. 51] mentioned only one in designating the lectotype).

Gnathophryne dubia: MÉHELÿ, 1901, pp. 182, 231.

Hylophorbus dubius: VAN KAMPEN, 1923, p. 143.

Asterophrys dubia: PARKER, 1934, p. 63.

DIAGNOSIS: The poor state of preservation of the only specimen I examined prevents satisfactory diagnosis of this species. Presumably the following combination of characters is diagnostic: small size (*ca.* 24 mm. snout to vent); discs on fingers and toes small, those on toes slightly the larger; hind legs unusually long (TL/S-V, 0.48). The only other species of *Phrynomantis*

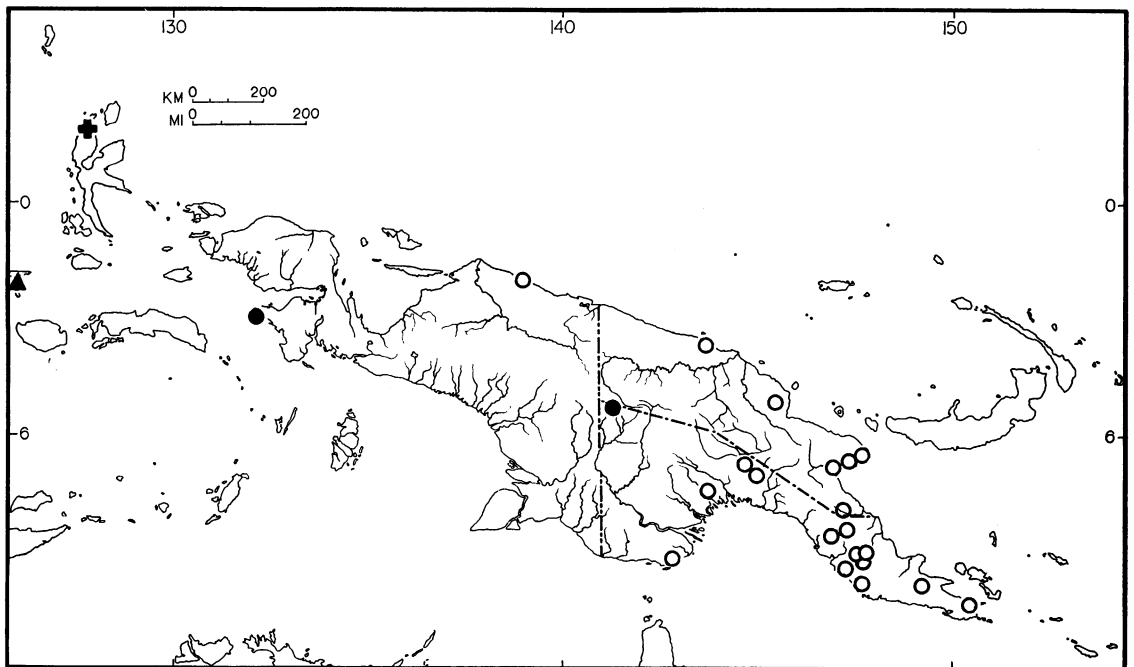


FIG. 25. Distribution of four species of *Phrynomantis*. Cross, *P. boettgeri*; triangle, *P. kopsteini*; closed circles, *P. eurydactyla*; open circles, *P. lateralis*.

known from Halmahera, *P. boettgeri*, has large digital discs, with the one on the third finger larger than the one of the fourth toe. The other Moluccan species, *P. fusca* and *P. kopsteini*, are shorter-legged (TL/S-V less than 0.40), and larger (to at least 45 mm. S-V).

DESCRIPTION: The following description is based on the original description and on additional information from Méhely (1901, p. 231), who examined the syntypes, as well as on my examination of the lectotype. See Boettger (1900, pl. 16) for an illustration.

This is a small (*ca.* 24 mm. snout to vent length), thick-set frog with a moderately broad head (HW/S-V, 0.39). The nasal openings are much closer to the tip of the rather pointed snout than to the eye, the canthus rostralis is rounded, and the loreal region is oblique. The interorbital space is approximately one and one-half times the width of an upper eyelid. The tympanum is indistinct and about two-fifths of the diameter of the eye. The skin is smooth except for the supratympanic fold and some wartiness on the sides of the body.

Very small discs are present on both fingers and toes, although this is not evident in Boettger's (1900, pl. 16) illustration. The toe discs are slightly larger than those of the fingers. In the original description Boettger (1895, p. 134) stated: "Fingertips blunt, without discs . . .," but Méhely (1901, p. 231) differed: "Fingers and toes free and provided with very small discs." The results of my examination of the rather dried lectotype agree more closely with Méhely's statement. Subarticular tubercles are weakly developed; a weak, inner metatarsal tubercle is present.

The palate has the usual two skin folds, the smooth anterior one and the serrate posterior. Méhely (*loc. cit.*) did not specifically state so, but presumably the skull is symphygnathine; I infer this from his reference of the species to the genus *Gnathophryne*. The pupil is horizontal. The terminal phalanges are T-shaped.

The dorsal color is "blackish gray, unicolor or indistinctly lightly flecked or marbled, the limbs with a few indistinct, light gray bars, transverse flecks and rings. Undersides brownish-yellow, entirely washed with chestnut brown, or chestnut brown with brownish-yellow marbling and rounded flecks" (Boettger, 1895, p. 135).

MEASUREMENTS OF LECTOTYPE SPECIMEN: S-V, 20.1; TL, 9.6; HW, 7.8; Eye, 2.2. Presum-

ably this specimen is the smaller of the two syntypes, for which Boettger (1895, p. 135) gave a length ("head length" plus "body length") of 22 mm. The difference in our measurements probably relates to shrinkage of the specimen.

DISTRIBUTION AND SPECIMENS EXAMINED: The species is known only from the two syntypes from the northern part of the island of Halmahera in the Moluccas, Indonesia (fig. 28). In the original description, Boettger (1895, p. 134) was no more specific than this regarding locality, but later (1900, p. 369) he listed one from "Nord-Halmahera" and the other from "Soah Konorah" (presumably Soakonora). I examined the lectotype, SMF 4201, from North Halmahera.

Phrynomantis eurydactyla, new species

Figure 26

HOLOTYPE: BBM 1014, collected by J. L. Gressitt at Danowaria, 70 m., near Fak Fak on the Onin Peninsula, West Irian, on June 2, 1959.

PARATYPE: MCZ 81692, Wangbin, 4800 ft. (1460 m.), (20 mi. W, 11 mi. N Olsobip), Western District, Territory of Papua.

DIAGNOSIS: *Phrynomantis eurydactyla* is the only species of its genus in which the discs of the

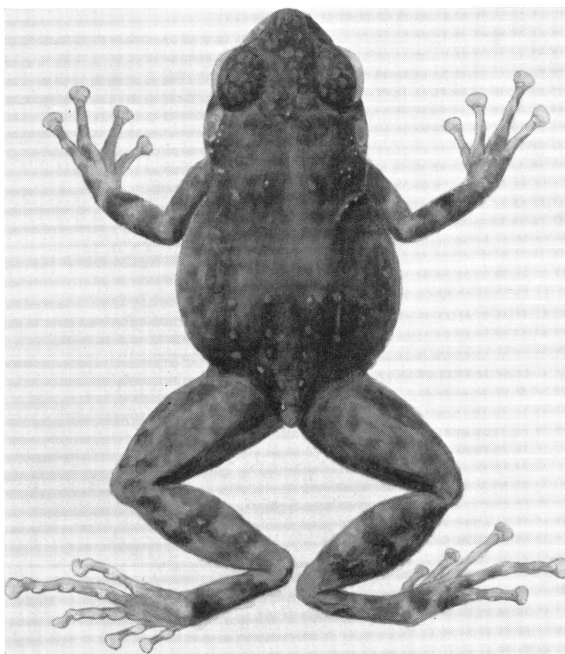


FIG. 26. *Phrynomantis eurydactyla* (BBM 1014, holotype), dorsal view. $\times 1.5$.

third finger and fourth toe are more than twice the width of the penultimate phalanges and are equal in size or essentially so. The only other species with similarly enlarged finger discs are *P. slateri* and *P. boettgeri*, and in these species the finger disc is distinctly broader than that of the toe.

DESCRIPTION OF TYPE-SPECIMEN: The body is moderately slender for an antrophryine, only slightly wider than the head. The snout is truncate, the canthus rostralis rounded, and the loreal region is vertical and concave. The nostrils are closer to the tip of the snout than to the eye and open laterally, so that they are scarcely visible from directly above. The internarial distance is greater than the distance from eye to naris. The eyes are large, equal to the length of the snout, with the width of an upper eyelid greater than the interorbital distance. The tympanum is large (more than one-half the diameter of the eye) and moderately distinct.

The dorsal surface of the body is somewhat warty, more so on the sides and posterior portion of the back than in the middorsal region. The lower surfaces of the body and limbs are smooth. A supratympanic fold is only barely indicated.

The relative lengths of the fingers are $3 > 4 = 2 > 1$; all have broad discs with terminal grooves (fig. 27A). The disc of the third finger is slightly more than twice the width of its penultimate phalange. The relative lengths of the toes are $4 > 3 > 5 > 2 > 1$. The disc of the fourth toe is more than twice the width of its penultimate

phalange and equal in size to that of the third finger. The other toes also bear broad discs, and all have terminal grooves. There are prominent, rounded subarticular tubercles on both hands and feet. Low, rounded inner, middle, and outer metacarpal tubercles are present (the first the most prominent), but the foot bears only an inner metatarsal tubercle. The fingers and toes are unwebbed.

The tongue is broad, somewhat pouched posteriorly, and not free posteriorly. There are the usual two palatal folds, the anterior one smooth, the posterior denticulate.

The specimen is a male with a subgular vocal sac and with small vocal slits placed posteriorly and laterally in the floor of the mouth.

The maxillary bones broadly overlap the premaxillae and are joined by a narrow band of connective tissue. The pectoral girdle lacks clavicles and procoracoids. There are no vomerine spikes or odontoids.

The head and body are brown dorsally with irregular darker brown spotting and mottling. Small rugosities of the head, eyelids, and body have tips lighter than the ground color. The limbs are colored and patterned much as is the body. The ventral surfaces have a light tan ground color, immaculate in the abdominal region but lightly mottled with light brown on the chin and undersides of the hind limbs.

MEASUREMENTS OF THE HOLOTYPE (followed, in parentheses, by those of the paratype): S-V, 37.1 (41.0); TL, 16.2 (18.7); HW, 14.5 (14.4); E-N, 3.0 (2.5); IN, 3.7 (3.4); eye, 4.8 (5.1);

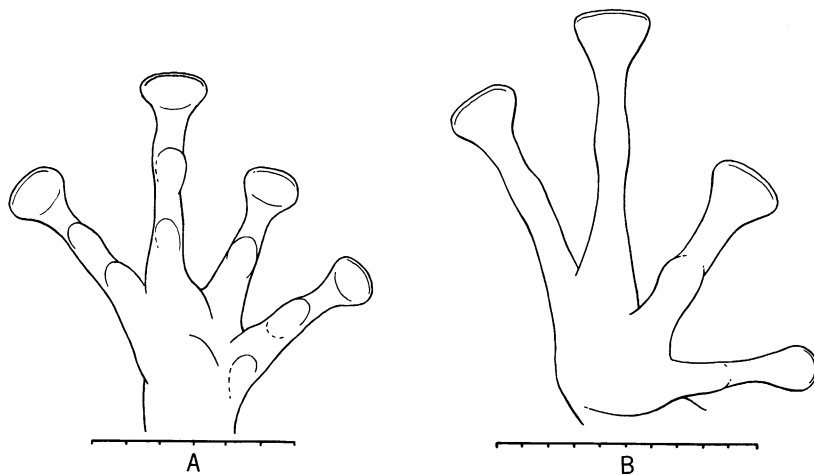


FIG. 27. Hands of *Phrynomantis* in palmar view. A. *P. eurydactyla*. B. *P. slateri*. Scale lines subdivided in millimeters.

EAR, 3.0 (not distinct in paratype); disc of third finger, 1.7 (1.5), penultimate phalange, 0.8 (0.8); disc of fourth toe, 1.7 (1.7), penultimate phalange, 0.7 (0.8). Proportions are as follows: TL/S-V, 0.437 (0.456); HW/S-V, 0.391 (0.351); E/N/IN, 0.81 (0.73); Eye/S-V, 0.129 (0.124); EAR/Eye, 0.625.

VARIATION: The single paratype, which was collected by Fred Parker, differs insignificantly from the holotype in proportions (see foregoing section). The color pattern resembles that of the holotype but the shades are more gray than brown, probably because the paratype was first preserved in formalin and the holotype in alcohol.

COMPARISON WITH OTHER SPECIES: Although most species of *Phrynomantis* have the tips of the toes and (less often) the fingers broadened into discs, the discs are usually relatively small. The expansion of the finger tips amounts in most cases to one and one-half or less of the width of the penultimate phalange. The three known exceptions are *P. boettgeri*, *P. eurydactyla*, and *P. slateri*. As pointed out in the diagnosis, *boettgeri* and *slateri* differ from *eurydactyla* in that their finger discs are larger than the corresponding toe discs, whereas in *eurydactyla* the discs are virtually the same size. The disc of the third finger of *boettgeri* and *slateri* is approximately three times the width of the penultimate phalange, compared with two times in *eurydactyla*.

The difference in disc size is not the only one distinguishing *P. eurydactyla* from the other two species. The internarial distance of *slateri* is less than the distance from eye to naris (E-N/IN mean 1.24), whereas in *eurydactyla* the proportions are reversed (E-N/IN=0.73, 0.81). The difference between these two ratios is greater than that to be expected within the range of variation of one species. The two may differ in eye size, although this character is too variable to be trusted without a larger sample (Eye/S-V in *eurydactyla* 0.124, 0.129; mean of *slateri* 0.102).

Phrynomantis boettgeri is an exceptionally long-legged microhylid with a ratio of tibia length to length from snout to vent of 0.52, compared to 0.42, 0.46 in *eurydactyla*. The E-N/IN ratio may be higher in *boettgeri* (0.97 compared to 0.73, 0.81), but because the only specimen of *boettgeri* has had the skull removed, the measurements made on the skinned head may not be too reliable.

The specific distinctness of *Phrynomantis eurydactyla* is strongly indicated by the nature of the digital discs and is supported by the differences in other proportions.

ECOLOGICAL NOTES: The only information on this species is that the type-specimen was found in a limestone cave.

DISTRIBUTION AND SPECIMENS EXAMINED: This species is known only from the holotype and paratype (localities cited above). The two localities are about 650 miles apart, one on the Onin Peninsula of West Irian and the other in the northwestern corner of the Territory of Papua (fig. 25). Presumably the species ranges all along the southern foothills of the main mountain mass of West Irian.

ETYMOLOGY: The specific name combines the Greek words *eury*s (broad) and *dactylos* (toe, finger), in reference to the unusually well-developed digital discs.

Phrynomantis fusca Peters

Phrynomantis fusca PETERS, 1867, p. 35 (type locality, "Amboina," Indonesia; syntypes [2], ZMB 5648, collected by von Martens).

Oreophryne celebensis (part): VAN KAMPEN, 1923, p. 112.
Hylophorbus amboinensis MERTENS, 1930, p. 145, fig. 1 (type locality, "Ambon, Molukken"; holotype, RMNH 5315, collected by F. Kopstein in April, 1922).

Asterophrys amboinensis: PARKER, 1934, p. 61.

Asterophrys fusca: PARKER, 1934, p. 63.

DIAGNOSIS: Among the four species of *Phrynomantis* recorded from the Moluccas, *P. fusca* is distinguished by the combination of relatively short legs (TL/S-V mean 0.37), discs on fingers and toes small and essentially equal in size, and nostrils moderately widely spaced (E-N/IN mean 0.85).

Phrynomantis boettgeri and *P. dubia* of Halma-hera are relatively long-legged (TL/S-V in each unique specimen, respectively, 0.52 and 0.48), and *boettgeri* differs in addition in having finger discs much broader than those of the toes. *Phrynomantis kopsteini* has a lower E-N/IN ratio (mean 0.75) and may have relatively larger discs on the toes (see section on comparisons).

Phrynomantis robusta of the mainland of New Guinea closely resembles *P. fusca*. Possible differences include smaller size of *fusca* (to 54 mm. snout-vent length in *fusca* compared with 73 mm.) and relatively slightly larger finger discs in *fusca*; see following discussion.

DESCRIPTION OF TYPE-SPECIMENS: The two syntypes are sufficiently similar that a composite description will suffice. The body is relatively slender, with the head only slightly narrower than the body. The eyes are large, longer than the snout, and an upper eyelid is wider than the interorbital space. There is no obvious canthal angle; rather, the rounded canthus slopes to a very shallowly concave loreal region. The nares are closer to the tip of the snout than to the eye, and the internarial distance is greater than the distance from eye to naris. The tympanum is scarcely visible and is less than half the diameter of the eye. The body is smooth above and beneath, lacking even the postocular fold common to so many species.

The relative lengths of the fingers are $3 > 4 > 2 > 1$ and of the toes $4 > 3 > 5 > 2 > 1$. All fingers and toes bear small grooved discs, with those of the toes being slightly the larger (fig. 51F). Subarticular tubercles are present only as low, rounded elevations. There is a low, inner metatarsal tubercle, but no outer one. The toes are unwebbed.

Clavicles and coracoids are lacking. The anterior processes of the maxillae meet on the midline (symphygnathine). There are no vomerine spikes. Noble (1926, pp. 19–20) examined one of the syntypes and noted: "vomers large bearing a crenulated ridge along their posterior margins transverse to the body axis [see Noble's fig. 7] . . . a denticulated fold between the eustachian tubes . . . tongue entire . . . sacrum moderately dilated . . . terminal phalanges T-shaped, no intercalary . . . pupil horizontal."

The faded color pattern is brown dorsally and slightly darker on the sides. Faint traces of lumbar ocelli are present. The limbs show some mottling but no distinct crossbarring. The undersurfaces are pale tan, faintly mottled or spotted with a lighter shade. Peters (1867, p. 35) stated, "ventral side with irregular white flecks and lines."

The smaller of the two syntypes is a male with a subgular vocal sac and paired slits in the floor of the mouth; the larger specimen has not been sexed.

MEASUREMENTS OF SYNTYPE SPECIMENS: S-V, 23.8, 22.8; TL, 8.9, 8.2; HW, 7.8, 8.0; Eye, 2.7, 2.9; E-N, 1.7, 1.8; IN, 2.1, 2.0; EAR, 1.0, 1.0; disc on third finger, 0.6 (penultimate phalange, 0.4), 0.4 (0.3); disc on fourth toe, 0.7 (0.4), 0.6 (0.3).

VARIATION: Proportional variation is summarized in table 6. Peters and Doria (1878, p. 429) referred a specimen from Batanta Island (MSNG 29131) to this species. This specimen, which I have examined, agrees closely with the syntypes of *fusca* in pertinent skeletal features, proportions, and pigmentation. The dorsum is brown with numerous tiny white spots on the flanks, lips, forelegs and hind legs, and some larger white spots in the head and shoulder region. The ground color of the chin is dark brown, washing to a paler shade at the posterior of the abdomen. The undersides of the hind legs are dark brown, and all ventral surfaces are liberally spotted with white. I regard the locality as peculiar for this species, since Batanta is a satellite of New Guinea 150 miles from Seram. With the information available, however, there is no reason other than the biogeographic one for suspecting the co-identity of the populations of Amboina and Batanta.

The holotype of *H. amboinensis* closely resembles the syntypes of *P. fusca* in most ways (see following section), but has larger ears (62 per cent of eye diameter, compared with 34 to 37 per cent in the syntypes). Mertens (1930, p. 146) mentioned whitish flecks on the flanks, but stated "abdominal surface dirty yellow brown."

COMPARISON WITH OTHER SPECIES: Mertens (1930, pp. 147–149) considered *H. kopsteini* very closely related to *amboinensis* (= *fusca*), but different principally in having finger discs smaller than toe discs, whereas *amboinensis* was said to have discs of the same size. My examination of the type-specimens confirms that the toe discs of *kopsteini* are relatively larger than in *amboinensis*, although I find the toe discs of *amboinensis* measurably if only slightly larger than the finger discs. With an average E-N/IN ratio of 0.75 (three specimens), *kopsteini* apparently differs from *fusca* (mean 0.85, five specimens). Mertens also cited differences in pattern and in the length of the second finger (longer in *kopsteini*).

Recent acquisition of two fresh, large specimens of *fusca* from Seram has made apparent a closer relationship between this species and *P. robusta* of the mainland of New Guinea than previously was evident. The two forms are closely similar in proportions (table 6) and general appearance. The largest specimen of *fusca*, an adult female, measures 54 mm. snout to vent. The sample of *robusta* includes specimens

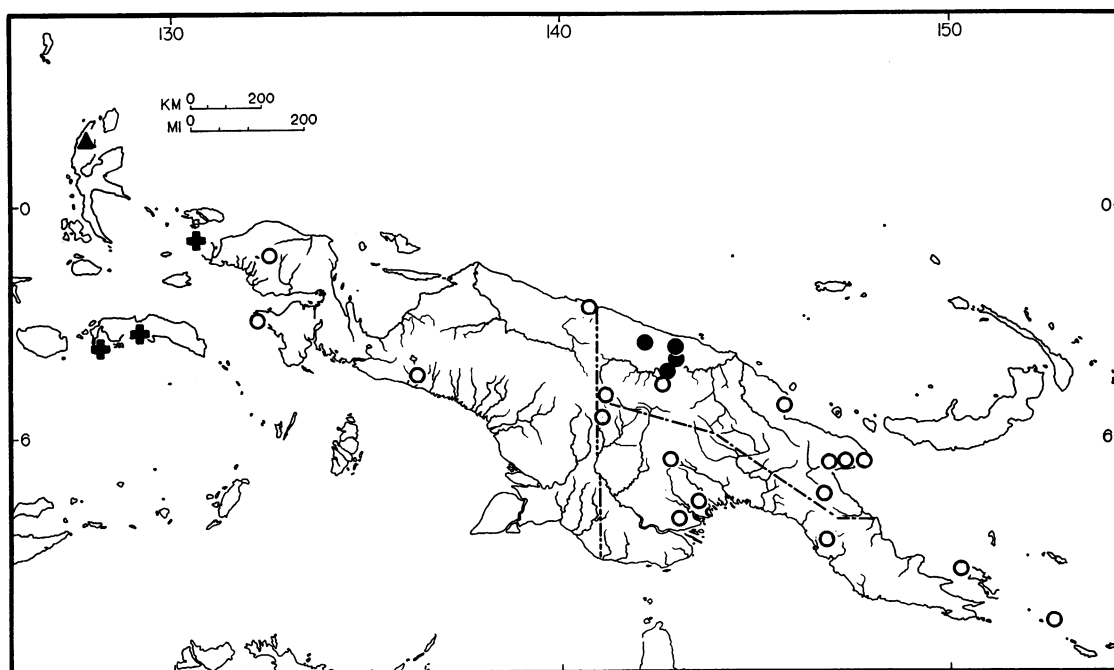


FIG. 28. Distribution of four species of *Phrynomantis*. Triangle, *P. dubia*; crosses, *P. fusca*; open circles, *P. robusta*; closed circles, *P. personata*.

up to 73 mm. long, and 18 of the 35 specimens in the sample are larger than the largest of five *fusca*. Although this is not conclusive evidence, it strongly suggests that *robusta* is a larger form.

TAXONOMIC NOTES: I regard *Hylophorbus amboinensis* Mertens, 1930 as a synonym of *P. fusca*. I examined the types of both species (but have not compared them directly) and can find no differences of diagnostic significance. Parker (1934) treated the two as distinct species, but he did not examine the types of either species and had to rely on the published descriptions. The original description of *fusca* is cursory in the extreme. Mertens's description of *amboinensis* is characteristically thorough, but he made no mention of *fusca*, and may have overlooked this, the only other species of microhylid recorded from Amboina. The holotype of *amboinensis* closely resembles the two syntypes of *fusca* in proportions (those of *fusca* given in parentheses): TL/S-V, 0.39 (0.37, 0.36); HW/S-V, 0.35 (0.33, 0.36); Eye/S-V, 0.112 (0.113, 0.127); E-N/IN, 0.82 (0.81, 0.90). Color pattern of *fusca* is of little use because of fading that has taken place in more than 100 years since the syntypes of

fusca were preserved. I see no reasonable alternative to regarding the two names as synonymous.

DISTRIBUTION AND SPECIMENS EXAMINED: *Phrynomantis fusca* is known only from Amboina, Seram, and Batanta islands (fig. 28). In addition to the specimens I have examined, Schijfsma (1932) reported two specimens from Amboina as *Hylophorbus ocellatus*. Parker (1934, p. 70) referred this record with question to *Metopostira kopsteini* (= *Phrynomantis kopsteini*); I think it more likely that the frogs were *P. fusca*.

Indonesia, Moluccas Islands: Amboina Island (ZMB 5648, [2 syntypes of *Phrynomantis fusca*]; RMNH 5315, holotype of *Hylophorbus amboinensis*). Seram Island, Ruhowa, 30 km. E Amahai (BMNH 1970.1868); Seram Island, River Upa, 29 km. E Amahai (BMNH 1970.1869). West Irian: Batanta Island (MSNG 29131).

***Phrynomantis glandulosa*, new species**

Figure 29

HOLOTYPE: RMNH 16667, collected by W. Vink on Mt. Kerewa, 3340 m. (10,960 ft.),

Southern Highlands District, Territory of Papua, in July, 1966.

DIAGNOSIS: This species differs from most other *Phrynomantis* in lacking terminal discs on fingers and toes, and differs from all others in having a well-developed glandular area above and behind the ear.

Only two species in addition to *P. glandulosa* have fingers and toes without terminal discs. The presence of a small tubercle between the eye and the nostril and the lack of a conspicuous glandular fold above and behind the ear will serve to distinguish *P. stictogaster* from *P. glandulosa*. The glandular fold is feeble or absent also in *P. wilhelmana*, which differs from *P. glandulosa* in addition by having the ventral surfaces uniformly colored (or nearly so), instead of pale with coarse darker mottling.

DESCRIPTION OF TYPE-SPECIMEN: The holotype is a male and presumed to be adult from the sizes of the testes. Because the specimen is the only one of its species known to me, I did not make the deep dissections necessary to examine the shape of the vomers or to establish the presence of a vocal sac. The upper jaw is firmly symphygnathine; procoracoids and clavicles are lacking. The large size of the eyes and general body form leave little doubt that the species is properly assigned to *Phrynomantis*.

The body is stout and only slightly wider than the head. The snout is bluntly rounded, slightly shorter than the eye. The canthus rostralis is rounded and the loreal region is nearly vertical and slightly concave. The internarial distance is broader than that from eye to naris. The nostrils are directed laterally. The eyes are large, with the upper eyelids almost twice the width of the

interorbital space. The tympanum is indistinct and has a horizontal diameter slightly more than one-half the length of the orbit.

Glandular areas that commence behind each eye and extend over the back become indistinct slightly past the level of the arm insertion and are most conspicuous where they overhang as prominent folds above and behind the ears. The glandular surface is conspicuously pitted. Similar but less obvious pitting is present elsewhere on the dorsal body surface, but the venter is smooth. Whereas the borders of the glandular areas are well marked in the tympanic region, there are no clear lines of demarcation posteriorly or toward the midline.

The relative lengths of the fingers are $3 > 4 = 2 > 1$. The tips are rounded, not enlarged, and show no terminal grooves (fig. 51I). There is no webbing, and there is scarcely a trace of sub-articular or metacarpal tubercles. The relative lengths of the toes are $4 > 3 > 5 > 2 > 1$. The tips are rounded, not enlarged, and lack terminal grooves. The feet resemble the hands in lacking webbing and in the virtual absence of development of tubercles; only the inner metatarsal tubercle shows as a faint, rounded elevation.

The dorsal surfaces—head, body, and limbs—are medium brown with both lighter and darker mottling. The chin, chest, abdomen, and under-surfaces of the limbs are pale tan with coarse, darker mottling.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 38.3; HW, 13.8; TL, 11.9; Eye, 3.9; E-N, 2.1; IN, 2.8; EAR, *ca.* 2.4. Proportions are: TL/S-V, 0.31; HW/S-V, 0.36; Eye/S-V, 0.102; E-N/IN, 0.75.

COMPARISON WITH OTHER SPECIES: *Phrynomantis glandulosa* most closely resembles *P. wilhelmana*. With respect to body size, head width, leg length, eye size, snout shape, and digital morphology, the two are not distinguishable. In common with many other asterophryines, *P. wilhelmana* has a more or less distinct fold of skin above and behind the tympanum, but this does not develop the conspicuously bulging, glandular character (especially behind the tympanum and above the arm) seen in the new species. More superficial but equally useful as a key character is the difference in color pattern, especially of the lower surfaces. The underside of *wilhelmana* is typically dark and nearly uniform. Rarely is spotting or mottling developed, and then principally in the posterior

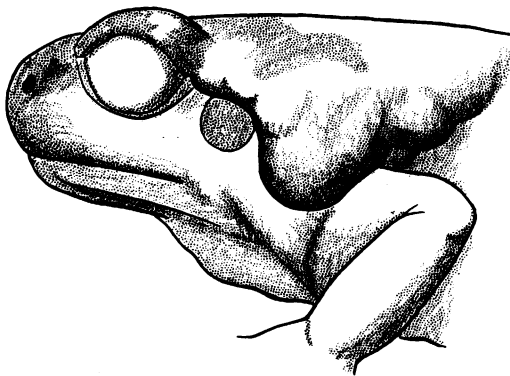


FIG. 29. *Phrynomantis glandulosa* (RMNH 16667, holotype), side of head. $\times 3.5$.

region. The holotype of *glandulosa* differs from all *wilhelmana* examined in being pale beneath with darker mottling on all surfaces. Occasional individuals of *wilhelmana* have pale ventral surfaces, but these lack the conspicuous mottling of *glandulosa*.

I am confident that *glandulosa* and *wilhelmana* are more closely related to each other than either is to any other *Phrynomantis*. Their relationship may be subspecific, but the evidence presently available favors assignment of specific rank to *glandulosa*. The locality closest to Mt. Kerewa from which *wilhelmana* is known is on the west flank of Mt. Giluwe about 45 miles to the east.

ECOLOGICAL NOTES: Kalkman and Vink (1970) described and illustrated the region of the type locality. Mt. Kerema is a Pleistocene volcano with a maximum elevation of 3555 m. "The altitude of both Kerewa and Ambua is such that without human interference the forest would extend right to the summits, probably in a lower, more open form . . ." (Kalkman and Vink, 1970, pp. 121-122), although repeated fires have degraded the vegetation to shrubbery and grassland around the summits.

DISTRIBUTION AND SPECIMENS EXAMINED: *Phrynomantis glandulosa* is known only from the holotype specimen. The locality is about 33 miles west and 10 miles north of Mendi (fig. 58). There are numerous high peaks northwest of Mendi that are virtually unexplored herpetologically, and it is likely that *P. glandulosa* occurs at high elevations on mountains other than the one it is known to inhabit.

ETYMOLOGY: The specific name is derived from the Latin *glans* (gland) and *-osa* (full of), and refers to the principal diagnostic character.

***Phrynomantis humicola humicola*,**

new species and subspecies

Figures 30, 31

HOLOTYPE: AMNH 66261, an adult female, collected by H. M. Van Deusen on the Sixth Archbold Expedition on Mt. Otto near Kotuni between 7000 and 8000 ft. (2130-2440 m.) above sea level, Eastern Highlands District, Territory of New Guinea, on August 17, 1959.

PARATYPES: AMNH 66224-66239, 66241-66279 + 125 untagged specimens, 84441, 84442, collected by the Sixth Archbold Expedition;

AMNH 76464, MCZ 52910-52921, 53077-53082, collected by Fred Parker, all from the type locality. Additional paratypes are from these localities in the Territory of New Guinea: Chimbu District: Igindi (MCZ 60807); Oruge (MCZ 81679); Dumun (MCZ 53016-53018, 53025-53029, 64407-64409, 64411, 64273); Masul (MCZ 53035, 53037, 53038); Sikuri Pass (MCZ 53039, 53040, 53042-53044, 79944, 79945); Tuna Pass (MCZ 53061, 64268, 64269); Derim (MCZ 53066, 53069, 53071, 53073). Eastern Highlands District: Mt. Michael, 10,200 ft. (AMNH 66509-66513); Orumba (AMNH 76469-76470; MCZ 81680-81684); Mt. Kerigomna (AMNH 76966); Daulo Pass (AMNH 76967-76972; MCZ 52922-52926, 52928-52946, 52948-52951, 52953-52966, 52968, 52970-52981, 52983-52986, 52989, 52990, 52992-52994, 52996, 52998-53013, 59873-59882, 59884-59890).

DIAGNOSIS: *Phrynomantis humicola humicola* is characterized by uniform brown dorsum, lightly but distinctly mottled ventral surfaces, small, grooved discs on fingers and toes (those on the fingers sometimes scarcely broader than the penultimate phalanges), and moderate body size (maximum snout-vent length, 59 mm.).

Phrynomantis robusta is the species most similar to *P. h. humicola*. It reaches a larger size (to 73 mm.) and has uniform rather than lightly mottled or reticulated ventral surfaces.

Phrynomantis wilhelmana superficially resembles *P. h. humicola* in dorsal color and habitus, but lacks grooved discs on the fingers and toes and has uniformly colored ventral surfaces.

The presence of a yellow to orange postocular stripe distinguishes *P. h. compta* (described below) from *P. h. humicola*, and the two also differ in proportions.

DESCRIPTION OF HOLOTYPE SPECIMEN: The head is almost as broad as the relatively short, chunky body (HW/S-V, 0.37) and the legs are moderately long (TL/S-V, 0.38). The eyes are relatively large (Eye/S-V, 0.11), with the horizontal diameter slightly longer than the snout and with the interorbital space slightly narrower than an upper eyelid. The nostrils are near the end of the blunt snout and are directed largely laterally, although the openings are visible from directly above. The internarial distance is distinctly greater than the distance from eye to naris (E-N/IN, 0.79). The canthal area is rounded and the lores are flat and slope steeply.

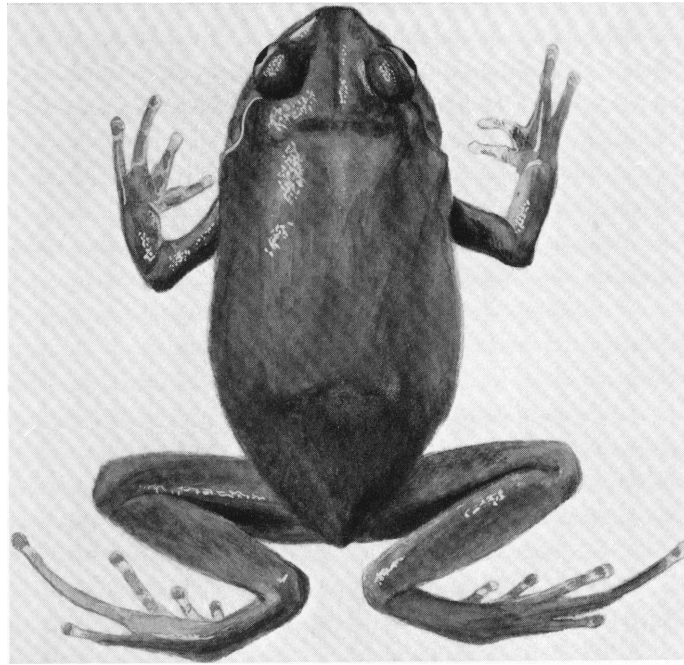


FIG. 30. *Phrynomantis humicola humicola* (AMNH 66261, holotype), dorsal view. $\times 1.5$.

The tympanum is indistinct and has a horizontal diameter less than one-half that of the eye. A strong fold of skin passes from the posterior corner of the eye along the upper edge of the tympanum before turning down toward the forelimb. The skin of the dorsal surfaces is slightly rugose, that of the ventral surfaces quite smooth.

The maxillary bones are in loose contact anteriorly, being connected by a ligament. The palate bears an anterior smooth fold followed by a serrate one.

The relative lengths of the fingers are $3 > 4 > 2 > 1$. The subarticular tubercles are low and rounded; indistinct inner and middle metacarpal tubercles are present. All fingers have grooved discs, but these are scarcely wider than the penultimate phalanges (fig. 51D). The relative lengths of the toes are $4 > 3 > 5 > 2 > 1$. The subarticular tubercles are low, rounded elevations and the inner metatarsal tubercle is scarcely distinct. The toes bear grooved discs slightly wider than the penultimate phalanges. The disc on the fourth toe is slightly broader than that on the third finger.

The dorsal surfaces (head, body, and limbs)

are dark purplish brown without pattern. The chin and chest show moderately heavy brown mottling, and there is similar but lighter mottling on the abdomen and undersides of the limbs. The dorsal and ventral patterns are not sharply demarked on the side of the body, but grade relatively abruptly.

The specimen has enlarged oviducts and ova 5 mm. in diameter.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 52.2; HW, 19.3; TL, 20.2; Eye, 5.9; E-N, 3.3; IN, 4.2; EAR, 2.5; disc of third finger, 1.2 (penultimate phalange, 1.0); disc of fourth toe, 1.4 (1.1).

VARIATION: Variation in proportions among three samples is set forth in table 6. The means for the proportions representing tibia length, head width, and eye size vary no more than 1 per cent within each category, so the samples are closely similar. There is a slight indication that frogs from Daulo Pass have an average higher E-N/IN ratio than is seen in the other two samples.

The largest specimen among 137 of this subspecies measured is a female from Mt. Otto 54.4 mm. in length from snout to vent; numerous other

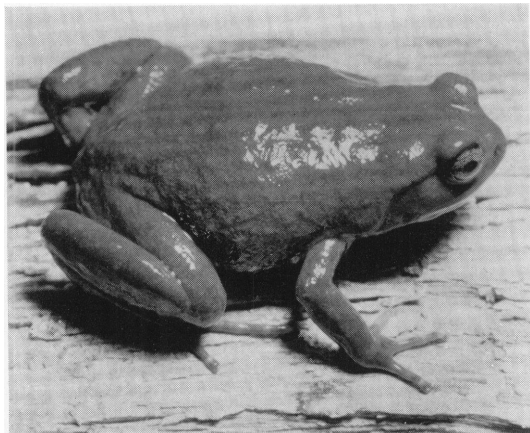


FIG. 31. *Phrynomantis humicola humicola* (AMNH 76470).

individuals have a length greater than 50 mm. Among 57 adult and juvenile specimens of both sexes from Mt. Otto, the largest male measures 44.2 mm., but one of five specimens from Mt. Michael is a male measuring 47.4 mm. Evidently female frogs attain sexual maturity at a snout-vent length of about 45 mm. In the series from Mt. Otto, several specimens 46 mm. and greater in length have enlarged ova. A specimen measuring 44.1 mm. has slightly enlarged ova, probably indicating the onset of sexual maturity, whereas no individual smaller than this shows any indication of maturity.

There is remarkably little variation in color pattern among the numerous individuals assigned to this subspecies. Rarely a faint trace of darker mottling shows through the purplish brown dorsal color. The mottling of the ventral surfaces varies in intensity from specimen to specimen, but even in the lightest individuals the ventral pattern is not uniform. A trace of the light postocular stripe characteristic of adult *P. h. compta* often is present in small *P. h. humicola*.

The color in life is dark purplish gray, and thus little different from the color in preservative. The iris is silvery gray with black lines.

COMPARISON WITH OTHER SPECIES: Because of superficial similarities in color pattern, frogs of this subspecies are perhaps more easily confused with those of two other species, *P. robusta* and *P. wilhelmana*, than with individuals of the other subspecies of *P. humicola*.

In regard to *Phrynomantis robusta*, nothing can

be added here to the comparisons made in the account of that species and in the present diagnosis. The resemblance of *P. humicola* and *P. wilhelmana* stems from similarities in dorsal color and general habitus. On close examination, the two can invariably be distinguished by the absence of grooved digital discs in *wilhelmana* and their presence in *humicola*. Differences in ventral pigmentation and in proportions also exist.

ECOLOGICAL NOTES: No specific data accompanied the specimens of the type series most of which were obtained from native collectors. Brass (1964, pp. 193–195) described the conditions around the Kotuni base camp, where much of the forest had been disturbed or cleared in logging operations.

A specimen in the paratype series, 48 mm. in snout to vent length, contained 21 ovarian eggs 4.2 to 5.0 mm. in diameter; a second group of eggs 1.5 mm. in diameter also was present.

DISTRIBUTION AND SPECIMENS EXAMINED: This subspecies has been found only in the Chimbu and Eastern highlands districts of the Territory of New Guinea, from Mt. Michael north to Daulo Pass and from Mt. Otto west to the vicinity of Koge (fig. 33). Sympatry with *P. humicola compta* evidently exists at Igindi; see the account of that subspecies for further discussion.

Probably the population on Mt. Michael is disjunct from that in the area of distribution to the north, as the limited evidence suggests that this species does not range below an elevation of about 6000 feet. Some extension of range to the southeast of Mt. Otto may be anticipated, but no *humicola* are present in large collections made to the northwest at high elevations on Mt. Wilhelm. All specimens examined are cited above under Holotype and Paratypes.

ETYMOLOGY: The specific name is derived from the Latin *humus* (soil) and *colo* (to inhabit), and refers to the inferred terrestrial habitat of the species.

***Phrynomantis humicola compta*,
new subspecies**

Figure 32

Asterophrys wilhelmana: TYLER, 1963, pp. 15–17 (part).

HOLOTYPE: AMNH 82887, an adult female collected by R. G. Zweifel 1.6 mi. (by road) NE Tambul, elevation 7400 ft. (2250 m.), Western Highlands District, Territory of New Guinea, on July 26, 1969.

PARATYPES: (all from Territory of New Guinea): Western Highlands District: AMNH 82888–82891, same locality as holotype; AMNH 82892, vicinity of Tambul, 7300 ft. (2230 m.); AMNH 65309–65318, Wahgi Dividing Range near Nondugl, 8000 ft. (2440 m.); BMNH 1961.839, 1961.842–1961.860, 1961.876, 1961.880, Wahgi Dividing Range near Nondugl, 6300–9500 ft. (1920–2900 m.); AM 22757, 22759–22761, 22763, 22764, 22766, 22767, 22769, 22770, 22772, 23119, 23120, 23122, 23177, 23178, Kaironk Valley, Schrader Mountains; AMNH 82251, 82252, Schrader Mountains above Kaironk Valley, *ca.* 7300 ft. (2230 m.). Chimbu District: MCZ 53959, 53060, Mintima; Igindi, AMNH 76963, MCZ 59897, X 06958, X 06959, X 07020.

DIAGNOSIS: *Phrynomantis humicola compta* differs from *P. h. humicola* in the presence in both adults and juveniles of a broad, yellow to orange post-ocular bar (absent in *P. h. humicola*, or faintly indicated in juveniles) and in having relatively shorter hind legs (see table 6).

DESCRIPTION OF HOLOTYPE SPECIMEN: The head is narrower than the relatively stout body (HW/S-V, 0.34), and the hind legs are relatively short (TL/S-V, 0.34). The eyes are of moderate size (Eye-S-V, 0.096), with the inter-orbital space slightly broader than the width of an upper eyelid. The snout is bluntly rounded, with the nostrils near the tips and directed largely laterally, but visible from directly above. The internarial distance is greater than the distance from eye to naris (E-N/IN, 0.81). The canthal region is rounded, and the loreal area is

angularly rather than smoothly concave. The tympanum is scarcely distinct and is vertically oval, with the horizontal diameter nearly two-thirds that of the eye. A weak fold of skin passes from the posterior corner of the eye, above and down behind the tympanum. Slight rugosity of the dorsal surface of the body is evident only under magnification; the ventral surfaces are smooth.

The anterior processes of the maxillary bones are in contact. There is an anterior smooth palatal fold and a posterior serrate one.

The relative lengths of the fingers are $3 > 4 > 2 > 1$. The subarticular tubercles are quite low and rounded, and the metacarpal tubercles (inner, middle, and outer) are present but not at all prominent. The fingers have grooved terminal discs, but only that of the third finger is slightly wider than the penultimate phalange. The relative lengths of the toes are $4 > 3 > 5 > 2 > 1$. The subarticular tubercles are even less well developed than those of the fingers, and the inner metatarsal tubercle is the only distinctive one on the foot. The discs on the toes are slightly wider than the penultimate phalanges; that on the fourth toe is slightly wider than the one on the third finger.

The holotype had the following color pattern in life: Dorsal color of head, body, and limbs dark brown with no pattern evident; a pale orange bar passing from near posterior corner of eye to angle of jaw and thence posteriorly beneath tympanum (with borders slightly diffused) to underside of forelimb; facial area and area immediately above orange bar slightly darker than general ground color of back and head; chin, chest, and belly light brown, mottled with numerous greenish yellow markings of irregular and commonly angular shape; undersides of hind limbs similar to rest of venter but with fewer and larger light spots; anterior and posterior surfaces of thighs immaculate brown; soles dark, upper surfaces of hind feet yellow with brown markings; iris black with abundant gold flecks.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 57.5; HW, 19.5; TL, 19.6; Eye, 5.5; E-N, 3.5; IN, 4.4; EAR, 3.5; disc of third finger, 1.2 (penultimate phalange, 1.0); disc of fourth toe, 1.4 (1.2).

VARIATION: The two principal samples are those from the Wahgi Dividing Range (collected by William Hosmer in 1959 and by Michael

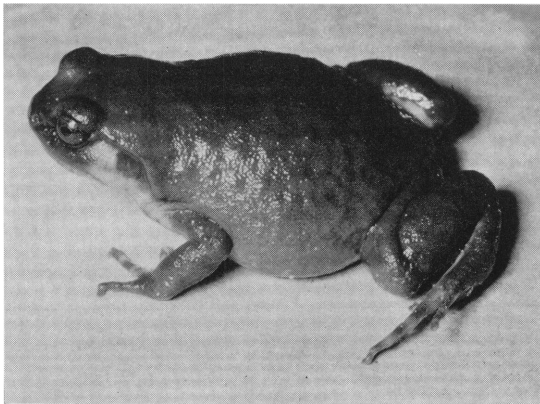


FIG. 32. *Phrynomantis humicola compta* (MCZ X7020, field number). Photo by Fred Parker.

Tyler in 1960) and the Kaironk Valley, Schrader Mountains (collected by Harold Cogger in 1963). In the proportions indicative of relative internarial distance, eye size, and head width, the two samples are identical or insignificantly different (table 6), whereas the mean ratios of tibia length to snout-vent length differ significantly as measured by the *t* test ($P \leq 0.001$). The sample from the Wahgi Dividing Range is intermediate both in leg length and geographically between that of the frogs from the Schrader Mountains and the relatively long-legged *P. h. humicola*. The small sample from the vicinity of Tambul, equidistant from the Schrader and Wahgi mountains, agrees with the former in proportions.

I have seen living individuals only from the vicinity of the type locality, but judging from the appearance of the preserved material, the postocular stripe and mottled ventral surfaces are constant throughout this subspecies.

The largest of 54 specimens measures 59.5 mm. in length from snout to vent.

RELATIONSHIP TO *Phrynomantis humicola humicola*: Fred Parker obtained 10 specimens of *Phrynomantis* at Igindi, a locality about 10 miles south of Kundiawa, between the major portions of the ranges of *P. h. humicola* and *P. h. compta* (fig. 33). Four of the specimens are readily recognized as *P. wilhelmana* by their lack of grooved digital discs, short hind legs (TL/S-V range 0.29–0.34, mean 0.31), and absence of any trace of a postocular light stripe. The ventral surfaces are paler and slightly less uniform than in topotypic *wilhelmana*, but this is the case in other southern populations of the species. Five specimens in the series are *P. h. compta*, having strong postocular stripes, short hind legs (TL/S-V range 0.31–0.33, mean 0.32), and at least some toes with small, grooved discs. The remaining specimen has the characteristics of *P. h. humicola*: no postocular stripe, long hind legs

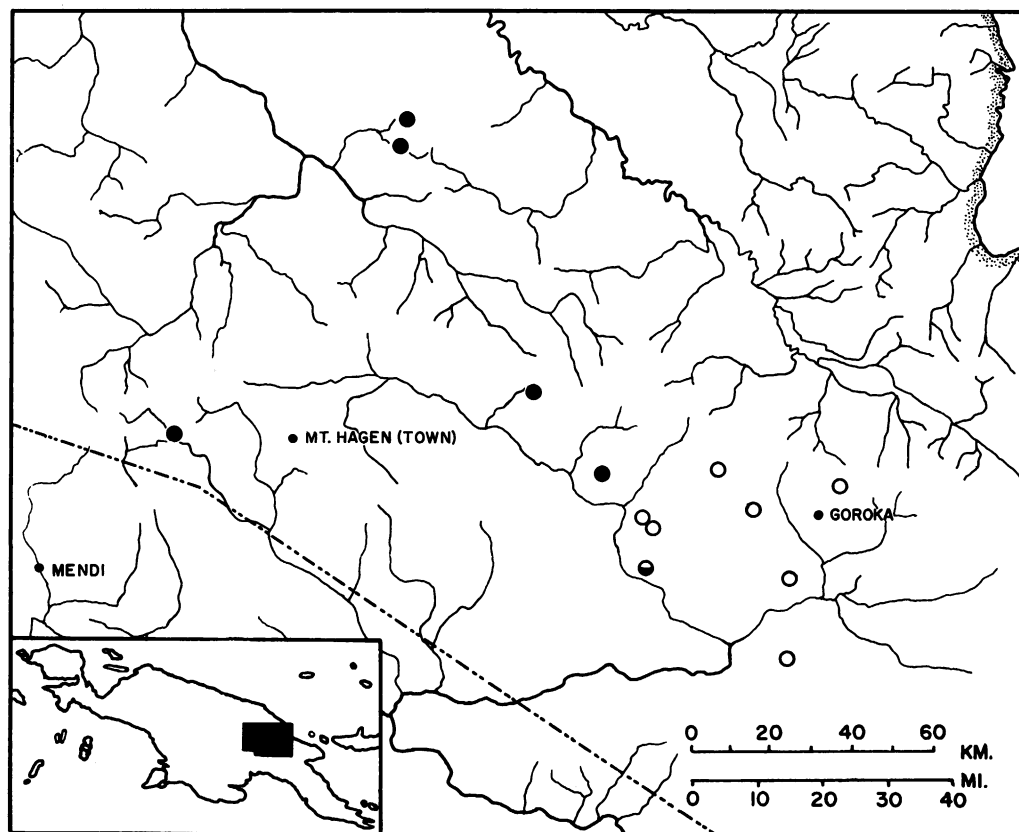


FIG. 33. Distribution of *Phrynomantis humicola*. Open circles, *P. h. humicola*; closed circles, *P. h. compta*; half-filled circle, apparently sympatric populations at Igindi (see text).

(TL/S-V, 0.41), and some digits with grooved discs.

This is the only evidence of sympatry between *compta* and *humicola*. It could reasonably be argued that these forms should be recognized as different species. Yet the two are so similar in most respects (even the characteristic postocular stripe of *compta* is somewhat developed in young *humicola*) that I prefer to regard them as subspecies pending more evidence that they in fact are reproductively isolated.

ECOLOGICAL NOTES: *Phrynomantis humicola compta* is, as are most of its congeners, a ground frog. I found the holotype at night in the mouth of a burrow and after an initial failure to do so manually returned two days later with a shovel and dug out the creature. The burrow was in an area of secondary forest in humic, dark soil in a mossy, nearly vertical road cut. The burrow had a total length of about 36 inches and ran about 12 inches into the bank, ending some 18 inches higher than the entrance. Tyler (1963, p. 16) secured specimens "beneath rotting wood and in other damp situations in moss-forest. . . ."

Tyler (1963, p. 16) briefly described eggs laid in captivity by "*Asterophrys wilhelmana*," but his sample of frogs included both *P. humicola compta* and *P. wilhelmana*, so it is possible that the description applies to *humicola*. The frog that

laid the clutch of 55 eggs measured 57 mm. The distinctive feature of the eggs Tyler described is that there was no mucilaginous cord connecting them. In *P. robusta* and apparently also in *P. wilhelmana* (see species accounts) such a cord is present.

DISTRIBUTION AND SPECIMENS EXAMINED: The known range of the subspecies includes the Schrader Mountains, the Wahgi-Sepik Dividing Range and the Tambul area, between Mt. Giluwe and Mt. Hagen (fig. 33). Probably this subspecies occurs in the Kubor Mountains, although it is not yet recorded there. The extent of the range to the west of Tambul remains to be determined.

All typical specimens of *Phrynomantis humicola compta* examined are listed above (holotype and paratypes).

ETYMOLOGY: I chose the Latin word *compta* (ornament or adornment of the head) to refer to the characteristic postocular stripe.

Phrynomantis infulata, new species

Figure 34

HOLOTYPE: AMNH 66687, an adult female, collected by H. M. Van Deusen on the Sixth Archbold Expedition at Arau, Kratke Mountains, elevation 4600 ft. (1400 m.), Eastern Highlands District, Territory of New Guinea, on October 14, 1959.

PARATYPES: AMNH 66684–66686 and 66688–66703, collected at the type locality between October 13 and November 8, 1959.

DIAGNOSIS: A small *Phrynomantis* with a maximum known length from snout to vent of 39 mm. The hind legs are unusually long (TL/S-V mean 0.49), the internarial distance is less than the distance from eye to naris (E-N/IN mean 0.79), and the disc of the third finger is narrower than that of the fifth toe. The distinctive characteristic of the color pattern is the presence of a dark brown, dorsolateral stripe that stands out from the much paler background.

The only species of *Phrynomantis* likely to be confused with *P. infulata* is *P. lateralis*. The latter has a similar dorsal pattern but reaches a larger size (55 mm.), has a relatively wider internarial spacing (E-N/IN mean 0.99), and shorter legs (TL/S-V mean 0.43).

Hylophorbus rufescens resembles *P. infulata* in size and to some extent color pattern. Positive identification can be made by determining the



FIG. 34. *Phrynomantis infulata* (AMNH 66687, holotype), dorsal view. $\times 1.25$.

condition of the maxillary bones—symphygnathine in *infulata* and eleutheroagnathine in *rufescens*. Externally, they are largely separable in the E-N/IN ratio, which is larger in *infulata* (mean 0.79, compared with 0.70 in *rufescens*).

DESCRIPTION OF HOLOTYPE SPECIMEN: This is a relatively slender, long-legged asterophryine with the head narrower than the body. The laterally directed nostrils are near the end of the snout, which is almost truncate in dorsal view and projects notably beyond the mouth. The canthus rostralis is rounded and the loreal region nearly vertical. The eyes are relatively large (Eye/S-V, 0.117), slightly longer than the snout, and the upper lid is slightly wider than the interorbital space. The tympanum is indistinct and is about one-half of the diameter of the eye. There is an indistinct supratympanic fold; the rest of the body is smooth dorsally and ventrally.

The fingers and toes have small, grooved discs (fig. 51B). The disc on the third finger is about twice the width of the penultimate phalange, whereas the disc of the fourth toe is larger and almost three times wider than its penultimate phalange. The relative lengths of the fingers are $3 > 4 > 2 > 1$, of the toes, $4 > 3 > 5 > 2 > 1$. There are large, rounded subarticular tubercles on the fingers and the toes. The hands have very low metacarpal tubercles (inner, middle, and outer), but the feet have only a small inner metatarsal tubercle.

The upper jaw is symphygnathine (fig. 35), with the anterior processes of the maxillary bones not fused but almost in contact and joined by a ligament. The usual two palatal folds are present, anterior smooth and posterior serrate.

The middorsal area is brown with indistinct darker mottling. On each side of this central area is a dark brown band that begins at the posterior corner of the eye and terminates in the groin. The upper (medial) edge of the band is somewhat obscure, but the wavy lower edge is abruptly differentiated from the light gray-brown of the sides and belly. The upper sides of the limbs have the same ground color as the middle of the back and are spotted and mottled with darker brown. There is no particularly distinctive pattern in the groin or on the posterior surfaces of the thighs. The throat is heavily mottled with brown. The mottling is somewhat reduced on the chest and markedly so posteriorly on the abdomen, but mottling is

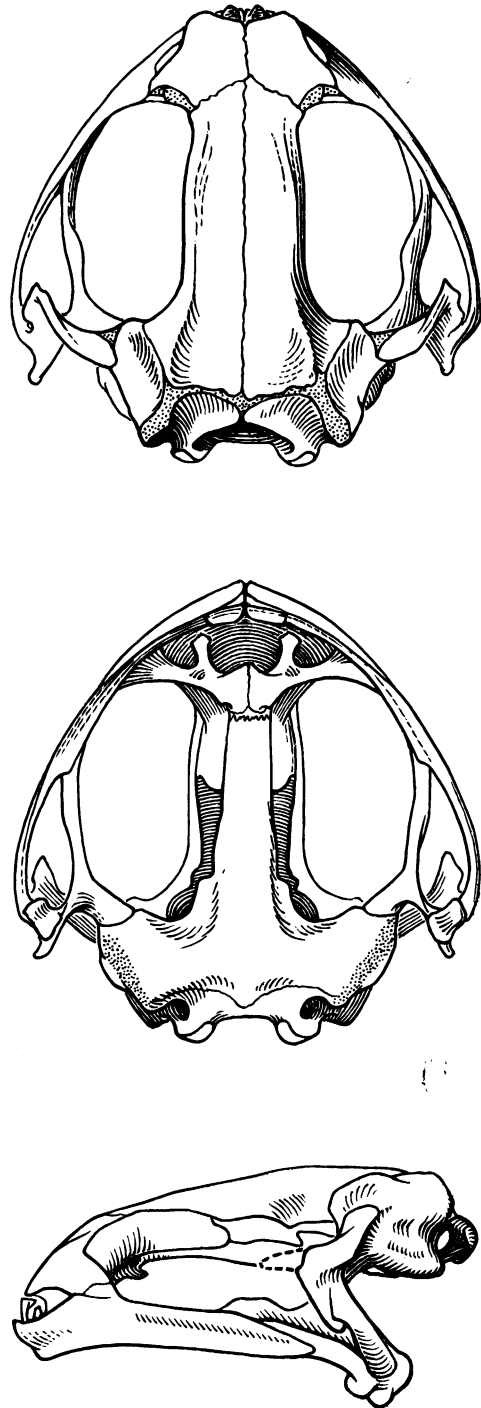


FIG. 35. Skull of *Phrynomantis infulata* (AMNH 66692) in dorsal (upper), ventral (middle), and lateral (lower) views. $\times 5$.

prominent on the undersides of forelimbs, and hind limbs.

The specimen is adult, with enlarged oviducts and ova up to 2.5 mm. in diameter.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 36.9; TL, 17.2; HW, 12.7; Eye, 4.3; E-N, 2.7; IN, 3.4; EAR, *ca.* 2; disc of third finger, 1.1 (penultimate phalange, 0.5); disc of fourth toe, 1.7 (0.6).

VARIATION IN THE TYPE SERIES: The paratypes differ in no significant way from the holotype. For variation in proportions, see table 6. Color patterns are identical in all important respects, with the only obvious difference being some variation in the waviness of the lateral margin of the dark stripe; occasionally, this margin is almost straight.

A male specimen has small, slitlike vocal sac openings in the floor of the mouth near the angles of the jaws. The vocal sac is single and

subgular. The tongue is broadly oval with only the margins free, and has a posterior pouch.

COMPARISON WITH OTHER SPECIES: Presumably the closest relative of *Phrynomantis infulata* is *P. lateralis*, for the two resemble each other in several aspects of morphology and color pattern and are more similar to each other than either is to any other species. To the distinguishing features noted in the foregoing diagnosis may be added the following: dark dorsolateral stripe generally wavy-edged laterally in *infulata*, straight in *lateralis*; chin and chest usually distinctly or diffusely spotted in *lateralis*, mottled in *infulata*; finger and toe discs relatively better developed in *infulata*.

ECOLOGICAL NOTES: Nothing specific is on record for the type series, but Brass (1964, pp. 200-213) described the site of collection. He noted that "the very extensive, little-disturbed forests represented a transition between mid-mountain

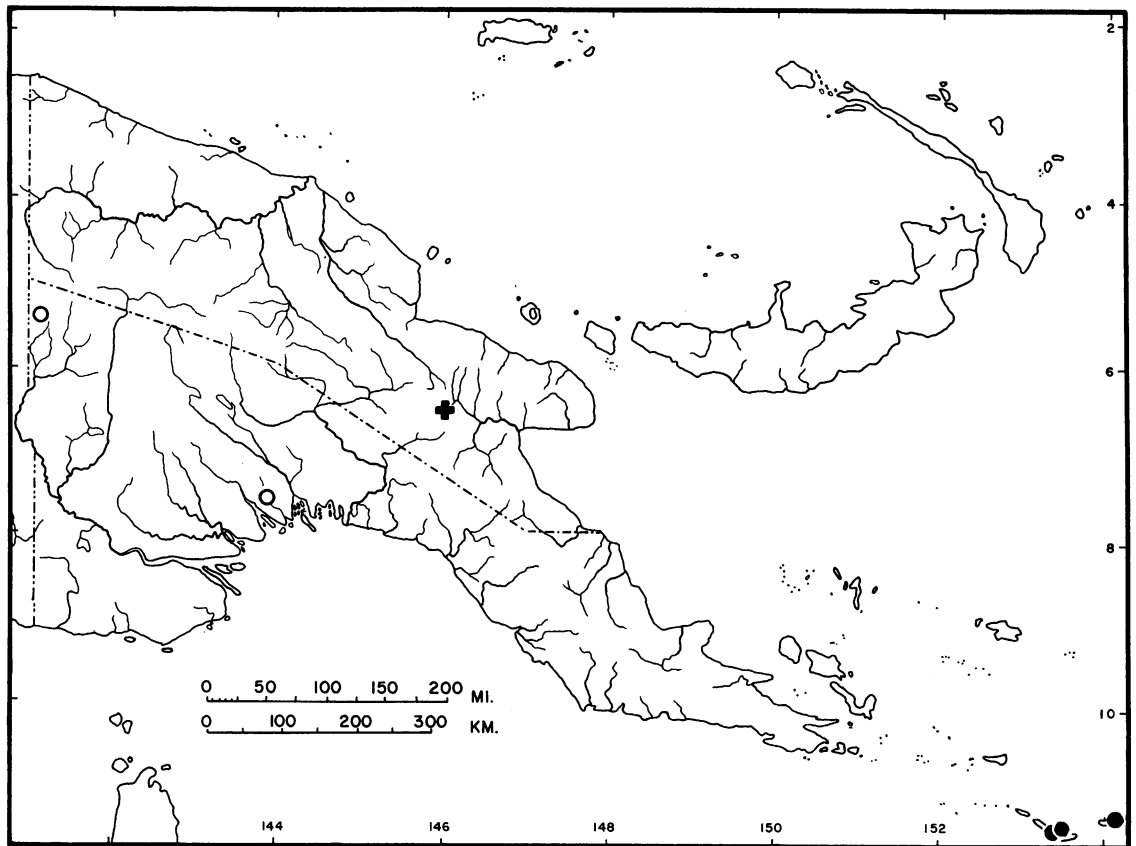


FIG. 36. Distribution of three species of *Phrynomantis*. Cross, *P. infulata*; open circles, *P. slateri*; closed circles, *P. louisiadensis*.

fagaceous forest and a lower montane mixed rain forest . . . ,” and that it “was a forest rich in herbaceous undergrowth, including ferns, but rather poor in woody undergrowth, epiphytes, and climbers.”

DISTRIBUTION AND SPECIMENS EXAMINED: This species is known only from the type locality (fig. 36) and type series of specimens, cited above.

ETYMOLOGY: The specific name is from the Latin *infulatus* (adorned with a band), and refers to the conspicuous element of the dorsal pattern.

Phrynomantis kopsteini (Mertens),
new combination

Hylophorbus kopsteini MERTENS, 1930, p. 147 (type locality, “Sanana, Soela-Inseln” [Sulabesi Island, Indonesia]; syntypes, RMNH 5310 [three specimens], collected by F. Kopstein in March, 1924).

Metopostira kopsteini: PARKER, 1934, p. 70.

DIAGNOSIS: The following characteristics will, in combination, distinguish *P. kopsteini* from the other three species of *Phrynomantis* found in the Moluccas: finger discs distinctly smaller than toe discs; hind legs relatively short, TL/S-V, 0.36 to 0.38; internarial space relatively broad, E-N/IN, 0.70 to 0.79. *Phrynomantis boettgeri* and *P. dubia* of Halmahera have much longer hind legs (TL/S-V, 0.52 and 0.48 in the two unique specimens) and *boettgeri* has finger discs larger than those on the toes. The finger and toe discs of *P. fusca* (Amboina, Seram, and Batanta islands) are more nearly equal in size, and the E-N/IN ratio is larger (0.79 to 0.90).

DESCRIPTION OF SYNTYPE SPECIMENS: The following description is taken from the original description by Mertens (1930, pp. 147–149), supplemented by my own observations and measurements. Mertens examined three specimens and designated one of two males (the other specimen being a gravid female) as the type. This published designation, however, has not carried over to the specimens, all of which bear one common number. I could not determine which specimen was intended as the holotype, so I treat all as syntypes.

The body is relatively thick-set, but is little wider than the head. The snout is short, as long as the horizontal diameter of the eye, with rounded canthus rostralis and oblique, somewhat concave loreal region. The nostrils are

rather widely spaced; E-N/IN mean 0.75. The diameter of the tympanum is slightly more than one-half the horizontal diameter of the eye. The skin is smooth except for a fold of skin running from the posterior corner of the eye above the tympanum and then down to the insertion of the forelimb, and for a fine median ridge passing from the tip of the snout to the anus.

The relative lengths of the fingers are $3 > 4 > 2 > 1$, of the toes, $4 > 3 > 5 > 2 > 1$. There is no outer metatarsal tubercle, but the inner metatarsal and subarticular tubercles are strong. All fingers and toes bear grooved discs, those of the toes being larger.

The anterior processes of the maxillae are only narrowly separated at the midline, so the condition is virtually symphagnathine. The tongue is broadly oval and scarcely free behind, with an entire margin and a furrow on the midline that is slightly deeper posteriorly. The usual two pharyngeal ridges are present, the anterior smooth and the posterior serrate.

The dorsal surfaces are dark brown with more or less distinct lumbar ocelli but no other pattern evident. The ventral surfaces are “gray brown with faded, bright gray flecks” (Mertens, 1930, p. 148).

Mertens (1930, p. 149) identified two specimens as males and one as a female, the last containing about 30 ova about 3.5 mm. in diameter.

MEASUREMENTS OF SYNTYPE SPECIMENS: S-V, 41.1, 45.5, 42.1; TL, 15.4, 16.5, 16.0; HW, 15.3, 15.6, 15.5; Eye, 4.7, 5.0, 5.0; EAR, 2.4, —, —; E-N, 3.0, 3.0, 3.1; IN, 4.0, 4.3, 3.9; disc on third finger (penultimate phalange), 1.0 (0.9), 1.2 (0.9), 1.1 (0.7); disc on fourth toe, — (—), 1.4 (0.8), 1.4 (0.8).

VARIATION: Data on proportions are presented in table 6; no other information is available.

COMPARISON WITH OTHER SPECIES: Comparisons with *P. dubia* and *P. fusca* are made in the accounts of those species, and further comparison with the other Moluccan species, *P. boettgeri*, is unnecessary.

TAXONOMIC NOTES: Parker (1934) presumably placed *kopsteini* in the genus *Metopostira* because of its superficial similarity to *Metopostira ocellata* (= *Hylophorbus rufescens*), but he did not examine specimens of *kopsteini*. Externally, *kopsteini* is readily distinguished from *rufescens* by its shorter hind legs (maximum TL/S-V in *kopsteini* 0.38;

minimum in *rufescens* 0.42). The virtually symphagnathine condition of *kopsteini* leads me to refer this species to *Phrynomantis* rather than to the clearly eleutherognathine *Hylophorbus*.

DISTRIBUTION AND SPECIMENS EXAMINED: *Phrynomantis kopsteini* is known only from Sanana or Sulabesi Island in the Sulu Islands, Indonesia, and is the westernmost species of its genus and subfamily (fig. 25). I have examined the three syntype specimens (RMNH 5310).

Phrynomantis lateralis (Boulenger),
new combination

Figure 37

Mantophryne lateralis BOULENGER, 1897, p. 12 (type locality, "Mount Victoria, Owen Stanley Range, New Guinea"; lectotype [by present designation; see following discussion], BMNH 1947.2.11.2, collected by A. S. Anthony).

Manthophryne lateralis: VOGT, 1911b, p. 427.

Hylophorbus rufescens: FRY, 1913, p. 48.

Asterophrys rufescens: PARKER, 1934, p. 62.

DIAGNOSIS: *Phrynomantis lateralis* has the following unique combination of characters: body of moderate size, up to 55 mm. snout to vent; fingers and toes with small but distinct, grooved discs; dorsal pattern of two broad, dark brown bands running from snout to groin and sharply set off laterally from gray of sides; internarial and eye to naris distances virtually equal (E-N/IN mean 0.99, minimum 0.83). The only species of *Phrynomantis* that closely resembles *P. lateralis* is *P. infulata*, which has a similar dorsal pattern but which is smaller (maximum snout to vent length, 39 mm.) and has the internarial distance always greater than the distance from eye to naris (E-N/IN mean 0.79, maximum 0.84).

DESCRIPTION: The description of external characteristics is based on AMNH 81060, a male from approximately 30 miles southwest of the type locality.

The snout is truncate and projects well beyond the lower jaw. The nostrils are lateral, near the end of the snout, and are not visible from directly above. The loreal region is almost vertical and slightly concave, with rounded canthus. The eye and snout are equal in length, and the interorbital space is broader than an upper eyelid. The head is narrower than the relatively broad body. The tympanum is barely visible; its horizontal diameter is approximately two-thirds that of the eye. There is only a faint

trace of a supratympanic fold. The skin of the dorsal and ventral surfaces of the body is smooth except for some slight wartiness on the posterior one-third of the dorsum and on the sides. Also, there are two slight projections made by the mento-meckelian bones behind the mandibular symphysis. The pupil is horizontal.

The fingers and toes bear small but distinct, grooved discs (fig. 51A); the disc on the third finger is smaller than that on the fourth toe. The hands and feet have large, prominent, rounded subarticular tubercles. The hands in addition have palmar, inner, and outer metacarpal tubercles. The feet have only inner metatarsal tubercles; the soles are smooth. The relative lengths of the fingers are $3 > 4 = 2 > 1$, of the toes, $4 > 3 > 5 > 2 > 1$.

The dorsal color pattern in life consisted of two broad, dark brown dorsolateral bands that began on the top of the snout and passed to the groin. The area between these bands, slightly broader than a band, was a slightly lighter shade of dark brown so that there was relatively little contrast between bands and middorsum. Each band was edged below with a narrow white line, below which the sides were pale gray. The thighs were dark brown with little pattern, but the lower leg showed a tendency to brown and yellowish brown longitudinal striping. The front legs were mottled gray with a dark band proximal to the wrist region. The ventral ground color was light gray, spotted heavily with dark gray-brown on the chin and chest and less heavily with smaller, grayer spots posteriorly on the abdomen and on the undersides of the hind

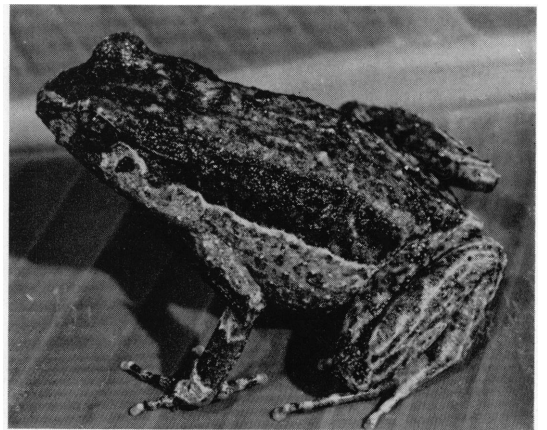


FIG. 37. *Phrynomantis lateralis* (AMNH 81059).

limbs. Each mento-meckelian protuberance was emphasized by a white spot.

MEASUREMENTS OF LECTOTYPE SPECIMEN: S-V, 42.4; TL, 17.4; HW, 16.2; Eye, 4.7; E-N, 4.1; IN, 3.5; EAR, 3.9; disc of third finger, 0.7; disc of fourth toe, 0.9.

The skull (as exemplified by AMNH 81059) is similar to that of other *Phrynomantis* with minor exceptions. The nasals are large, smooth, and in contact, but a small, triangular area of the ethmoid is exposed on the midline between the nasals and the frontoparietals. At least one other *Phrynomantis* (*P. lousiadensis*) is similarly rugose. The frontoparietals are slightly concave and bear rugose sculpturing. A small amount of sculpturing also is present on the posterior parts of the squamosal arms. The vomers show only a slight amount of mesial expansion. In his illustrations that otherwise agree closely with AMNH 81059, Méhely (1901, pl. 4; Parker, 1934, fig. 27, copied Méhely's illustration) shows the vomers much more expanded than in the skull I examined (fig. 3B). It is possible that Méhely's illustration does not differentiate between the vomers and the heavily calcified cartilage of the nasal region.

VARIATION: The observed variation in proportions is summarized in table 6. The largest among 30 specimens I measured is a female that measures 51 mm. from snout to vent, but Parker (1934, p. 62) recorded a length of 55 mm. This species may reach a larger size in the northern part of its range (Territory of New Guinea and West Irian) than in the southern and eastern region (Territory of Papua). Considering only specimens 35 mm. or greater in snout to vent length, there are 10 from the first area and 15 from the second. The northern specimens range up to 51 mm., and only one is smaller than 40 mm.; the largest of the other 15 specimens measures 43.5 mm., and only seven are 40 mm. or greater in length. In addition, Méhely (1901, p. 220) recorded four specimens from the Huon Peninsula that measured 43 to 55 mm.

Variation in dorsal color pattern chiefly involves the color of the middorsal area, between the dark dorsolateral bands. All specimens from moderate to low elevations in the southern drainage of the Territory of Papua resemble the individual described in detail above, in that there is little contrast between the middorsal area and the dorsolateral bands. This is also true of an individual from Garaina in the Huon Gulf

drainage, but specimens from the northern part of the range have the middorsal area distinctly paler than the dorsolateral bands. One from Lae is described in my field notes: "The dorsal ground color is light brown. . . . There is a broad dark brown lateral stripe beneath which the color of the side of the body is the same as that of the middle of the back." Another from Lae had "Top of head and broad middorsal band brown. . . . A broad lateral band from eye to groin is dark gray, almost black, and bears a faint trace of an ocellus at the posterior end."

The pattern of the ventral surfaces varies in a geographically similar fashion. Most specimens from the southern drainage (Territory of Papua) have a pattern of irregularly rounded dark spots, some of which may be several millimeters in diameter. Spots on the northern frogs tend to be smaller, lighter, and more diffuse. In some individuals there is no distinct spotting at all: "The throat and chest are rather uniform brown. This color becomes slightly mottled on the abdomen. The posterior of the abdomen and the under sides of the hind legs are grayish brown with a light overlay of brown mottling" (field notes on a specimen from Lae).

Two specimens from Mt. Dayman, in eastern Papua, appear closest to the northern type, but are somewhat darkened by preservative. Boulenger's (1897, pl. 2) illustration of a syntype shows the contrasting northern dorsal pattern.

COMPARISON WITH OTHER SPECIES: No species other than *Phrynomantis infulata* appears similar enough to *P. lateralis* to warrant comparison; these species are compared in the description of *P. infulata*.

TAXONOMIC NOTES: There are two principal taxonomic complications involving this species; the first concerns the presence of specimens of three genera in the syntype series. Parker (1934, pp. 62, 69, 178) identified three syntypes as *Asterophrys rufescens*, one as *Metopostira ocellata* and one as *Cophixalus oxyrhinus*. He noted (p. 62): "The five cotypes of *Mantophryne lateralis* Boulenger are not all conspecific, but the name must be applied to the present species [*Asterophrys rufescens*]; the description and figure are clearly drawn up from one of the specimens listed below [B.M.(N.H.) Nos. 96.10.31.32-96.10.31.34, now B.M.(N.H.) Nos. 1947.2.11.2-1947.2.11.4]." I have examined the specimens cited and concur with Parker's determinations. My

choice of a lectotype (see synonymy, above) follows Parker's restriction and is refined to the extent that the specimen selected most closely agrees with Boulenger's (1897, p. 12) statement, "From snout to vent 43 millim."

The second complication concerns the identity of *Hylophorbus rufescens* Macleay, 1878. As I have explained in the account of that species, *H. rufescens* is not, as Fry (1913, p. 48) thought, a senior synonym of *Mantophryne lateralis*, but is a senior synonym of *Metopostira ocellata* Méhely. Parker (1934), unable to examine the type-specimen of *H. rufescens*, followed Fry and hence assigned the name *Asterophrys rufescens* to the species here called by the new combination *Phrynomantis lateralis*.

ECOLOGICAL NOTES: *Phrynomantis lateralis* inhabits the floor of the rain forest. Judged from the frequency with which its voice may be heard it is not rare, but because it is solitary and secretive it is not readily collected. On three occasions in the daytime I found individuals under cover on the leaf litter—twice under rocks and once under a log. A male found calling at night was on the ground beneath a thin layer of leaf litter. Another called from the shelter of leafy debris lying against a log, and a third called from an exposed position at the foot of a stump.

An individual captured at Lae ate a smaller microhylid frog of the genus *Oreophryne* while in the collecting sack.

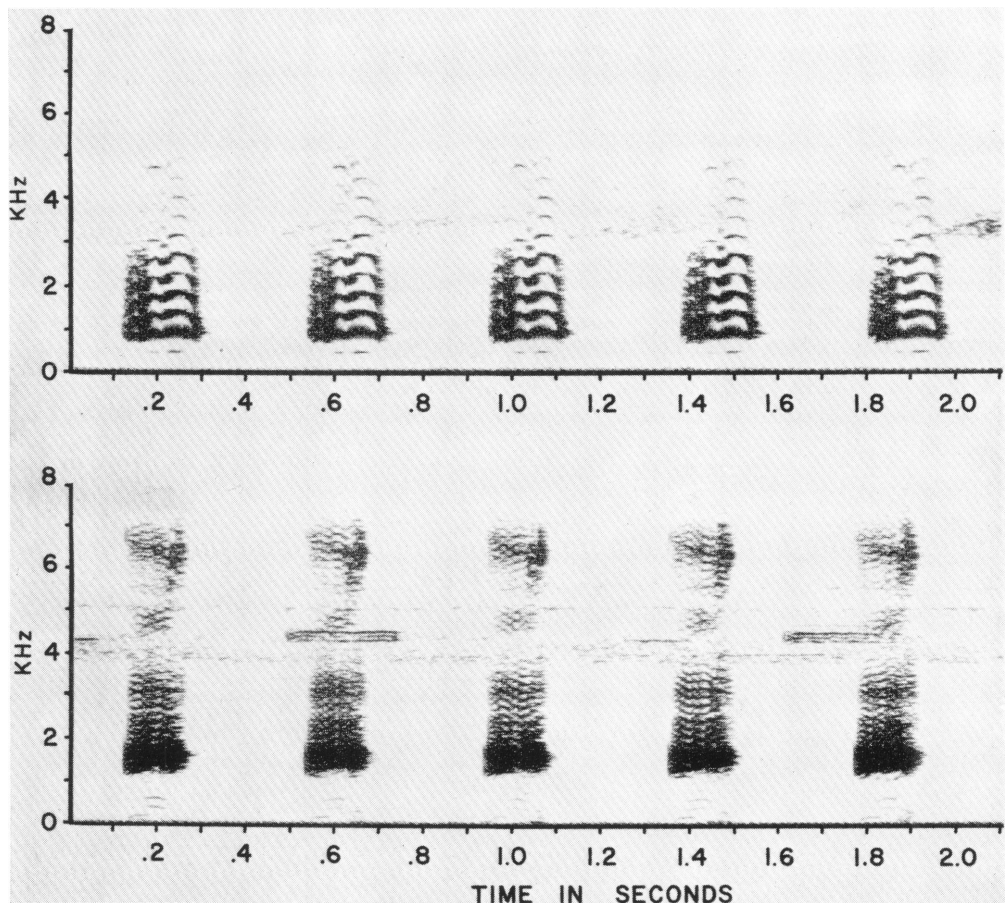


FIG. 38. Sound spectrograms of calls of *Phrynomantis lateralis*. *Upper*: Portion of call of AMNH 81058, recorded at Lae, Morobe District, July 24, 1968, body temperature 23.8°C. *Lower*: Portion of call of AMNH 81060, recorded 7 mi. N, 21 mi. E Port Moresby, Central District, August 18, 1968, air temperature 22.3°C. Both spectrograms made with 45 Hz. filter.

MATING CALL: The typical call is a series of loud, clear, melodious notes. Generally, several minutes elapse between calls. Two complete sequences that I recorded from different frogs comprised 30 and 25 individual notes and lasted, respectively, 13 and 10 seconds. The individual notes are slightly less than 0.2 second in length, and separated by intervals slightly longer than the notes themselves (fig. 38, upper). There is no clearly dominant frequency band in the one recording of high enough quality to merit analysis, and the fundamental frequency is about 440 Hz.

I have heard calls of the sort described near Alexishafen, near Lae, at Garaina, and near Port Moresby, and James Menzies has kindly furnished me with a tape-recording of this call (and a photograph of the caller) made at Alotau on Milne Bay. At Ower's Corner, near Port Moresby, two sorts of calls were being given by *P. lateralis*. Several individuals called in a way that to my ear was not distinguishable from the typical call, but others gave a much harsher call with a lower fundamental frequency, about 200 Hz. in the individual recorded (fig. 38, lower), and a distinctly dominant band centered on about 1600 Hz. Two complete sequences from the same frog each lasted 28 seconds and included 65 and 66 single notes. The repetition rates and lengths of individual notes do not differ noticeably from those in typical calls. Elsewhere, I have heard this call only on a

recording made by James Menzies near the Purari River; he heard other frogs giving the same sort of call at this locality (personal commun.).

The differences between the two calls are essentially the same as those I observed in the two-call types of *Hylophorbus rufescens*, but in that species I did not hear the two types at one locality. The harsher call recorded at Ower's Corner could conceivably emanate from a frog calling with the vocal sac only partly inflated, but if this was the case, it is curious that I heard several other frogs giving the same sort of call at this locality but none doing so elsewhere.

In common with many other anurans, *P. lateralis* produces a "distress" call (fig. 39) when grasped.

DISTRIBUTION AND SPECIMENS EXAMINED: This species is widely distributed throughout the eastern part of New Guinea, from virtually sea level (as at Lae and Katau) to an elevation of 6000 ft. in the Albert Edward Mountains (fig. 25). There is an isolated record far to the west at Toem on the north coast of West Irian.

West Irian: Toem (USNM 124645).

Territory of New Guinea: East Sepik District: Passam, 9 mi. S Wewak (HC 432). Morobe District: Masba Creek near Pindiu, 2000 ft. (610 m.) (AMNH 76007, 76008); Lae, 50 m. (160 ft.) (AMNH 74888, 81058; MCZ 52908, 52909); Busu logging area, ca. 18 mi. (by road) N Lae, 800 ft. (240 m.) (AMNH 81059);

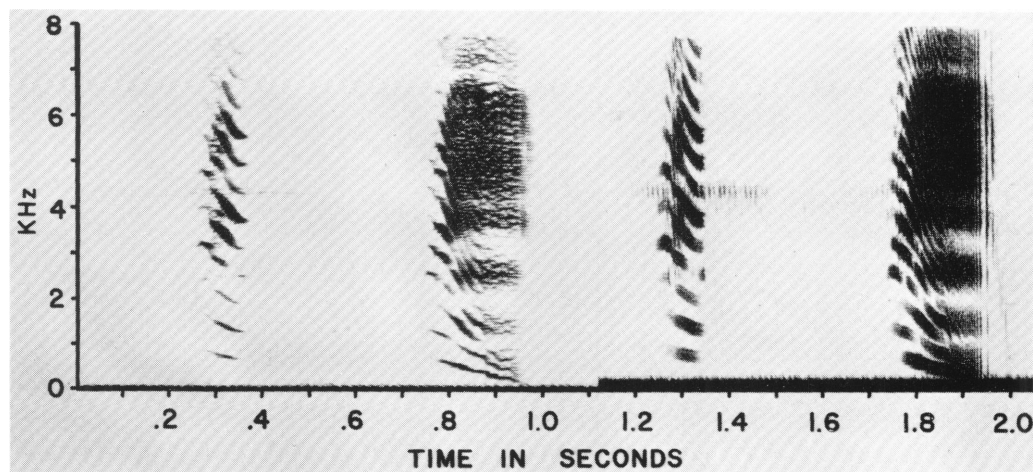


FIG. 39. Sound spectrograms of distress call of *Phrynomantis lateralis*, AMNH 81060, recorded 7 mi. N, 21 mi. E Port Moresby, Central District, August 18, 1968, air temperature 22.3°C. Same two-note call is shown in spectrograms made with 45 Hz. (left) and 300 Hz. filters (right).

Garaina, 2500 ft. (760 m.) (AMNH 81057); Sattelberg (Méhely, 1901, p. 220); Saurere, 4700 ft. (1430 m.) (AMNH 82893). Madang District: Maratambu, Adelbert Mountains, 2300 ft. (700 m.) (AMNH 64244).

Territory of Papua: Central District: Kokoda Trail below Ower's Corner, 7 mi. N, 21 mi. E Port Moresby, 440 m. (1440 ft.) (AMNH 81060); Efogi (UPNG 1051); Rigo (MSNG 29933); Moroka (MSNG 29933); Albert Edward Mountains, 6000 ft. (1830 m.) (MCZ 2894); Mt. Victoria (BMNH 1947.2.11.2 [lectotype], 1947.2.11.3, 1947.2.11.4 [syntypes]);

Mafulu (Parker, 1936, p. 73). Chimbu District: Soliabeda (MCZ 79515, 79516); Weiana, 1500 ft. (460 m.) (MCZ 79512). Gulf District: Omati (MCZ 28330); Gibiteri Village, Omati River (SW 351); Uraru, Purari River, 200 ft. (60 m.) (MCZ 79513 [4 specimens]); Koni, Purari River, 150 ft. (50 m.) (MCZ 79514). Milne Bay District: North slope, Mt. Dayman, 700 m. (2300 ft.) (AMNH 57112, 57361); Alotau (UPNG 2619: photo and tape-recording; specimen not examined). Northern District: Kokoda (Parker, 1936, p. 73). Western District: Katou (MSNG, 1 uncatalogued specimen).



FIG. 40. *Phrynomantis lousiadensis* (AMNH 60137), dorsal view. $\times 1$.

Phrynomantis lousiadensis (Parker),
new combination

Figure 40

Asterophrys lousiadensis PARKER, 1934, p. 62 (type locality, "Rossel Island, Louisiadé Archip.," Milne Bay District, Territory of Papua; holotype, BMNH 1947.2.11.1 [formerly 99.4.25.22] collected by Albert Meek).

DIAGNOSIS: *Phrynomantis lousiadensis* is the only large species of the genus that has long legs. The minimum ratio of tibia length to length from snout to vent in *lousiadensis* is 0.40, whereas in the other species known to reach a length greater than 70 mm. (*P. personata*, *P. robusta*, and *P. stictogaster*) the mean TL/S-V is less than 0.40. No species of *Phrynomantis* is known to be sympatric with *P. lousiadensis*. *Xenorhina doriae*, which is sympatric and of similar size, has shorter legs and much smaller eyes (Eye/S-V mean 0.075 compared with 0.119 in *lousiadensis*) in addition to other differences (see description of *X. doriae*).

DESCRIPTION: *Phrynomantis lousiadensis* is a large microhylid (up to 82 mm. S-V length) with the head as wide as the body and a trun-

cate, slightly overhanging snout. The nostrils open laterally and are closer to the end of the snout than to the eyes. The canthus is rounded and the loreal region is almost vertical and shallowly concave. The eyes are relatively large. (Eye/S-V mean 0.119), with the diameter greater than the distance from eye to naris and greater than the internarial distance. The interorbital space is broader than an upper eyelid. The angles of the jaws flare outward somewhat, especially in large individuals, so that the tympanum is at an angle of about 60 degrees to the horizontal. The border of the tympanum may be indistinct and the diameter difficult to measure accurately. The horizontal diameter of the tympanum ranges from 37 per cent to 61 per cent of that of the eye, mean 47.8 per cent in 27 specimens.

The limbs are relatively long, but the length of the hind limb is subject to both ontogenetic and geographic variation (see following section). There are well-developed discs on both fingers (fig. 51C) and toes; that of the fourth toe is about one and one-half times the width of the disc of the third finger. The disc of the third finger is one and one-half times the width of the

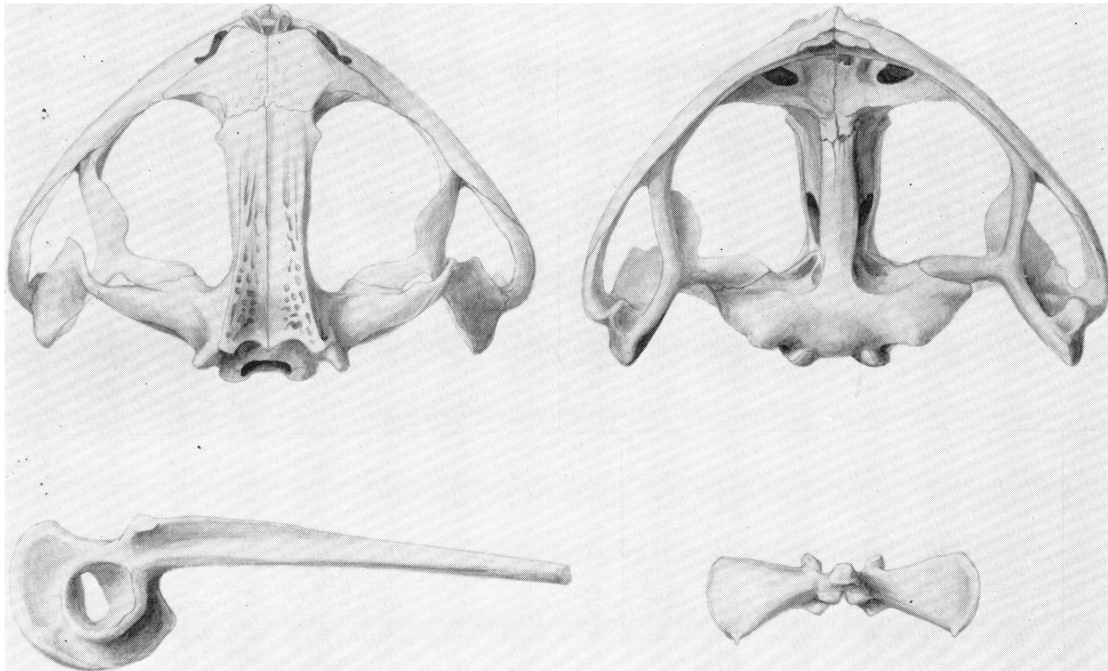


FIG. 41. Skeletal elements of *Phrynomantis lousiadensis* (AMNH 60134). Upper left, skull, dorsal view; upper right, skull, ventral view; lower left, pelvic girdle, right lateral view; lower right, sacral vertebra, ventral view. All $\times 2$.

penultimate phalanx, whereas that of the fourth toe is double the width. All discs have well-developed terminal grooves. The fingers and toes bear large, rounded subarticular tubercles. There is a low, rounded inner metacarpal elevation and less prominent elevations in the middle and outer positions. The inner metatarsal tubercle is about twice as long as wide. There is no outer metatarsal tubercle, and there are no tubercles on the soles or palms. The relative lengths of the fingers are $3 > 4 > 2 > 1$, of the toes, $4 > 3 > 5 > 2 > 1$.

The skin of both dorsal and ventral surfaces may be quite smooth, although in some individuals the dorsal skin is slightly roughened. The only skin fold is a weak one above and behind the tympanum.

The dorsal color in preservative is dark purplish gray with no pattern evident in most

individuals. Light individuals show traces of a dark-spotted pattern, and an inguinal ocellus may be faintly indicated. The chin and chest are dark gray with few to many light speckles. This pattern changes posteriorly to one of blotching and mottling on the abdomen and undersides of the hind limbs, with the least dark pigment in the lower region of the abdomen. The anterior and posterior surfaces of the thighs may be uniformly dark or mottled.

The male possesses vocal slits in the floor of the mouth near the angles of the jaws. The vocal sac is single, median, and subgular. There is no obvious external indication of the vocal sac.

The skull (fig. 41) resembles that of other *Phrynomantis* in most particulars. In that the frontoparietals are slightly rugose, it differs from most but not from *P. lateralis*.

VARIATION: The series of specimens from

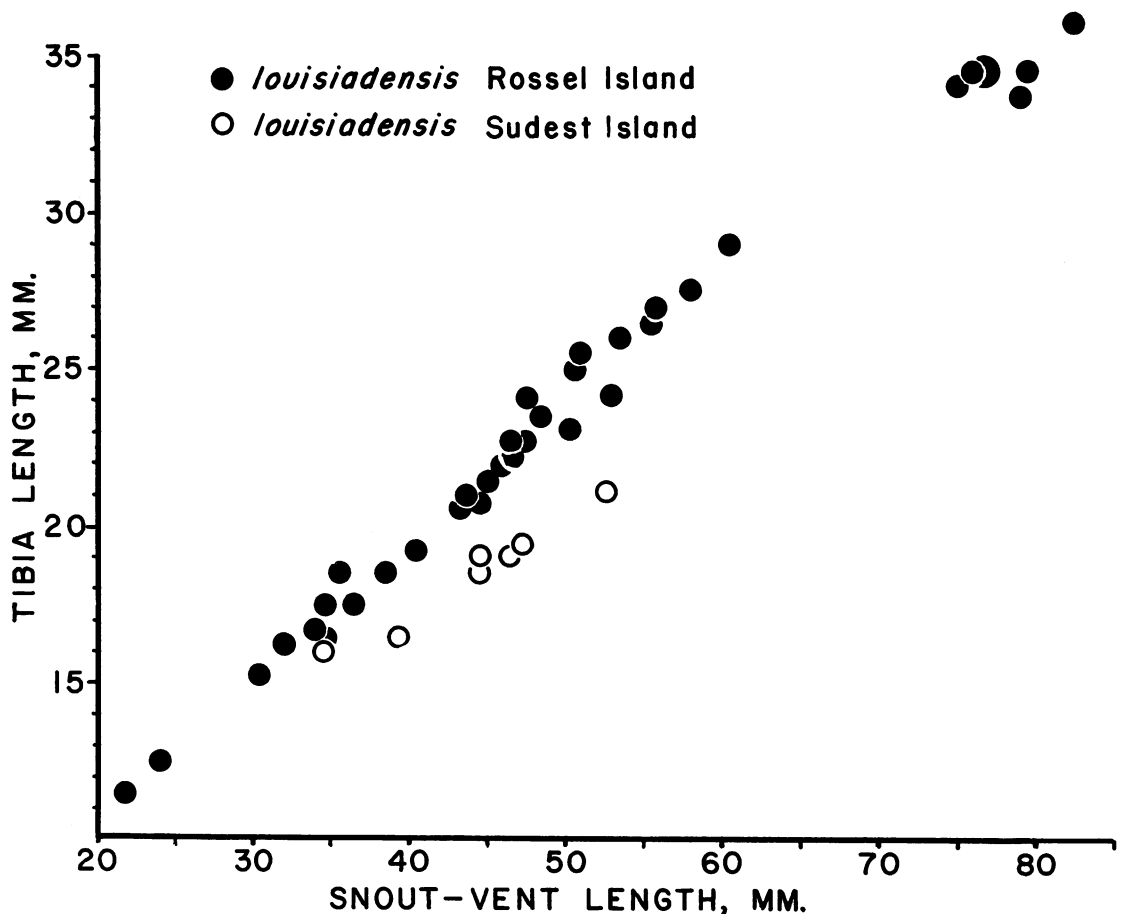


FIG. 42. Relationship of tibia length to snout-vent length in two populations of *Phrynomantis lousiadensis*.

Rossel Island includes individuals of a wide range of sizes, which makes it possible to demonstrate ontogenetic variation in proportions. Differences in proportions between populations of Rossel and Sudest islands also are evident (table 6).

The difference in relative leg length between specimens from Rossel and Sudest islands is clearly evident in the scatter diagram (fig. 42). Not so obvious is the change in proportions that takes place with growth, but this is shown well in figure 43, where the ratio of tibia length to length from snout to vent is plotted against snout-vent length. The average of this ratio in the sample from Rossel Island declines from 0.51 in juveniles to 0.44 in the largest adults.

An ontogenetic increase in head width takes place in the Rossel Island population (fig. 45).

There is some indication that the frogs of Sudest Island mature at a smaller size than those of Rossel Island. The two largest individuals in the small sample from Sudest Island measure 43 and 53 mm. and are gravid with ova 2.5 to 3.0 mm. in diameter. Eight females from Rossel Island measuring 50 to 61 mm. appear to be immature, for none has ova greater than 1 mm. in diameter. This is not merely a seasonal phenomenon, for larger females in the same samples are gravid.

If additional specimens from Sudest Island confirm the apparent differences between the

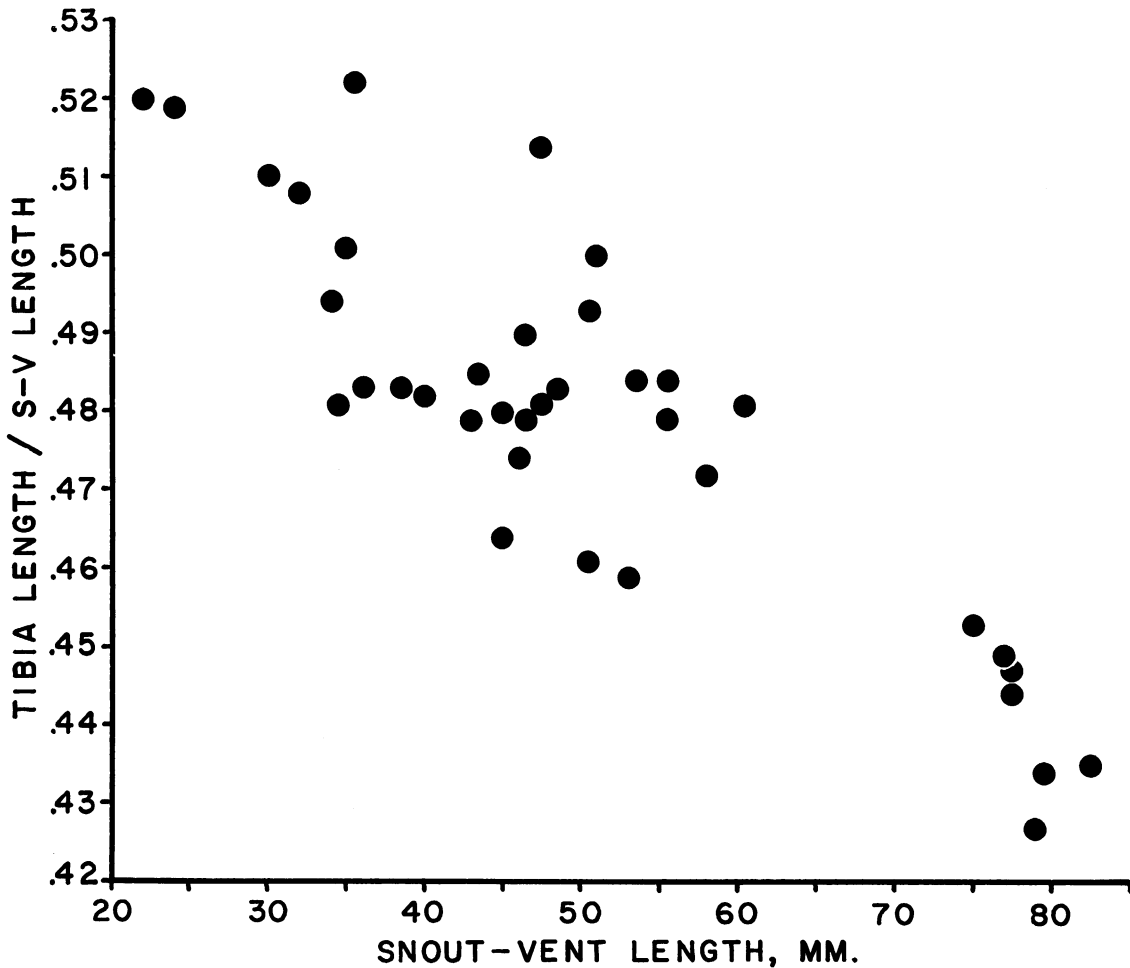


FIG. 43. Relationship of the ratio of tibia length/snout-vent length to snout-vent length in *Phrynomantis lousiadensis* from Rossel Island, showing relative decrease in tibia length with increased body size.

populations, it may prove desirable to accord subspecific status to the two insular groups.

COMPARISON WITH OTHER SPECIES: Comparisons made in the foregoing diagnosis should suffice to distinguish *P. lousiadensis* from other species of its genus. There is a superficial similarity between *P. lousiadensis* and *Hylophorbus ocellatus extimus* of Sudest Island, but any doubt as to the identity of a particular specimen can be resolved by examining the premaxillae, which are symphygnathine in *Phrynomantis* and eleuthernognathine in *Hylophorbus*.

ECOLOGICAL NOTES: Nothing specific regarding the ecology of this species is on record. See

Brass (1959) for descriptions of the localities at which this species was collected.

DISTRIBUTION AND SPECIMENS EXAMINED: This species is known only from Rossel and Sudest (Tagula) islands in the Louisiade Archipelago (fig. 36). It was known only from the type-specimen until members of the Fifth Archbold Expedition collected 29 specimens on Rossel Island and seven on Sudest Island. Later, Mr. Hugh Osborne donated an additional six specimens from Rossel Island.

TERRITORY OF PAPUA: Milne Bay District: Rossel Island (no specific locality: BMNH 1947. 2.11.1 [holotype]; AMNH 69116–69119); south

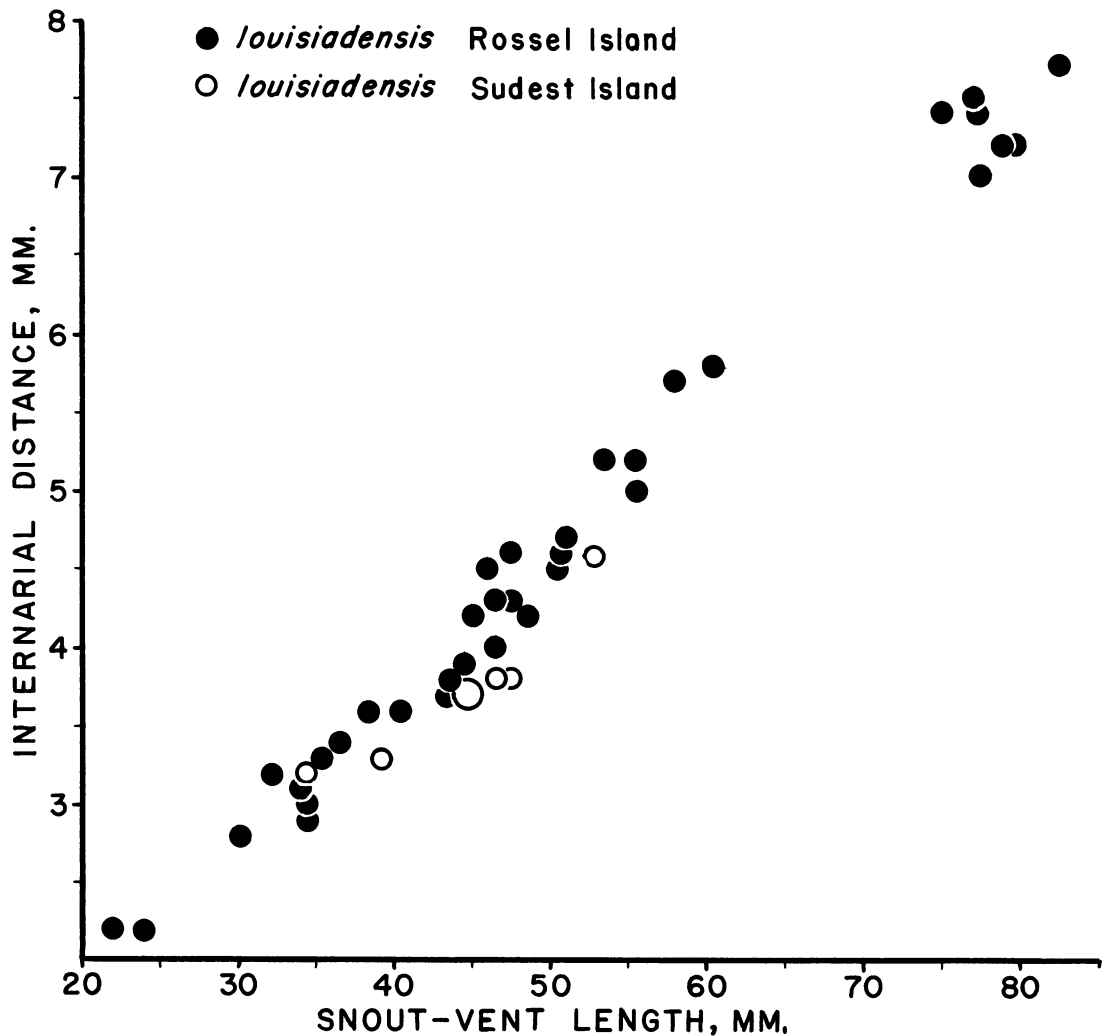


FIG. 44. Relationship of internarial distance to snout-vent length in two populations of *Phrynomantis lousiadensis*.

slope of Mt. Rossel, 700 m. (2300 ft.), Rossel Island (AMNH 60128, 60134–60142+19 untagged specimens); Abaleti, Rossel Island (AMNH 69347, 69348); west slope of Mt. Riu, 250–350 m. (820–1150 ft.), Sudest Island (AMNH 60060–60065); Rambuso, 100 m. (330 ft.), Sudest Island (AMNH 60034).

***Phrynomantis personata*, new species**

Figures 48, 49

HOLOTYPE: AMNH 74903, an adult male collected by R. G. Zweifel and G. Sluder at Maprik, elevation 800 ft. (240 m.), East Sepik District, Territory of New Guinea, on August 12, 1964.

PARATYPES: AMNH 74902 from the type locality; SAM 5888 from Jama, East Sepik District (23 mi. S of type locality); AMNH 78090–78093, Lumi, 1750 ft. (530 m.), AMNH 78094–78096, Miliom, 1500 ft. (460 m.), and AMNH 78097, Mt. Nibo, all from West Sepik District.

Diagnosis: This is a heavy-bodied *Phrynomantis* of large size (up to 72 mm., snout to vent) that is readily distinguished from all other species of the genus by its color pattern; the head, from the posterior corner of the eyes to the tip of the snout (except for the loreal region in some specimens), is black in marked contrast to the reddish brown ground color of the remainder of the dorsal surfaces. Comparisons with species

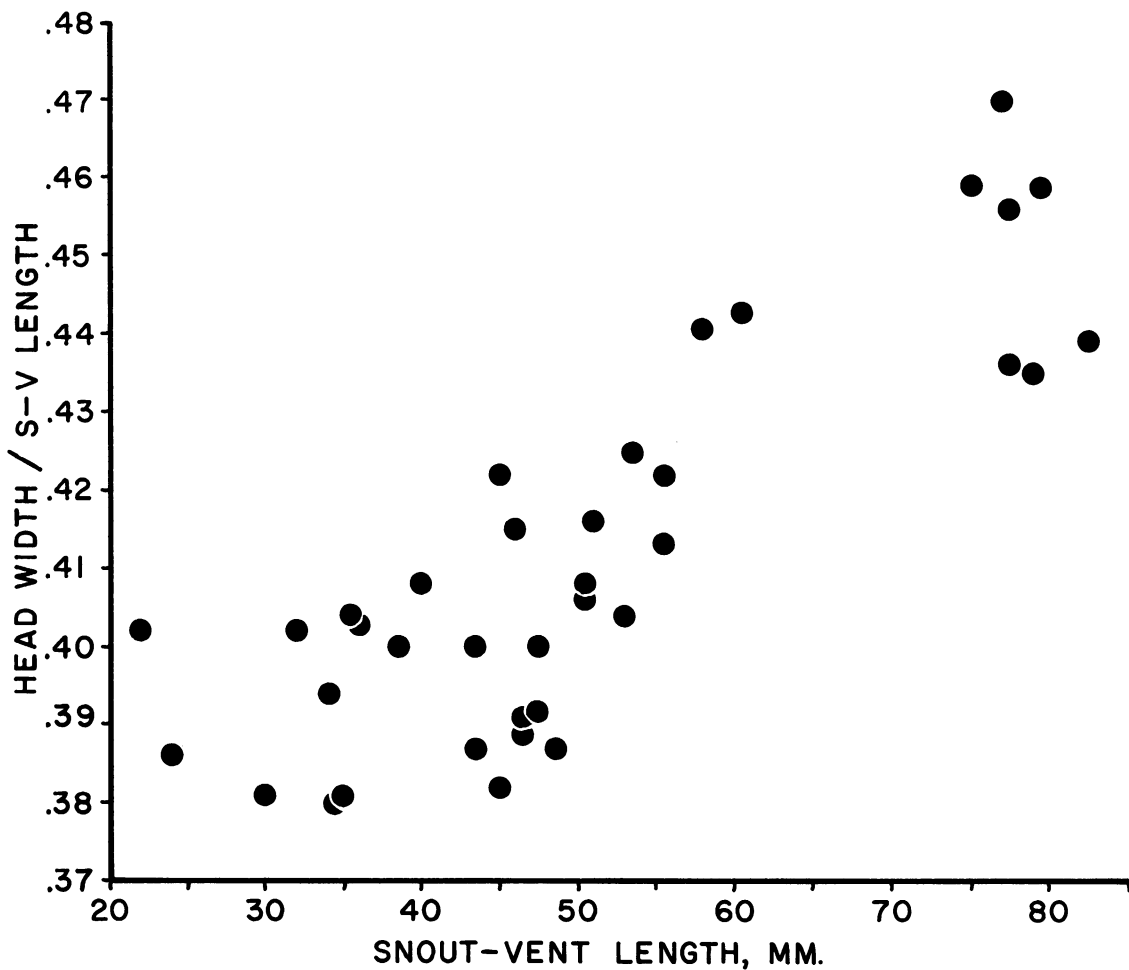


FIG. 45. Relationship of the ratio of head width/snout-vent length to snout-vent length in *Phrynomantis lousiadensis* from Rossel Island, showing relative increase in head width with increased body size.

similar in morphology (but not in color pattern) are made in a following section.

DESCRIPTION OF TYPE-SPECIMEN: The head, although moderately broad ($HW/S-V=0.37$), is narrower than the relatively heavy-set body. The snout is truncate and the canthus curved and rounded. The loreal region is nearly vertical and slightly concave. The nostrils are situated laterally at the end of the snout and the openings

are scarcely visible from directly above. A fold of skin passes from the posterior corner of the eye across the upper margin of the tympanum (which is indistinct) and then downward behind the tympanum. Except for this fold, the body is smooth both dorsally and ventrally.

The relative lengths of the fingers are $3 > 4 > 2 > 1$, of the toes, $4 > 3 > 5 > 2 > 1$. All fingers and toes have grooved terminal discs. Those of the

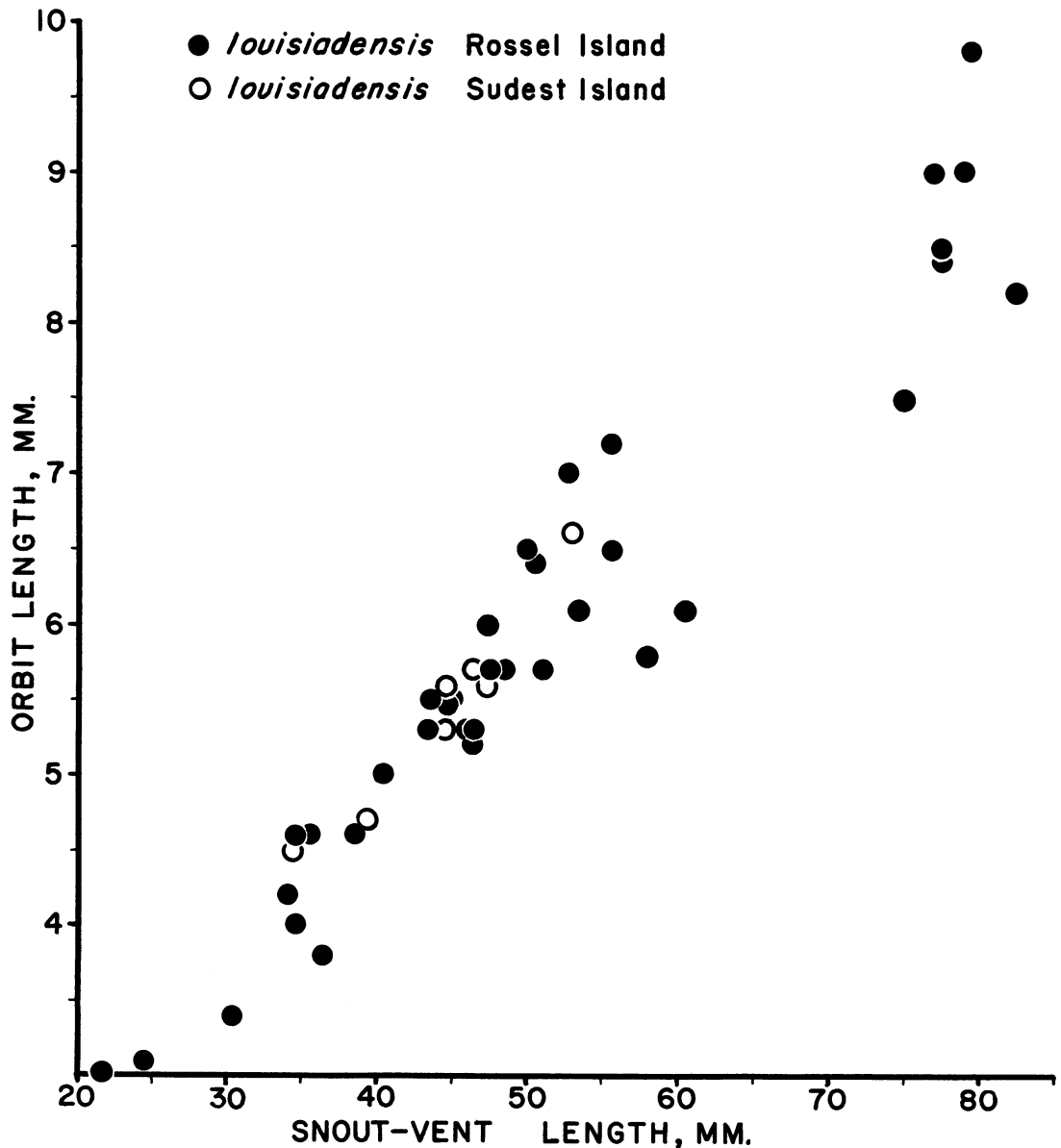


FIG. 46. Relationship of eye size to snout-vent length in two populations of *Phrynomantis louisiadensis*.

fingers are slightly broader than the penultimate phalanges, whereas those of the toes are more noticeably broadened and are larger than the finger discs. Hands and feet bear low, rounded subarticular tubercles. Low, rounded, inner, middle and outer metacarpal tubercles are present, but the foot has only an inner metatarsal tubercle about twice as long as wide. The fingers and toes are without webbing.

In life the anterior half of the head (except for a patch of reddish ground color in the loreal region) was black. In the preserved specimen the dark pigment is less intense and the rich reddish brown, almost orange, of the body and limbs has

faded to pale tan. An indistinct pattern of gray flecks and blotches on the body and limbs was more nearly black in the living animal, but not of the intensity of the head coloring. Lumbar ocelli are faintly indicated. The chin and undersurfaces of the hind limbs are slightly mottled with gray-brown on a light tan ground color; the belly is immaculate. In life the ground color of the chin was much the same as that of the back, and the belly had an orange rather than a tan tint.

MEASUREMENTS OF HOLOTYPE: S-V, 64.7; TL, 22.6; HW, 24.1; Eye, 7.5; E-N, 5.2; IN, 5.6; EAR, *ca.* 4.0; width of disc of third finger, 1.7

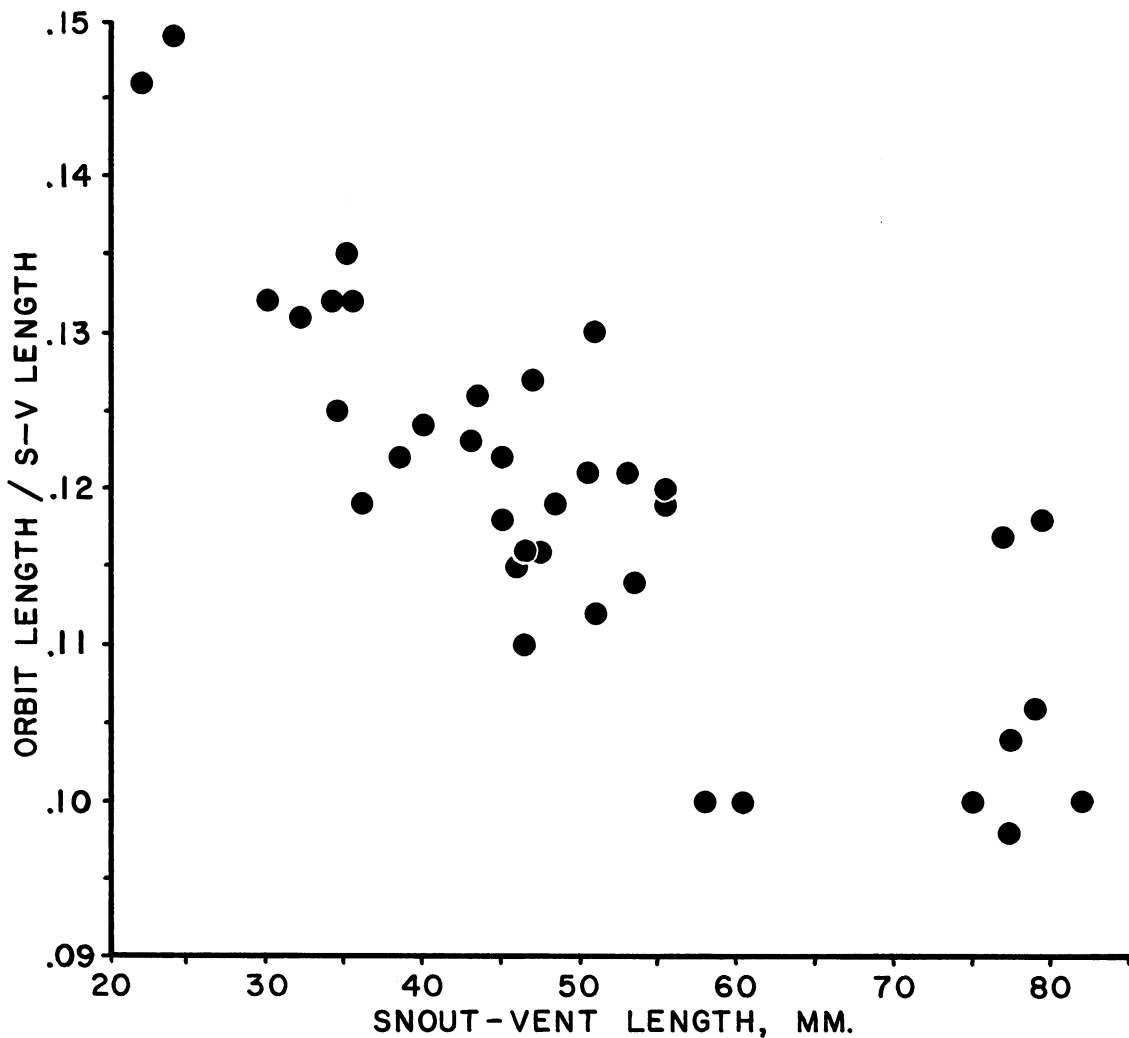


FIG. 47. Relationship of the ratio of orbit length/snout-vent length to snout-vent length in *Phrynomantis louisiana*, showing relative decrease in eye size with increased body size.

(penultimate phalange, 1.2); width of disc of fourth toe, 2.1 (1.4).

VARIATION: The largest of the 11 specimens in the type series is a male with a snout to vent length of 72.5 mm. Females 67 mm. and 71 mm. long are gravid, with ova up to 5.3 mm. in diameter. Variation in selected proportional measurements is presented in table 6.

The female paratype collected at the same spot as the male closely resembled the male holotype in dorsal color and pattern. It differed somewhat ventrally in that the chin and hind limbs were more uniform gray rather than mottled, and the belly was grayish white, lacking the orange tint of the male. It should not be inferred that there is sexual dimorphism in ventral pattern, for other males in the type series have (in preservative) a pattern much like that of the female paratype described above. The chin may be dark gray with scarcely a trace of lighter mottling, or may be heavily mottled with gray on white. The undersides of the thighs show the same range of variation. The central region of the belly usually is immaculate, although mottling may impinge on this region from both front and rear. The dark head pattern is common to all specimens, adult and juvenile

(at least down to 43 mm. snout-vent length). The intensity of dark markings on the back varies considerably; some individuals show as little as the holotype, whereas others are fairly heavily speckled with dark brown (probably black in life) and show fairly distinct lumbar ocelli.

I have excluded from the type series a juvenile specimen with a snout to vent length of 17 mm., captured at Ambunti (BBM 1018). The belly is more heavily spotted than in other *personata*, and the back is dark enough that the dark anterior part of the head is not well distinguished. Probably it represents *personata*, but the record needs to be confirmed with additional specimens, preferably adults. The spotted venter lends a superficial similarity to *P. stictogaster*, but the loreal tubercle characteristic of that species is lacking, and the toe tips are expanded and grooved.

COMPARISON WITH OTHER SPECIES: *Phrynomantis personata* and *P. robusta* are virtually identical in size and proportions, but no specimen of *robusta* from over its wide range has anything like the color pattern of *personata*. The anterior part of the head of *robusta* may be darker than the rest of the body, but does not show the sharp black and red distinction of *personata*. The ventral surfaces of *robusta* show little or none of the mottling commonly seen on the chin and hind legs of *personata*.

Phrynomantis personata may be no more than a geographic race of *robusta* (so far as known the ranges are allopatric), but I think that at the present state of knowledge it would be presuming too much to relegate the distinctive *personata* to subspecific status. Specimens from the region of

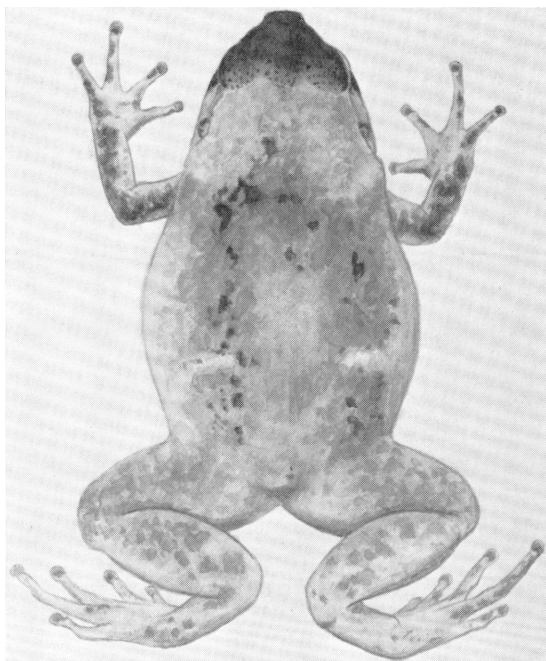


FIG. 48. *Phrynomantis personata* (AMNH 74903, holotype), dorsal view. $\times 1$.



FIG. 49. *Phrynomantis personata* (AMNH 74902).

Djayapura in West Irian may prove significant in this regard (see account of *P. robusta*).

Another possible close relative of *P. personata* is *P. stictogaster*. The latter has its own distinctive color pattern, particularly the dark venter with numerous tiny white spots, and possesses a loreal tubercle that *personata* lacks. Most important for diagnostic purposes, the digits of *stictogaster* lack discs and terminal grooves.

ECOLOGICAL NOTES: The type locality is in the southern foothills of the Prince Alexander Mountains at an elevation of 800 feet. The original forest has largely been cleared, and the vegetation is a mosaic of second growth forest and grassland. We found the female paratype from Maprik at night in the mouth of a hole in the edge of a gully on a grassy hillside. The immediate area was almost unshaded and the grass was cut to a height of about 6 to 10 inches. We had been attracted to the site by the calling of a frog and assumed we had caught the vocalist, but the following night calling resumed from the same spot and we found the male (holotype) in the mouth of the same burrow. The burrow into which the frog retreated was about 1 foot deep with an entrance in the shape of a horizontal ellipse. A similar burrow that we excavated in search of a calling frog held only a crab. I doubt that these frogs could dig such burrows in the dense clay soil and suspect that they utilize holes made by crabs or other animals.

A mention of blood parasites in "*Asterophrys* sp." by Ewers (1968) refers, in part at least, to a specimen of *P. personata* from Jama.

MATING CALL: I recorded two complete call sequences uttered by the individual designated as holotype. Each call consists of five loud, harsh notes (fig. 52, upper). The initial note is slightly greater than 0.1 second long, and subsequent notes increase to almost 0.3 second. Intervals between notes range from 0.3 to 0.6 second, and the entire sequence lasts 3 seconds. I have no precise data on the rate of calling, but at least several minutes passed between calls. The call is closely similar in most respects to that of *Phrynomantis robusta*, but the rate at which individual notes are repeated is almost twice as rapid in *robusta* as in *personata*; a five-note sequence in *personata* took 3 seconds, and in *robusta*, only 1.6 seconds at almost the same temperature (24.0–25.3°C.). These data suggest a true difference in mating calls, but with only two individuals of *robusta* and one of *personata*

recorded, the data are too few to justify a firm conclusion.

DISTRIBUTION AND SPECIMENS EXAMINED: The localities for this species lie between the Sepik River and the summit of the north coastal ranges, the Torricelli and Prince Alexander mountains, from Maprik and Jama on the east to Lumi, some 70 mi. to the west (fig. 28). The elevation at Jama is probably less than 200 ft. (available maps do not show sufficient detail), and the specimen from Mt. Nibo came from at least 2100 ft.; other specimens are from intermediate elevations. The only specimen examined other than the holotype and paratypes listed in foregoing paragraphs is one from Ambunti, West Sepik District (BBM 1018).

Evidently the first specimens to be collected were those Sluder and I caught at Maprik in August, 1964. Ewers (1968) obtained one at Jama in October, 1964, and Jared Diamond obtained the balance of the paratype series in July, 1966.

ETYMOLOGY: The name for this species is from the Latin adjective *personatus* (masked), and refers to the head coloration.

Phrynomantis robusta (Boulenger),
new combination

Figure 50

Mantophryne robusta BOULENGER, 1898b, p. 480 (type locality, "St. Aignan I., south of Fergusson I., British New Guinea" [Misima Island, Louisiade Archipelago, Milne Bay District, Territory of Papua]; three syntypes, BMNH 1947.2.11.5–1947.2.11.7 [formerly 98.3.31.9–98.3.31.11], collected by A. S. Meek).



FIG. 50. *Phrynomantis robusta* (AMNH 82895).

- Gnathophryne robusta*: MÉHELÿ, 1901, p. 225.
Mantophryne microtis WERNER, 1901, p. 102 (type locality, "German New Guinea" [the present Territory of New Guinea]; holotype, ZMB 16499, collected by E. Tappenbeck, now lost or destroyed).
Pomatops valvifera BARBOUR, 1910, p. 89 (type locality, "Fak Fak, Northwestern Dutch New Guinea" [West Irian]; holotype, MCZ 2577, collected by A. E. Pratt).
Manthophryne microtis: VOGT, 1911b, p. 429.
Liophryne kampeni BOULENGER, 1914, p. 252 (type locality, "Mimika R.," West Irian; holotype, BMNH 1947.2.11.8 [formerly 1913.10.31.349], collected by the British Ornithologists' Union Expedition in 1910 or 1911).
Hylophorbus microtis: VAN KAMPEN, 1919, p. 54.
Hylophorbus robustus: VAN KAMPEN, 1919, p. 54.
Asterophrys microtis: PARKER, 1934, p. 64.
Asterophrys robusta: PARKER, 1934, p. 64.
Asterophrys valvifera: PARKER, 1934, p. 64.

DIAGNOSIS: *Phrynomantis robusta* is a large species (snout-vent length up to 73 mm.), typically with the dorsal surfaces uniform purplish brown (sometimes with more or less distinct darker markings or faint lumbar eyespots), ventral surfaces paler than dorsal and without conspicuous spotting or mottling, and distinct discs on fingers and toes, those on the toes being slightly larger.

Phrynomantis robusta is closely similar to *P. humicola*, which differs in smaller maximum size (59 mm. snout to vent) and in ventral color pattern. A more detailed comparison of the two forms is made in a following section. *Phrynomantis fusca* closely resembles *robusta* but appears to be a smaller species (to 54 mm., snout-vent); *robusta* and *fusca* are compared in the account of the latter species. Other species of *Phrynomantis* known to reach the large size of *P. robusta* are *P. personata*, *P. stictogaster*, and *P. louisianensis*. Comparisons with these three species are made in a following section.

DESCRIPTION: Except for its relatively large size (maximum snout-vent length 73 mm., 11 of 40 specimens greater than 60 mm.), *Phrynomantis robusta* is a rather generalized asterophryine. The body is moderately stout, neither as rotund as most *Xenobatrachus* nor as relatively slender as *Hylophorbus*. The head width (HW/S-V mean 0.37) and tibia length (TL/S-V mean 0.36) are moderate, and the eyes are relatively large (Eye/S-V mean 0.12). The maximum width of the upper eyelid approximately equals the narrowest interorbital distance. The snout is shorter

than the eye and is truncate or bluntly rounded. The loreal region is vertical and slightly concave. The canthal area is rounded. The nostrils are lateral, closer to the tip of the snout than to the eye, and only slightly visible from above. The horizontal diameter of the tympanum may be as great as half the length of the orbit, but usually is less, and the tympanum is indistinct. An inconspicuous fold passing from the posterior corner of the eye above and behind the tympanum is the only fold on the otherwise smooth body.

The relative lengths of the fingers are $3 > 4 > 2 > 1$, of the toes, $4 > 3 > 5 > 2 > 1$. All fingers and toes have grooved terminal discs. The disc of the fourth toe is twice as wide, or nearly so, as the narrowest part of the penultimate phalange. The discs of the fingers (fig. 51E) are smaller than those of the toes, both in absolute dimensions and relative to the penultimate phalanges. The subarticular tubercles of both the fingers and toes are low and rounded. Metacarpal tubercles are only faintly indicated. The inner metatarsal tubercle is distinct, although low and rounded; there is no outer tubercle.

See the following section for description and discussion of color patterns. Measurements of syntypes and holotypes assigned to *P. robusta* are in table 7.

VARIATION: Most specimens of *Phrynomantis robusta* are dark purplish brown dorsally and a paler shade of the same color ventrally. The dorsum may be uniform or may show obscure, darker vermiculate markings. Faint inguinal eyespots may be present. Generally the facial region assumes a darker, blackish tint, but there is little contrast to the rest of the dorsal ground color, and the change from one shade to the other is gradual. The ventral surfaces are uniformly colored or show at the most very faint mottling. The limbs are without markings.

Frogs with the sort of color and pattern described above occur widely throughout New Guinea. The type-specimens of *M. robusta*, *P. valvifera*, and *L. kampeni* are of this general type. Frogs from the vicinity of Alexishafen on the north coast and from near Wau, in the Huon Gulf drainage are brown with small white spots on the back and sides. Probably this is the color-pattern type on which *M. microtis* was based. Two adult frogs obtained by Fred Parker at Bankim and Derongo, localities 3 miles apart in the extreme northwestern corner of the Terri-

tory of Papua, are unusually pale for *robusta*. Two juveniles from Derongo are darker than the adults but are paler and much more heavily marked dorsally than is usual in *robusta*.

Variation in proportions is presented in table 6. There appears to be geographic variation in relative leg length. Ten specimens from Western and Gulf districts of the Territory of Papua have relatively long legs: TL/S-V mean 0.403 (0.34–0.44). The sample of 14 specimens from the Huon Peninsula has a distinctly lower average, 0.353 (0.32–0.37), and scattered small samples from elsewhere in eastern New Guinea fall in the same range as the latter.

COMPARISON WITH OTHER SPECIES: *Phrynomantis robusta* must be compared with four other moderately large species: *humicola*, *lousiadensis*, *personata*, and *stictogaster*. It is not known to be sympatric with any of these.

The most evident difference between *Phrynomantis robusta* and *P. humicola* is in size: *robusta* reaches a length of at least 73 mm., and 11 of 40 specimens are longer than 60 mm.; the largest among 161 specimens of *humicola* measures 59.5 mm. The finger discs of *robusta* are only slightly expanded but are noticeably wider than their penultimate phalanges. There is a tendency for these discs in *humicola* to be relatively narrower, and in many instances they are no wider than the penultimate phalanges. The chest and abdomen of *robusta* (in preservative) vary from virtually white (unpigmented) to uniform light tan. The ventral surfaces of *humicola* are basically quite pale, and darkening involves a coarse reticulum of melanophores rather than an essentially uniform darkening. Some trace of the reticulum invariably is present.

Phrynomantis lousiadensis differs from *P. robusta* in color pattern, is larger than *robusta* (up to 82 mm.), and has longer hind legs (TL/S-V minimum in *lousiadensis* 0.40; maximum in *robusta* 0.44). The dorsal color patterns of the two species may be similar, but *lousiadensis* has more dark pigment ventrally, the hind legs being especially heavily marbled or spotted. The subarticular tubercles of *lousiadensis* are prominent, in contrast with the low, rounded elevations of *robusta*.

Phrynomantis personata cannot be distinguished from *P. robusta* in either size or proportions but has a distinctive color pattern. In *personata*, the entire head from the snout to the posterior corners of the eyes, occasionally excepting the

loreal region, is very dark brown (virtually black), and is abruptly differentiated from the rest of the head and body. Although *robusta* may show smudgy dark markings in the facial region, the pattern never gives the distinct masked effect of *personata*. The chin and chest of *personata* are much darker in most individuals than the belly, and mottling is prominent on the undersides of the hind legs and sometimes on the lower abdomen. These areas are much more uniform in color in *robusta*. The mating calls of *robusta* and *personata* may differ (see account of *personata* for a comparison).

Phrynomantis stictogaster also resembles *P. robusta* in size and proportions but has a distinctive ventral color pattern. The under surfaces of *stictogaster* typically are dark gray-brown with numerous tiny white spots or, rarely, a mottled pattern. An anatomical peculiarity of *stictogaster* is a tiny but distinct tubercle situated between the nostril and the eye (fig. 57).

TAXONOMIC NOTES: The three syntypes of *Mantophryne robusta* are in good condition, although the color, "Reddish or purplish brown above, uniform or with small black spots" (Boulenger, 1898b, p. 480), has faded to light tan with scarcely a trace of pattern. The only way in which these specimens differ noticeably from the average for the whole series is in eye size, the eyes being smaller than in mainland specimens of similar size. Unfortunately, there are no other specimens from the type locality (Misima Island), so the significance of the apparent difference cannot now be assessed.

There is nothing in the original description of *Mantophryne microtis* Werner, 1901 (type locality, "German New Guinea") that serves adequately to differentiate this form from *P. robusta* as I have defined the species. The holotype of *microtis* apparently has been lost or destroyed (G. Peters, *in litt.*). The morphological features attributed by Werner to *microtis* are held in common with *robusta*. Two specimens I collected near Alexis-hafen (in what was formerly German New Guinea) have the sides and hind limbs white-spotted, as Werner describes, and so do three from Kulolo Creek near Wau (also in the former German territory). I have not seen this pattern in *robusta* from other areas. The snout and eyelids are often blackish in *robusta*, as Werner describes for *microtis*, but the "rather dark olive green" of the upper surfaces and "greenish yellow" of the venter differ from the dark and

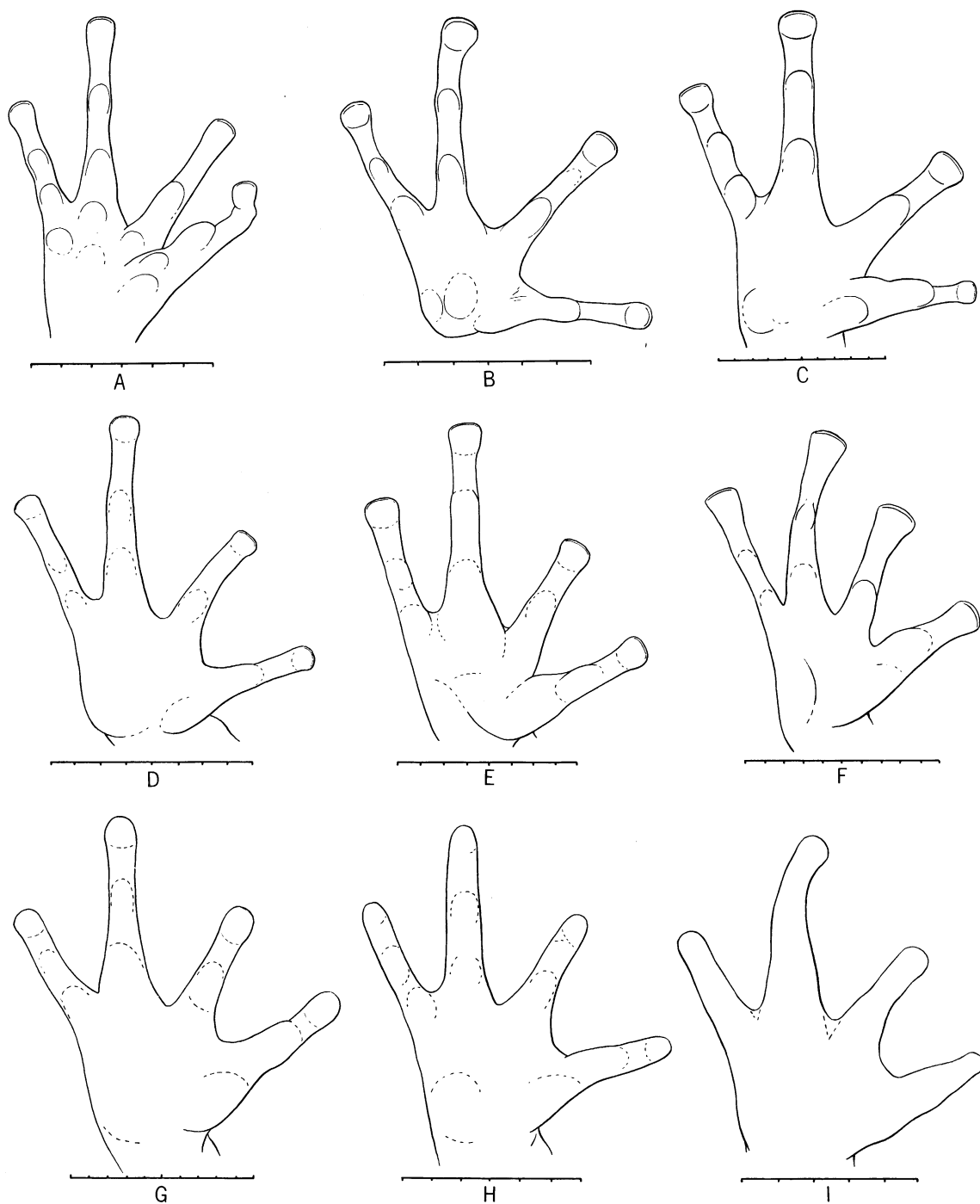


FIG. 51. Hands of *Phrynomantis* in palmar view. A. *P. lateralis*. B. *P. infulata*. C. *P. louisianensis*. D. *P. h. humicola*. E. *P. robusta*. F. *P. fusca*. G. *P. stictogaster*. H. *P. wilhelmana*. I. *P. glandulosa*. Scale lines subdivided in millimeters.

light brown in *robusta* I have seen alive. I can see no grounds for maintaining *microtis* as a distinct species, because the only apparent difference is in the color in the dorsal and ventral surfaces. It is true that the skeleton of the type was never examined to confirm the generic assignment, but Werner's description of the external anatomy and his assignment of the species to *Mantophryne* make it likely that it was a *Phrynomantis*.

Barbour (1910) based *Pomatops valvifera* on a small specimen, said to be "well preserved," taken from the stomach of a snake. The specimen is not now "well preserved," and to judge from Barbour's illustration may not have been in too good condition then. The toes are somewhat dehydrated, so the discs appear in Barbour's illustration smaller than they must have been in life.

In defining *Pomatops valvifera*, Barbour (1910, p. 89) emphasized supposed peculiarities in the eyelids: "The upper eyelids are involved in a flap of skin extending for some distance anterior and posterior to the position of the eye. These flaps are sufficiently developed so that they may be laid down and thus completely cover the whole eye." There is, in fact, nothing peculiar about the eyes or eyelids except that the eyeballs are retracted and probably partly collapsed in this slightly digested individual. I cannot find characters adequate to differentiate *valvifera* from *robusta*, so I consider *valvifera* a junior synonym.

The type-specimen of *Liophryne kampeni* is in good condition and closely resembles the syntypes of *M. robusta* in general appearance. The "Two long oblique series of vomero-palatine teeth" mentioned by Boulenger (1914, p. 252) are odontoids rather than true teeth, and although inconspicuous are readily felt with the tip of a needle. Parker (1934, p. 64) treated

kampeni as a synonym of *valvifera*, and I regard both as synonyms of *robusta*.

Kinghorn (1929, pp. 76-77) identified specimens from Mt. Lamington as "*Hylophorbus robustus*," but they are *Xenorhina doriae* (see account of that species).

Specimens tentatively associated with *P. robusta*: Four specimens from Busilmin in the Star Mountains of the East Sepik District resemble *robusta* in most respects. The dorsal and ventral colors are the almost uniform dark and light browns common to most *robusta*. Digital discs, hind leg length, eye size, and head width are also as in that species. The largest specimen measures only 48 mm. snout to vent, but the series is too small to attach significance to this. My reservations as to the identity of these specimens stem from two sources: the high montane locality (probably 7000 feet or higher, although I do not have precise data) would be most unusual for *robusta*, which elsewhere has been found from virtually sea level to perhaps 5000 feet; the E-N/IN ratio is unusually low for *robusta*. This ratio averages 0.75 (range 0.71-0.78) in the four specimens, compared to the mean 0.88 (0.74-1.12) for 38 *robusta*.

I have considered the possibility that the Busilmin specimens represent *Phrynomantis humicola*, the smaller, brown *robusta*-like species that replaces *robusta* at high elevations in the Central Highlands. However, the fit is no better here. The difference between the E-N/IN ratios is of similar magnitude, and the uniform ventral color is unlike the mottled pattern of *humicola*. Tentatively, I refer these montane frogs to *robusta*, but I would not be astonished if additional investigation shows them to represent a distinct form, with a relationship to *robusta* comparable to that between *humicola* and *robusta*.

A small, rather poorly preserved specimen

TABLE 7
MEASUREMENTS (IN MILLIMETERS) OF TYPE-SPECIMENS IN SYNONYMY OF *Phrynomantis robusta*

| Name | Catalogue Number | S-V | TL | HW | EYE | EAR | IN | E-N | Width of Discs | |
|----------------------------|------------------|------|------|------|-----|-----|-----|-----|-----------------|---------------|
| | | | | | | | | | Third Finger | Fourth Toe |
| <i>Mantophryne robusta</i> | BMNH 1947.2.11.5 | 69.5 | 23.0 | 24.1 | 6.3 | 3.2 | 4.6 | 4.5 | 1.7 | 1.9 |
| <i>Mantophryne robusta</i> | BMNH 1947.2.11.6 | 63.9 | 20.5 | 22.2 | 6.0 | 3.8 | 4.5 | 4.3 | 1.5 | 1.7 |
| <i>Mantophryne robusta</i> | BMNH 1947.2.11.7 | 61.7 | 21.2 | 23.3 | 5.9 | 3.1 | 4.1 | 4.6 | 1.4 | 1.5 |
| <i>Liophryne kampeni</i> | BMNH 1947.2.11.8 | 54.6 | 19.5 | 19.5 | 6.3 | 2.7 | 4.5 | 3.5 | 1.2 | 1.6 |
| <i>Pomatops valvifera</i> | MCZ 2577 | 30.1 | 11.2 | 8.9 | 3.7 | — | 2.4 | — | — | — |

from Djayapura (Hollandia) is much paler dorsally than is usual in *robusta*, and possesses dark markings on the face, back, and limbs. The facial markings lack the clarity and intensity seen in *personata*, so I refer this specimen to *robusta*. The taxonomic status of the frogs in this area will require investigation when a better sample becomes available. They may be *P. personata*, which would be geographically reasonable.

ECOLOGICAL NOTES: This species is a ground-dweller, but little is on record of its habits. One found at an elevation of 1600 m. on Goodenough Island on the Fourth Archbold Expedition was "under tree root in oak forest" (field notes). I found a juvenile at Tumnang, elevation 4400

feet, in a hole in the cut bank of a trail in second-growth forest. In August and September, 1969 I found two *robusta* calling from the mouths of burrows on the floor of lowland rain forest near Alexishafen. The burrows were in well-drained, slightly sloping sites and were $2\frac{1}{2}$ to 3 feet in length with a maximum depth of about 1 foot.

The only published information on the ecology of this species was given by Méhely (1901, pp. 228–229, translated): "Ludwig Biró found this frog together with a clump of eggs in a decaying tree stump lying on the ground in thick forest, 60–80 m. above sea level. 'The animal sat on the eggs, held them encircled with both hands, and covered them.' . . .

"The fortunate discoverer sent the eggs, 17 in

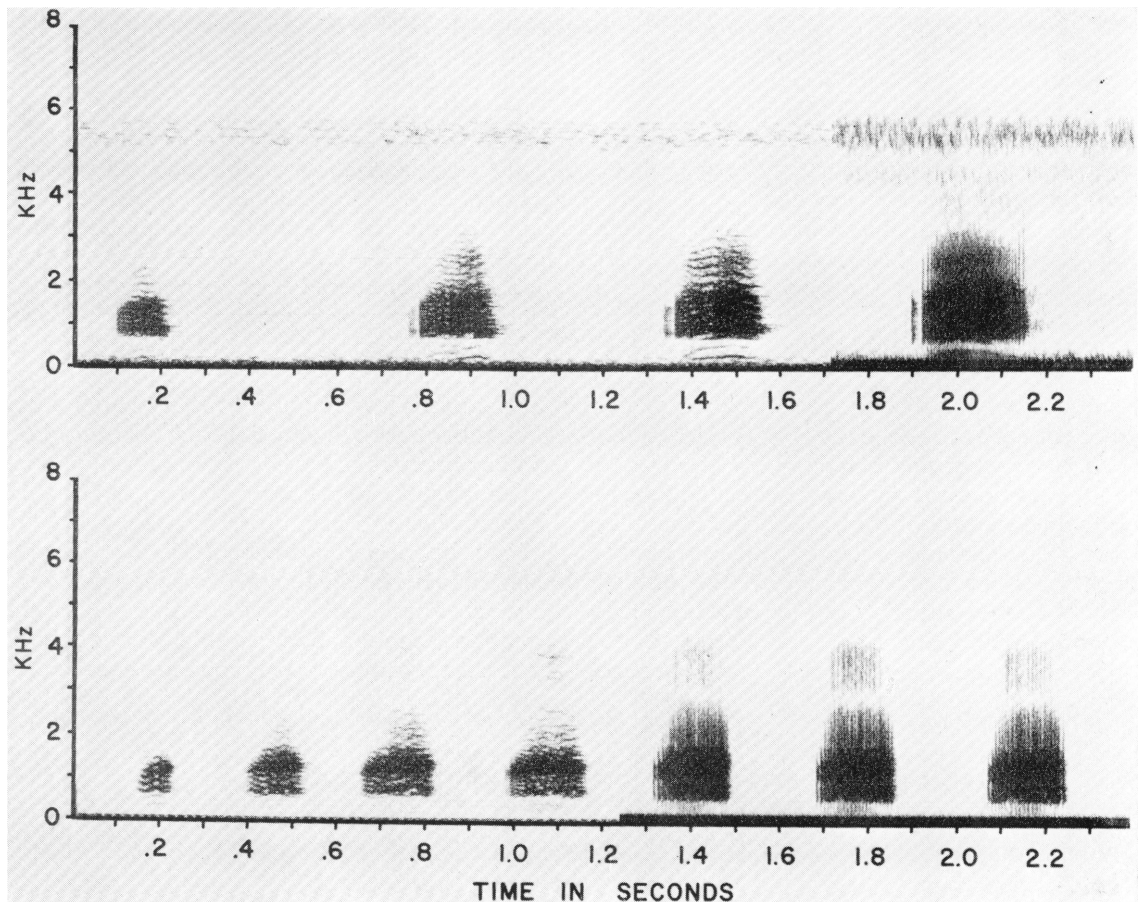


FIG. 52. Sound spectrograms of calls of *Phrynomantis*. *Upper*: Initial four notes of a five-note sequence uttered by *P. personata*, AMNH 74903 (holotype), recorded at Maprik, East Sepik District, on August 12, 1964, air temperature 24°C.; first three notes graphed with 45 Hz. filter, last with 300 Hz. filter. *Lower*: One complete call of *Phrynomantis robusta*, AMNH 82895, recorded 2 mi. NNW Alexishafen, Madang District, September 15, 1969, air temperature 24.7°C.; first four notes graphed with 45 Hz. filter, remainder with 300 Hz. filter.

number, with the frog [a male, 52 mm. in length] to the Hungarian National Museum. The eggs are typical frog eggs of comparatively large size, somewhat elliptical, in which the longer diameter amounts to 7 mm. but the shorter only to 6.5 mm. . . .

"The eggs of *Mantophryne robusta* are surrounded with a thin, golden-brown, horny covering; the connecting stalks are of the same character, and their longitudinal axes are repeatedly twisted (Plate IX, Fig. 7). The interior of each egg is filled with a liquid clear as water in which the embryo, about 5.5 mm. long and 4.5 mm. broad, floats. The embryo lies on the very large vitelline sphere in the form of a semicircle, so that the head and tail ends fall very close to one another. Clearly distinguished are: the large eyes, the four-fingered fore- and five-toed hindlimbs, the buccal cleft and very large tail, similar to an empty hemisphere. The limbs are quite normal in form; the hind limbs are folded crossed and pressed closely to the abdomen, the toe tips reach almost to the mouth opening and are completely covered by the tail (Pl. IX, Fig. 8). I can find no trace of external or internal gills; it is certain that the tail serves for respiration, as it shows a thick capillary net (Pl. IX, Fig. 9)."

MATING CALL: The call of this species, which I recorded twice near Alexishafen, is a series of five to seven very loud, harsh, croaking notes. The initial note in the series is shortest (ca. 0.1 second), and the subsequent notes are both louder and longer (to ca. 0.2 second). Intervals between notes are equal to or slightly longer than the notes themselves, so that sequences of five to seven calls occupy about 1.6 to 2.1 seconds. Calling is not regular or frequent, and usually at least a minute elapses between calls. Two individuals recorded called at fundamental frequencies of about 110 and 130 Hz., and the calls showed a slightly dominant band centered at about 1500 Hz. (fig. 52, lower).

DISTRIBUTION AND SPECIMENS EXAMINED: *Phrynomantis robusta* is widely distributed throughout New Guinea from the southeastern islands to the Vogelkop Peninsula (fig. 28). It ranges in elevation from virtually sea level to at least 1920 m. (6300 ft.).

West Irian: Aifat, Vogelkop Peninsula (RMNH, 1 uncatalogued specimen); Fak-fak (MCZ 2577, holotype of *Pomatops valvifera*); Djayapura [Hollandia] (AMNH 43695); Mi-

mika River (BMNH 1947.2.11.8, formerly 1913.10.31.349, holotype of *Liophryne kampeni*).

Territory of New Guinea: Madang District: 2 mi. NNW Alexishafen (AMNH 82895); 5 mi. N Alexishafen (AMNH 82894). Morobe District: Aregenang (AMNH 81061, 81062); Gevak, 4800 ft. (1460 m.) (AMNH 72554-72556); Kulolo Creek, Wau (BBM 3687-3689); Mindik (BBM 3690); Sarawaged Range, 1920 m. (6300 ft.) (BBM 1207-1212); Sattelberg (Lönnberg, 1900); Simbang, 60-80 m. (200-260 ft.) (Méhely, 1901, p. 225); Tewep, 4500 ft. (1370 m.) (AMNH 72557); Tumnang, 4400 ft. (1340 m.) (AMNH 74889; MCZ 28305). West Sepik District: Mt. Hunstein, 4000 ft. (1230 m.) (AMNH 77538, 77539); Busilmin (SAM 6384, 6406, 6407, 6415).

Territory of Papua: Central District: Mafulu, 1250 m. (4100 ft.) (AMNH 58188). Gulf District: Omati (MCZ 28196-28199). Milne Bay District: Goodenough Island, east slopes, 1600 m. (5250 ft.) (AMNH 56902); Misima (St. Aigan) Island (BMNH 1947.2.11.5-1947.2.11.7, formerly 93.3.31.9-93.3.31.11, syntypes of *Mantophryne robusta*). Western District: Aramia River (MCZ 28388); Didessa (SW 333); Derongo, 1300 ft. (390 m.) (MCZ 81685-81687); Bankim, 1200 ft. (370 m.) (MCZ 81688).

Phrynomantis slateri (Loveridge),
new combination

Figures 53, 54

Asterophrys slateri LOVERIDGE, 1955, p. 1 (type locality, "Omati, near Port Moresby, Papua" [Omati is in the Gulf District of the Territory of Papua, 20 mi. W Kikori and about 250 mi. NW Port Moresby]; holotype, MCZ 28205, collected by Kenneth R. Slater between January and April, 1954).

DIAGNOSIS: *Phrynomantis slateri* differs from all other *Phrynomantis* of the mainland of New Guinea in having finger discs that are broader than those of the toes, a character best measured by comparing the disc of the third finger to that of the fourth toe. One other species, *P. boettgeri* of Halmahera Island, Moluccas, has finger and toe discs similar to those of *slateri*; these species are compared below.

DESCRIPTION OF TYPE-SPECIMEN: The body is relatively heavy-set, with moderately broad head (HW/S-V=0.42), moderately long hind

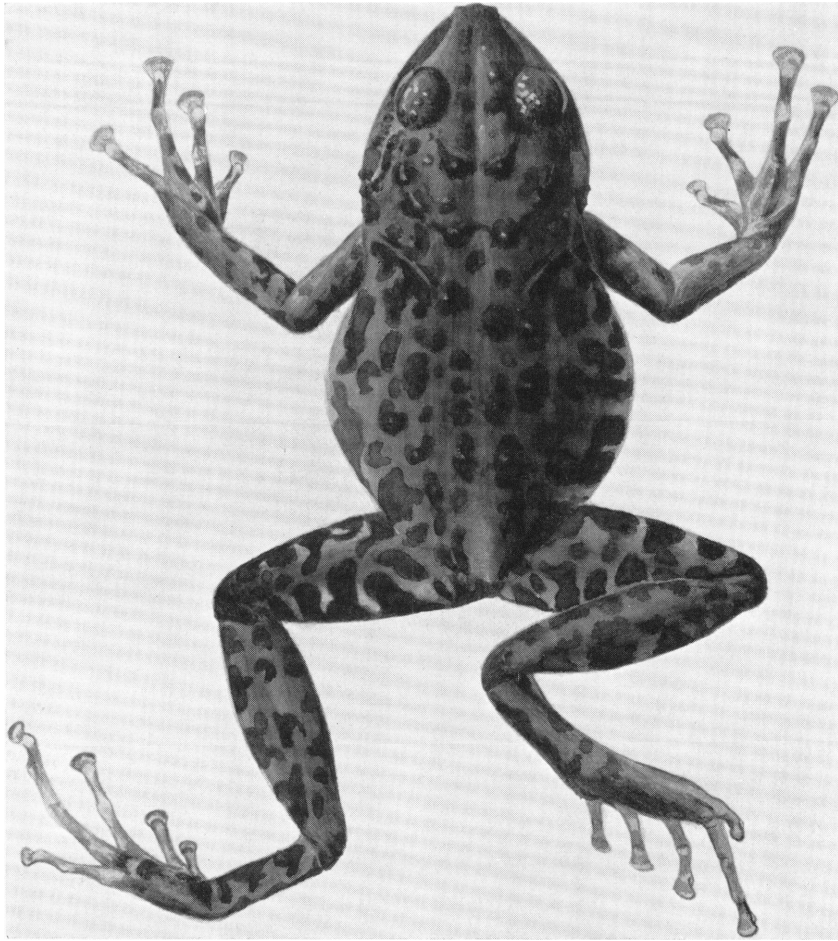


FIG. 53. *Phrynomantis slateri* (MCZ 28205, holotype), dorsal view. $\times 1.5$.

limbs ($TL/S-V=0.42$) and eyes of moderate size ($Eye/S-V, 0.101$). The internarial distance is slightly less than that from eye to naris ($E-N/IN=1.12$). The ear is not well marked externally, and its diameter is slightly more than half that of the eye ($EAR/Eye=0.58$). The loreal region is concave, the canthus rounded and the snout bluntly pointed. The snout projects only slightly beyond the lower jaw. The dorsal surface of the body bears low rounded warts that are neither numerous nor prominent enough to impart a pustulose appearance except on the eyelids where the warts are much denser. An indistinct ridge of skin over the tympanum does not continue past or behind it. The venter is smooth.

The relative lengths of the fingers are $3 > 4 > 2$

> 1 , of the toes, $4 > 3 > 5 > 2 > 1$. All fingers (fig. 27B) and toes bear well-developed discs with terminal grooves. The disc of the third finger is almost three times the width of the penultimate phalange, and that of the fourth toe more than twice. The disc of the fourth toe is 70 per cent of the width of that of the third finger. The hand bears prominent but smooth and rounded subarticular tubercles; those of the feet are similar in character but less prominent. There is a low, rounded inner metatarsal tubercle and an indistinct elevation in the place of the outer tubercle.

The dorsal surface of the body is purplish brown with irregular small, darker markings arranged in no definite pattern. The groin, anterior, and posterior surfaces of the thighs,

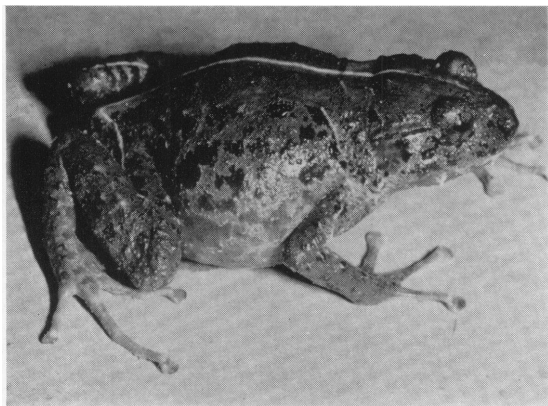


FIG. 54. *Phrynomantis slateri* (MCZ 81689). Photo by Fred Parker.

undersides of tibias, and anterior surfaces of the feet bear bold, dark markings outlined in a lighter reticulum. The ventral surfaces from chin to thighs (inclusive) are light brown with darker spots and a faint suggestion of a light reticulum. There are two light spots at the anterior edge of the chin where the mento-meckelian bones form slight projections beneath the skin.

The upper jaw is symphygnathine, the maxillae forming a firm suture. There are no projections on the vomers. There is a smooth anterior palatal fold followed by a serrate one bearing about 10 points.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 52.4; TL, 22.0; HW, 22.0; Eye, 5.3; E-N, 4.5; IN, 4.0; EAR, 3.1; disc of third finger, 2.8 (penultimate phalange, 1.0); disc of fourth toe, 2.1 (0.9).

The frog is an adult female with ova approximately 2 mm. in diameter.

VARIATION: Knowledge of this aspect of the biology of *Phrynomantis slateri* is inadequate, for there are only three specimens (recently captured by Fred Parker) in addition to the holotype. Variation in proportions is summarized in table 6). The color pattern of the holotype does not differ markedly from that seen in the other three specimens. The reticulate markings in the groin and on the underside of the hind legs are less pronounced in the new specimens, and two of these have light vertebral hairlines, but these are minor differences. In the characters important in the diagnosis and

definition of the species, especially the relative sizes of the finger and toe discs, there is complete agreement among the four specimens. The largest specimen measures 56 mm. snout to vent.

COMPARISON WITH OTHER SPECIES: The size of the finger discs relative to those of the toes sets *slateri* apart from all other *Phrynomantis* except *P. boettgeri*. Adequate comparison of the two is difficult because *boettgeri* is known only from the type-specimen, so nothing is known of the variation in this species. I examined the type-specimens of *P. boettgeri* and *P. slateri*, but have not compared the two directly. The skull has been removed from the type of *boettgeri*, so critical measurements of eye size and nostril position cannot be made accurately.

There is little of taxonomic use in the color patterns of the species. The close-set, large, vertically oval markings on the posterior surface of the thigh of *boettgeri* may be similar to the pattern of *slateri* in that region, as may the large, reddish brown spots on the side of the body.

The legs of *boettgeri* are distinctly longer than those of *slateri*, the ratios of tibia length to snout-vent length being, respectively, 0.52 and 0.37 to 0.42. A difference this great in sympatric populations could be of considerable significance, but because the samples come from remote localities, the possibility of geographic variation reduces the significance that may be attributed to the difference. The head width of *slateri* ($HW/S-V=0.37-0.42$) is not significantly different from that of *boettgeri* (0.37 by my measurement, 0.39 by the measurement published by Méhely).

Loveridge (1955, pp. 2, 3) recognized the greater leg length of *boettgeri* and its smaller size, and in addition distinguished *slateri* "in having a much longer (not shorter) snout [and] an interorbital space that is one and one-third times as broad as (instead of equal to) an upper eyelid." The condition of the type-specimen of *boettgeri* did not permit me to make measurements that would verify the alleged differences. Presumably Loveridge's comparisons are based on the original description of *boettgeri* (Méhely, 1901).

Insofar as morphology provides evidence, there is not a strong case for maintaining *slateri* and *boettgeri* as distinct species. The geographical situation, however, makes it seem more likely that two species are involved. Even allowing for the poor knowledge of distribution of most Papuan frogs, it is unlikely that a species

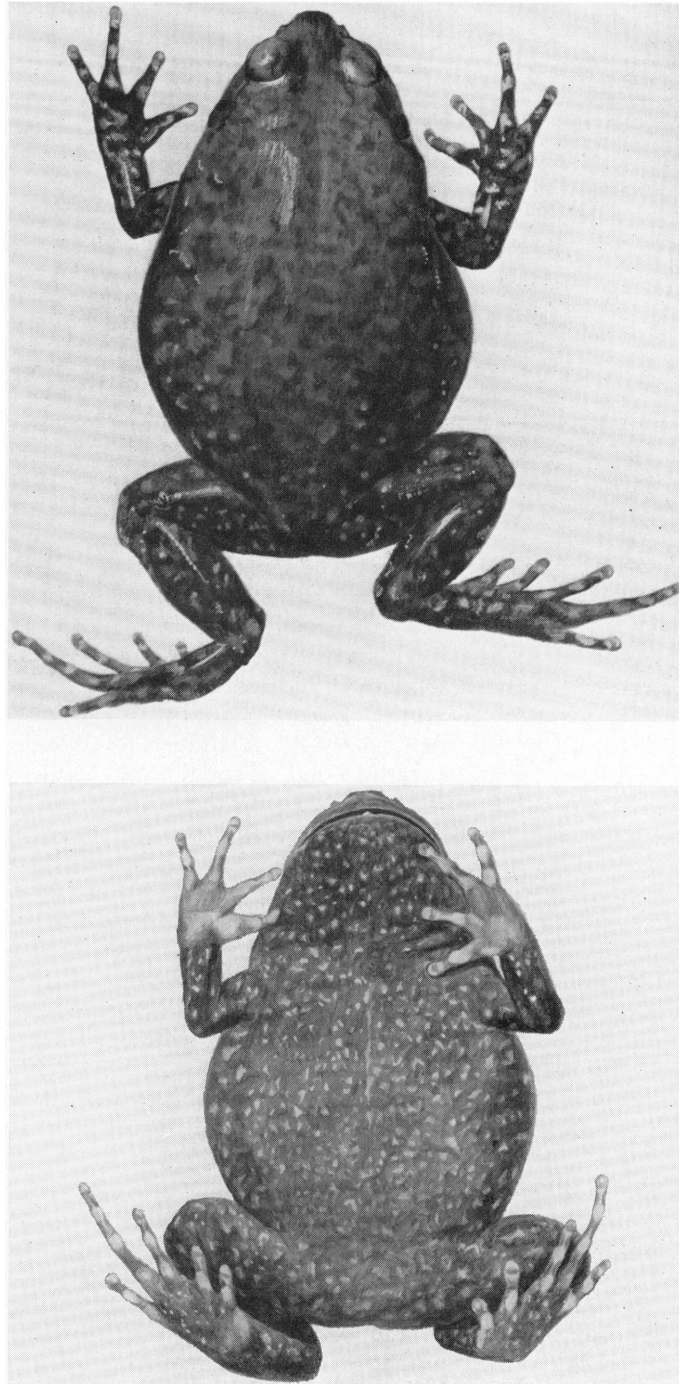


FIG. 55. *Phrynomantis stictogaster* (AMNH 74895, holotype), dorsal (upper) and ventral (lower) views. $\times 1$.

would be known only from localities 1000 miles apart. This is especially true when one of the localities lies in the Moluccas, a group of islands with a highly endemic fauna. Loveridge (1955, p. 2) recognized the similarity of *slateri* to *boettgeri* and suggested "Possibly it is only racially distinct." I do not think that anything would be gained by reducing *slateri* to subspecific status.

Phrynomantis slateri is similar in some respects to *P. eurydactyla*; the two are compared in the account of the latter species.

DISTRIBUTION AND SPECIMENS EXAMINED: *Phrynomantis slateri* is known from only two localities in southern New Guinea, in the territory of Papua (fig. 36). Undoubtedly, the range extends westward in West Irian, for one of the localities of capture lies within 10 mi. of the boundary.

Territory of Papua: Gulf District: Omati (MCZ 28205, holotype). Western District: Derongo (MCZ 81689, 81691; AMNH 84590).

***Phrynomantis stictogaster*, new species**

Figures 55, 56

HOLOTYPE: AMNH 74895, an adult female, obtained from native collectors by F. Parker, G. Sluder, and R. Zweifel at Irumbofoie, elevation ca. 6600 ft. (2010 m.), 9 mi. S and 10 mi. W Goroka, Eastern Highlands District, Territory of New Guinea, on July 11, 1964.

PARATYPES: AMNH 74891–74901 and MCZ 59511–59515, all from the type locality, and specimens from the following localities: Eastern Highlands District: Orumba, 8 mi. S, 6 mi. W

Goroka, 7000 ft. (2130 m.) (AMNH 74890, 76468; MCZ 59521–59526); Yaveyufa (AMNH 76465, 76466; MCZ 59517–59520, 59527); Nivi (AMNH 76467, MCZ 59516); northeast slopes of Mt. Michael, 6500 ft. (1980 m.) (AMNH 66514); Lufa, Mt. Michael, 7000 ft. (2130 m.) (MCZ 59529, 59530, 59908–59918); Moife, Kainantu (BBM 1002, 1003); Arau, Kratke Mountains, 4600 ft. (1400 m.) (AMNH 66683); Arona, Kassam Pass (AMNH 66924); Awande, 6300 ft. (1920 m.) (AMNH 77027, 77028); Okapa (MCZ 59531, 59532); Purosa (MCZ 81693, 81694). Chimbu District: Igindi (MCZ 59528). Western Highlands District: Banz (AMNH 68125–68129); Lake Iviva (Sirunki), 2580 m. (8460 ft.) (BBM 1019). Morobe District: Bulldog Road, 10 mi. S Edie Creek, 2500 m. (8200 ft.) (AMNH 84514); Edie Creek, 8000 ft. (2440 m.) (BBM 2546).

DIAGNOSIS: This large species, (up to 80 mm. snout to vent), is distinguished from all other *Phrynomantis* by the presence of a small ridge or tubercle situated between the eye and the nostril (fig. 57). In addition, it differs from other large species in that the tips of the fingers and toes are not expanded into discs and lack terminal grooves (fig. 51G).

DESCRIPTION OF HOLOTYPE SPECIMEN: A heavy-bodied frog with the head narrower than the body (HW/S-V, 0.38) and with relatively short hind limbs (TL/S-V, 0.31). The snout is bluntly rounded and shorter than the moderately large eye (Eye/S-V, 0.09); the width of the eyelid equals the interorbital distance. The nostrils are lateral and near the end of the snout with the openings scarcely visible from directly

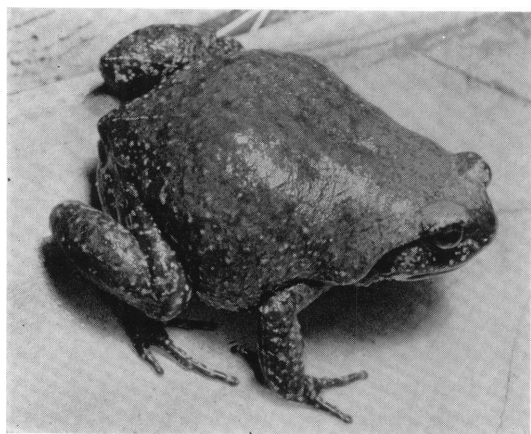


FIG. 56. *Phrynomantis stictogaster* (AMNH 76468).



FIG. 57. *Phrynomantis stictogaster*, side of head to show loreal tubercle.

above. The internarial distance is slightly greater than the distance from eye to naris (E-N/IN, 0.86). The canthus is straight and bluntly rounded. The loreal region slopes slightly and is indented beneath a prominent tubercle situated midway between eye and naris that points toward the naris (fig. 57). The tympanum is visible but not prominent and is about two-thirds of the diameter of the eye. A weak fold of skin passes from the posterior corner of the eye above the upper edge of the tympanum and becomes indistinct behind it. There are no other skin folds. The dorsal surface of the body is faintly textured, but the ventral surfaces are smooth.

The tips of the fingers and toes are bluntly rounded, without terminal grooves, and are scarcely broader than the penultimate phalanges (fig. 51G). The relative lengths of the fingers are $3 > 4 = 2 > 1$, of the toes, $4 > 3 > 5 > 2 > 1$. There are low, rounded subarticular tubercles on hands and feet. The inner metatarsal and inner metacarpal tubercles are the only other elevations present, and these are indistinct.

The ground color of the dorsal surfaces is (in preservative) light purplish brown. Darker variegations are present and are most prominent on the lower back, sides, and hind legs. There is light spotting on the same areas. The side of the head from snout through ear region is darker brown. The ventral ground color is brown, darker than that of the dorsum. All ventral surfaces except the palms (which are gray) are covered with numerous tiny white spots; even the soles, which have a somewhat lighter ground color, show these spots.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 72.2; TL, 22.7; HW, 27.3; Eye, 6.8; E-N, 4.5; IN, 5.2; EAR, 4.5; tip of third finger, 1.5 (penultimate phalange, 1.4); tip of fourth toe, 1.6 (1.5).

The frog is gravid with ova 5 mm. in diameter.

VARIATION IN THE TYPE SERIES: The paratypes show no unusual variation in proportions, so no discussion is needed to supplement the data tabulated (table 6).

There is little variation in dorsal patterns. A juvenile from Lake Sirunki has a nearly uniform dorsum. Specimens from Banz have more lichen-like dorsal markings, with the darker pigment predominating, but individuals from other areas more closely resemble the holotype.

There is some indication of geographic variation in the pattern of the ventral surfaces. The

pattern of the westernmost specimen, the juvenile from Lake Sirunki cannot clearly be distinguished, but appears to be coarsely mottled. Four specimens from Banz have a fine reticulum and the fifth is coarsely mottled. All specimens from the central part of the range around the type locality closely resemble the type in having numerous tiny, light spots on a dark background. The one from Arau in the Kratke Mountains resembles the holotype, but others from the eastern part of the range (Arona, Moife, Awande, Purosa, and south of Edie Creek) are boldly mottled beneath or have larger, irregular spots.

In life, a paratype from Orumba (AMNH 74890) had a yellowish brown ground color on the anterior part of the head and eyes, gradually darkening posteriorly and laterally on the body to virtually black on the hind limbs and the sides of the body. The side of the face was black with white spots. Light greenish flecks mixed with smaller white ones on the limbs and sides of the body. The chin was dark brown with white spots, the rest of the venter slightly lighter brown with abundant white spots. The iris was dark brown.

The largest specimens are two males from Awande with snout to vent lengths of 80 mm.

The tongue has a median furrow and posterior depression and is only slightly free behind. Smooth anterior and serrate posterior palatal ridges are present. The male possesses a median, subgular vocal sac (not particularly evident externally) with openings in the floor of the mouth beside the angles of the jaws. The upper jaw is strongly symphygnathine (fig. 2) and the pectoral girdle lacks clavicles and procoracoids.

Charles J. Cole (personal commun.) used the testicular squash technique to determine the haploid chromosome number of a male paratype (AMNH 74898) to be 13. This was reported by Cole and Zweifel (1971) under the name *Asterophrys* sp.

COMPARISON WITH OTHER SPECIES: *Phrynomantis stictogaster* most closely resembles *P. robusta*, *P. glandulosa*, *P. humicola*, and *P. wilhelmana*, and its evolutionary relationships probably lie within this group. The unique character of the loreal tubercle sets *stictogaster* apart, although the relatively small size of the eyes and the absence of digital expansions and grooves suggest that the closest relationship may be with *wilhelmana* and *glandulosa*.

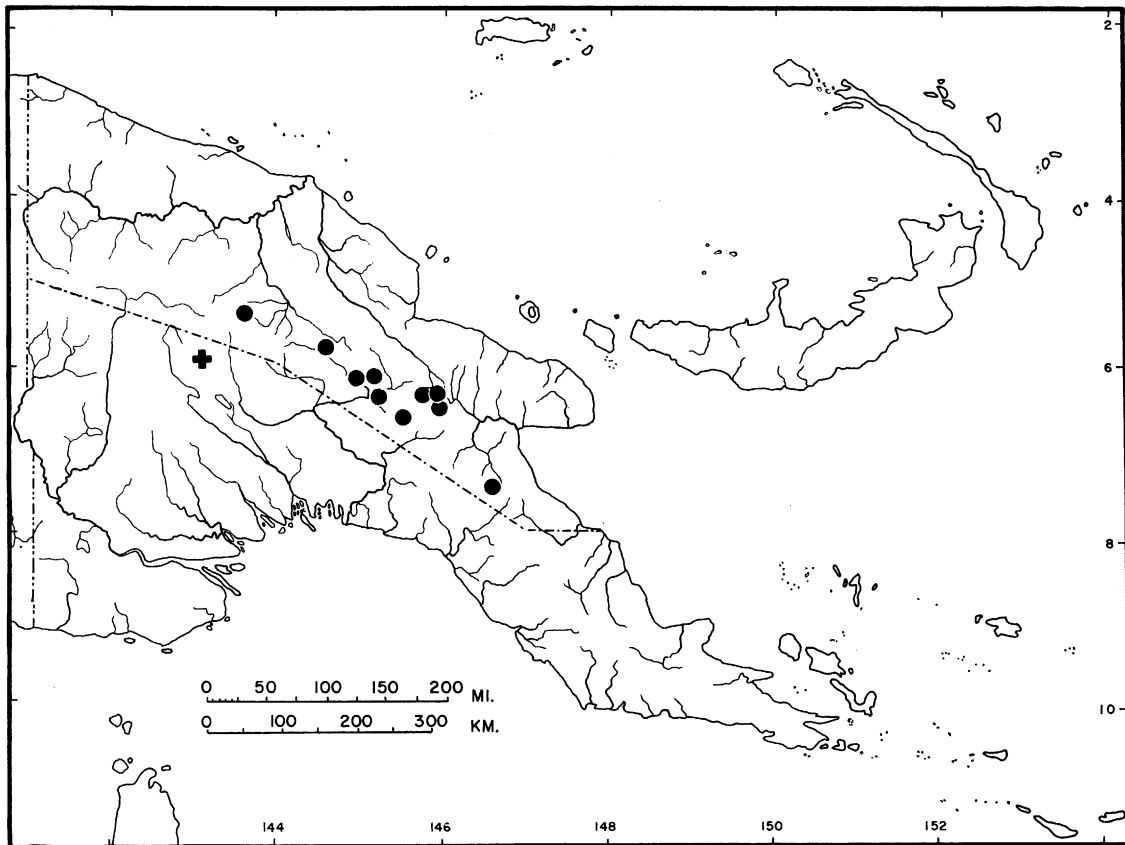


FIG. 58. Distribution of *Phrynomantis glandulosa* (cross) and *P. stictogaster* (closed circles).

ECOLOGICAL NOTES: The type locality, the native village of Irumbofoie, is situated on a mountain ridge in secondary grassland. This would appear to be unsuitable habitat for a large *Phrynomantis*, and I suspect that the native collectors obtained the frogs in forest nearby. Undoubtedly it is a terrestrial species. A collector who brought in a gravid female and an adult male found them occupying the same hole in the ground. The full complement of enlarged ova (diameter 4 mm.) in another female was 44.

ETYMOLOGY: The specific name is from the Greek *stictos* (spotted) and *gaster* (belly).

DISTRIBUTION AND SPECIMENS EXAMINED: The range of *Phrynomantis stictogaster* is in mountainous areas of the Territory of New Guinea, from the vicinity of Wau (10 mi. S Edie Creek) westward to Lake Iviva (Sirunki), west of Mt. Hagen at elevations of about 4600–8200 ft. (1400–2600 m.) (fig. 58). In addition to the

specimens listed as holotype and paratypes, I examined briefly several in the collection of the South Australian Museum from Okapa and Aiyura, Eastern Highlands District.

Phrynomantis wilhelmana (Loveridge),
new combination

Figure 59

Asterophrys pansa wilhelmana LOVERIDGE, 1948, p. 419 (type locality "Mount Wilhelm, 8000 feet, Bismarck Range, Madang Division, Australian New Guinea [Chimbu District, Territory of New Guinea]"; holotype, MCZ 25910, collected by Captain P. J. Darlington in October, 1944).

Asterophrys wilhelmana: ZWEIFEL, 1956, p. 9.

DIAGNOSIS: *Phrynomantis wilhelmana* differs from all congeneric species except *P. glandulosa* and *P. stictogaster* in that the tips of the fingers and toes are bluntly rounded without flattened, expanded

discs and terminal grooves. *Phrynomantis stictogaster* is much larger than *wilhelmana* (up to 80 mm. compared to 58 mm. snout to vent) and has a characteristic tubercle between the eye and the nostril. *Phrynomantis glandulosa* has a mottled rather than uniform belly, and a conspicuous glandular fold over and behind the tympanum.

DESCRIPTION: This description is based on specimens from Mt. Wilhelm in the general vicinity of the type locality.

Phrynomantis wilhelmana is a chunky, short-legged frog with the body distinctly wider than the head. The maximum length is approximately 58 mm. snout to vent. Variation in selected proportional measurements is presented in table 6. The snout is bluntly rounded and the nostrils are lateral but tilted slightly upward and are visible from the dorsal view. The nostrils are slightly closer to the tip of the snout than to the eye. The canthus rostralis is rounded. The loreal region directly anterior to the eye is slightly concave but is slightly convex above this region between the nostril and the anterior corner of the eye. An eyelid is about equal in width to the interorbital space, and the length of the eye is

about equal to that of the snout. The tympanum may be visible but often is hidden. A weak fold of skin passes from the posterior corner of the eye above the tympanum and then obliquely down to the arm. There are two palatal folds, the anterior smooth and the posterior serrate (fig. 4).

The fingers have bluntly rounded tips without terminal grooves (fig. 51H). The subarticular tubercles are low, rounded elevations and metacarpal tubercles are scarcely evident. The relative lengths of the fingers are $3 > 4 = 2 > 1$, of the toes, $4 > 3 > 5 > 2 > 1$. The toes also have bluntly rounded tips without terminal grooves and with inconspicuous subarticular tubercles. Only a faint trace of an inner metatarsal tubercle is present.

The dorsal surfaces are uniform slaty purple. There is no pattern except for a black spot covering the cloacal opening and an indistinct dusky line that commences at the posterior corner of the eye and passes posteriorly and downward over the tympanum; the upper border of this line coincides with the edge of the tympanic fold. The ventral surfaces from chin to hind feet resemble the dorsum in uniformity, but typically are slightly paler. There is no distinct line of demarcation between dorsal and ventral color.

VARIATION: There appears to be little variation in proportions (table 6). Average tibia length is slightly greater in the sample from Kup in the Kubor Mountains, but the size of the sample is small, and the range of variation is within that seen elsewhere.

Frogs from Mt. Wilhelm are remarkably uniform in color pattern, and the description given in the foregoing section could serve adequately for almost all of more than 100 specimens examined. I noted the following variations: The dark postocular stripe is never too distinct and may be absent. The ventral surfaces are usually paler than the dorsal, but a few individuals are virtually the same dorsally and ventrally. Two individuals had pale venters with small, irregular spots from chin to hind legs. Mottling or spotting in other specimens generally is confined to the hind legs and the posterior part of the abdomen. One peculiar specimen has the chin, chest, and legs typically dark, but the abdomen is pale with scarcely any dark pigment. Only two individuals show significant variation in dorsal pattern. In one, the

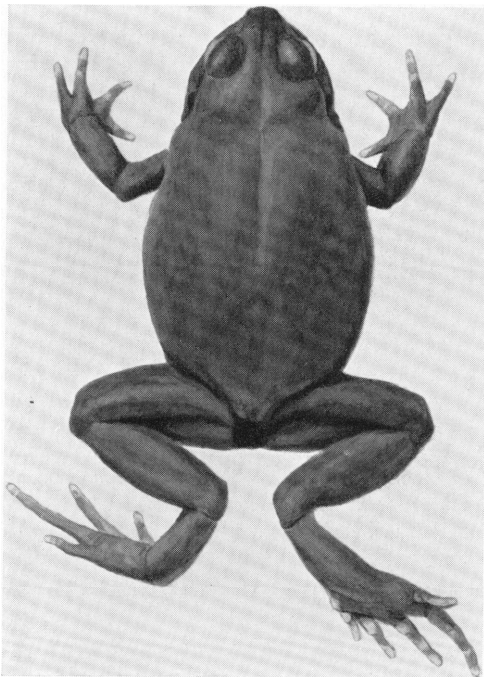


FIG. 59. *Phrynomantis wilhelmana* (AMNH 65868), dorsal view. $\times 1.25$.

background color is slightly paler than usual and numerous dark flecks are visible. The other specimen has the hind legs conspicuously mottled and irregular yellow spotting on the posterior part of the back.

The samples from Daulo Pass and Kotuni (Mt. Otto) east of Mt. Wilhelm do not differ significantly in pigmentation from topotypes from Mt. Wilhelm except that the dark postocular marking is in general less well developed. Frogs from localities south and southwest of Mt. Wilhelm are quite similar to the northern and northeastern specimens in dorsal pigmentation, but are commonly much paler beneath. Occasional individuals are as dark beneath as the typical Mt. Wilhelm specimens, and even the palest frogs have relatively uniform ventral pigmentation without conspicuous mottling.

I have examined four specimens of this species from the Wahgi Dividing Range west of Mt. Wilhelm. Two have the dorsal coloration typical of *P. wilhelmana* and have relatively dark ventral surfaces in which a trace of mottling can be detected. The collector of the two specimens, William Hosmer, noted that in life one was "uniform dark brown above, lighter below." The other two specimens are part of a series reported by Tyler (1963, pp. 15–17) as *wilhelmana*, but which actually includes both *P. humicola* and *P. wilhelmana*. One of these frogs, BMNH 1961.840, is a large female (52 mm. S-V) with the dorsal surfaces of body and limbs mottled with dark brown and pale yellow, the brown dominating. The other specimen, BMNH 1961.841, a male 44 mm. snout to vent, is mottled similarly on the head and anterior part of the body, but the posterior dorsal area is pale yellow with a few scattered, irregular dark spots. The ventral surfaces of both specimens are relatively dark but slightly more mottled than is usual in *wilhelmana*. The color patterns of these two specimens are unique among *wilhelmana* I have examined, but are approached by that of one specimen from Mt. Wilhelm described above. In morphology the four specimens from the Wahgi Dividing Range are good *wilhelmana* and agree with topotypes in the important characters of eye size (Eye/S-V less than 0.100 in three adults) and lack of digital discs.

Specimens from near the western edge of the known range in the vicinity of Tambul were uniform reddish brown dorsally in life. The ventral surfaces were mostly uniform, paler

brown with more of an orange tint and with a few pale, purplish brown splotches on the throat. A specimen from Kaguba on Mt. Giluwe, differed in being dark olive-green rather than brown dorsally.

COMPARISON WITH OTHER SPECIES: If the state of the finger and toe tips—both not expanded into discs and both lacking terminal grooves—is taken into consideration, *Phrynomantis wilhelmana* should not easily be confused with most other species. Only *P. glandulosa* and *P. stictogaster* lack discs and grooves; see the foregoing diagnosis for comparisons and refer to the account of *P. glandulosa* for additional information.

At some localities *P. wilhelmana* is sympatric with, and bears a superficial similarity to, *P. humicola*. On first examining a large, mixed sample from Mt. Otto, I noted that the frogs were divisible into two groups: one with uniformly colored ventral surfaces as in *wilhelmana* from Mt. Wilhelm, the other (described herein as *P. h. humicola*) with mottled venters. Closer examination revealed that the mottled frogs had longer legs and larger eyes (table 6), and differed with respect to the digital discs as well. In other localities *P. wilhelmana* may have a slightly mottled venter, but the structural differences remain.

TAXONOMIC NOTES: Loveridge (1948) described *wilhelmana* as *Asterophrys pansa wilhelmana* and also regarded *Asterophrys minima* (= *Xenorhina minima*) as a subspecies of *pansa*. Zweifel (1956) showed that *Aphantophryne pansa* Fry is not an asterophryine but is referable to the spheophryne genus *Cophixalus*, and considered *minima* and *wilhelmana* as full species.

ECOLOGICAL NOTES: The majority of specimens of *Phrynomantis wilhelmana* obtained on Mt. Wilhelm by the Sixth Archbold Expedition were acquired from native collectors, but notes accompanied some frogs captured by members of the expedition. Fourteen specimens found at the Pengagl Creek Camp, elevation 9100 ft. (2770 m.), were recorded as "under log," and four others as in "humus in forest." Brass (1964) gave a comprehensive description of this camp, which was in dense primary forest. A specimen found in "woods" about 2 miles east of Lake Aunde on Mt. Wilhelm at an estimated elevation of 3400 m. (11,150 ft.) comes from the highest elevation known for the species. The expedition captured

numerous *Sphenophryne brevicrus* but no *P. wilhelmana* in grassland around Lake Aunde at 11,700 ft. (3560 m.), which suggests that *wilhelmana* does not range above the upper altitudinal limits of forest. The type series was found "beneath logs in the forest at 8,000 feet" (Loveridge, 1948, p. 419).

I have collected this species only at the western edge of its range, near Kaguba on the west slope of Mt. Giluwe, and near Tambul north of that mountain. One individual was at an elevation of 8900 ft. (2710 m.) beneath a tree fern log in an area from which most of the large forest trees had been removed but where many tree ferns, pandanus, and much scrambling bamboo grew. Other frogs were beneath logs (daytime temperatures 14.4° and 15.5°C.) in unshaded, grassy sites near the edge of the forest at 8300 ft. (2530 m.). One found at night was at the mouth of a burrow in a deforested area shaded only by tall cane grass, elevation 7300 ft. (2230 m.).

One of the specimens found "under log" on Mt. Wilhelm on July 12, 1959, was "with eggs." Presumably the frog, AMNH 65866, was closely associated with the eggs (frog and eggs were preserved together), but whether the association was fortuitous or the frog, a male, was actually "guarding" the eggs cannot now be determined. There were 15 eggs in the group, each about 6.5 mm. in diameter. Each of the eggs bears two cordlike projections. Probably prior to preservation, the eggs were joined in a beadlike string such as Méhely (1901, pl. 9) illustrated for *Phrynomantis robusta*. The eyes of the embryos are conspicuous, and the head region and blood vessels radiating from it bear melanic pigment. Both front and hind limbs are evident, the latter better developed. The tail is relatively small, about twice as long as a hind limb, with the fins not conspicuously widened. I can find no trace of gills. Méhely (1901, pl. 9) shows the later embryo of *P. robusta* with a broad, highly vascular tail that presumably serves as an organ of

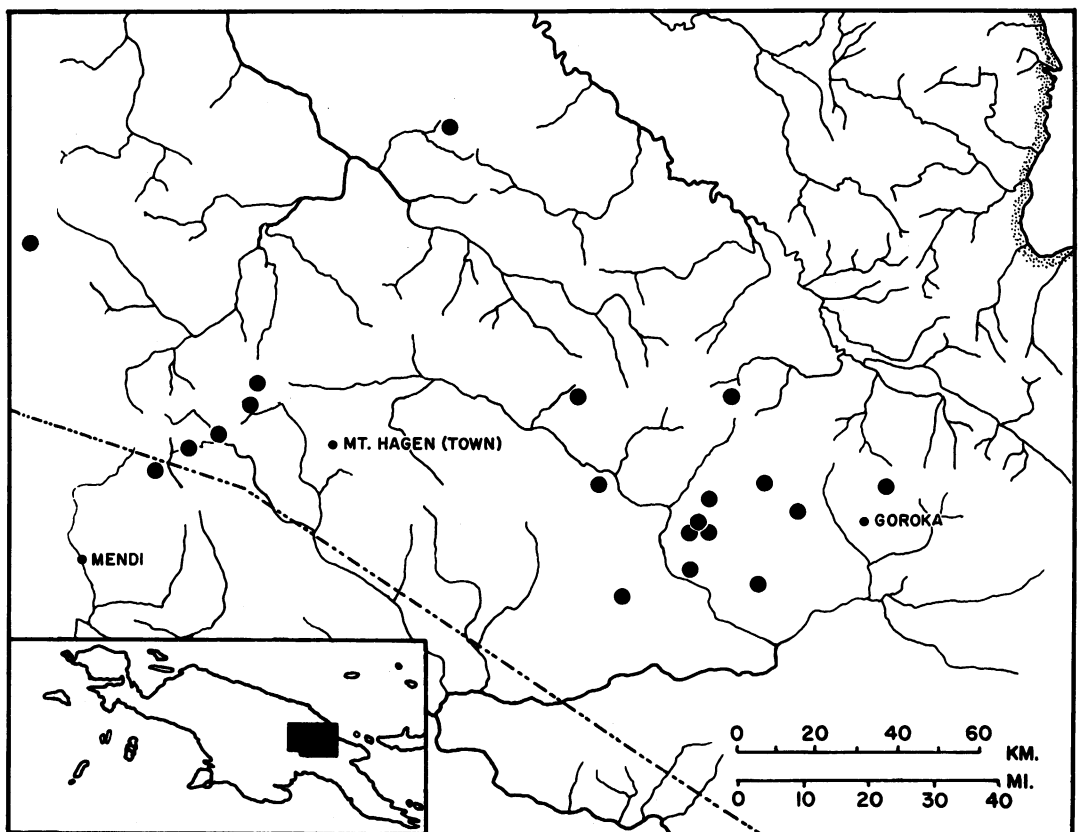


FIG. 60. Distribution of *Phrynomantis wilhelmana*.

respiration. Perhaps the tail of *P. wilhelmana* increases in size later in embryonic growth.

Tyler (1961, p. 220; 1963, p. 16) briefly described eggs that he attributed to *P. wilhelmana*, but they may not be of that species; see the account of *P. humicola compta*.

MATING CALL: The call I attribute to this species consists of two or three low-pitched croaks followed by up to several minutes of silence before repetition. I heard this call on several occasions in the vicinity of Tambul and once was able to associate it with a fair degree of certainty with a *wilhelmana* found sitting in the mouth of a burrow. I did not, however, actually see the animal call or tape-record it.

DISTRIBUTION AND SPECIMENS EXAMINED: *Phrynomantis wilhelmana* has been found in the Southern Highlands, Eastern Highlands, Western Highlands, and Chimbu districts of the Territories of Papua and New Guinea, from Lake Sirunki and Mt. Giluwe on the west to Mt. Otto in the east (fig. 60). The airline distance between the extremes is about 135 miles. Reliable data on elevation are not available for many specimens, but probably all came from above 7000 ft. (2130 m.), maximum, ca. 11,150 ft. (3400 m.). Throughout much of the region where these frogs have been collected, secondary grassland replaces forest at lower elevations. Under undisturbed conditions the species may range to lower elevations than now known.

Territory of New Guinea: Chimbu District: east slopes of Mt. Wilhelm, 8000–9000 ft. (2440–2740 m.) (AMNH 65866, 65868–65886 + 20 untagged specimens, 65887–65908 + 7 untagged specimens, 65909–65919, 84444); east slopes of Mt. Wilhelm, Pengagl Creek, 9100 ft. (2770 m.) (AMNH 65920–65928 + 6 untagged specimens, 78903); east slopes of Mt. Wilhelm, 2 mi. E Lake Aunde, 3400 m. (11,150 ft.) (AMNH 65867); Mt. Wilhelm, 8000 ft. (2440 m.) (MCZ 25910, holotype; MCZ 25911–25913, 25915–25917, paratypes; AMNH 58668, 58669, paratypes; MCZ 64412–64417, 64275–64289); Mt. Wilhelm, Dengaigu, 2500 m. (8200 ft.) (BBM 1016, 1017); Dumun (AMNH 76961; MCZ 53014, 53015, 53019–53024, 53030–53034, 64410); Nondiri Pass (AMNH 76962; MCZ 53057, 53058); Mt. Kerigomna (AMNH 76965; MCZ 79943); Masul (MCZ 53036); Igindi (AMNH 79964; MCZ 60805, 60806, 60808); Sikuri Pass (MCZ 53041, 53045, 53046); Derim (MCZ 53062–53065, 53067, 53068, 53070, 53072,

53074, 53075); Niglguma (MCZ 59902); Kubor Mountains, Kup (MCZ Y26301–Y26303, 60809–60814, 79930–79942); Mt. Elimbari (MCZ 59906, 59907); Koge (MCZ 59891–59896). Eastern Highlands District: Kotuni, Mt. Otto, 7000–8000 ft. (2130–2440 m.) (AMNH 66280–66294, 76463); Daulo Pass (MCZ 52927, 52947, 52952, 52967, 52969, 52982, 52987, 52988, 52991, 52995, 52997, 59883). Western Highlands District: Wahgi Dividing Range, Mt. Pollam, 8170 and 9000 ft. (2490 and 2740 m.) (AMNH 65319, 65320); Wahgi Dividing Range near Nondugl, 9500 ft. (2900 m.) (BMNH 1961.840, 1961.841); Mt. Hagen, 8000 ft. (2440 m.) (AMNH 56261); Schrader Mountains, 8000–8500 ft. (2440–2590 m.) (UPNG 839–847); 8–9 mi. (road) SW Tambul, 8300–8400 ft. (2530–2560 m.) (AMNH 82896, 82897, 82900); vic. Tambul, 7300 ft. (2230 m.) (AMNH 82898, 82899); Tomba, 8200 ft. (2500 m.) (MCZ 64272); Lake Sirunki, 2580 m. (8460 ft.) (BBM 3031).

Territory of Papua: Southern Highlands District: 1 mi. SE Kaguba, Mt. Giluwe, 8900 ft. (2710 m.) (AMNH 82901); Mt. Giluwe, 2550 m. (8370 ft.) (BBM 3029).

GENUS *XENOBATRACHUS* PETERS AND DORIA

Xenobatrachus PETERS AND DORIA, 1878, p. 432 (type-species by monotypy, *X. ophiodon* Peters and Doria). *Choanacantha* MÉHELÿ, 1898, p. 175 (type-species by monotypy, *C. rostrata* Méhelÿ).

DIAGNOSIS: *Xenobatrachus* differs from all other asterophryine genera in possessing one or two prominent toothlike spikes on each vomer. This is the only feature in which *Xenobatrachus* and *Xenorhina* differ. *Barygenys* resembles *Xenobatrachus* in external appearance, but has the eleutherognathine condition of the upper jaw. Most *Barygenys* may be distinguished from *Xenobatrachus* without recourse to dissection by noting the vertical snout ridges of the former. *Asterophrys*, *Pherohapsis*, and *Phrynomantis* resemble *Xenobatrachus* in being symphygnathine but differ in a number of ways in addition to the vomerine spikes as follows: nasal bones fused and rugose in *Asterophrys* and *Pherohapsis*; frontoparietal crest present in *Asterophrys*; squamosal-maxillary contact and squamosal-frontoparietal contact in *Pherohapsis*; eye relatively larger in *Phrynomantis* (Eye/S-V rarely as low as 0.09 in *Phrynomantis*,

TABLE 8
BODY PROPORTIONS IN ELEVEN SAMPLES OF THE GENUS *Xenobatrachus*

| Sample | N | TL/S-V | | | HW/S-V | | | Eye/S-V | | | E-N/IN | | |
|-----------------------------------|-----------------|-------------------|-------------|---------------|-------------------|-------------|---------------|-------------------|---------------|---------------|------------------|-------------|---------------|
| | | Mean | Range | $\pm\sigma_m$ | Mean | Range | $\pm\sigma_m$ | Mean | Range | $\pm\sigma_m$ | Mean | Range | $\pm\sigma_m$ |
| <i>X. bidens</i> | 3 | 0.418 | — | — | 0.313 | — | — | 0.070 | — | — | 1.28 | — | — |
| <i>X. giganteus</i> | 2 | 0.335 | — | — | 0.390 | — | — | 0.065 | — | — | 1.00 | — | — |
| <i>X. macroptera</i> ^a | 9 | 0.436 \pm 0.008 | (0.40-0.47) | — | 0.343 \pm 0.009 | (0.31-0.39) | — | 0.085 \pm 0.005 | (0.073-0.111) | — | 1.07 \pm 0.015 | (1.00-1.15) | — |
| <i>X. mehelyi</i> | 11 | 0.400 \pm 0.007 | (0.37-0.43) | — | 0.338 \pm 0.008 | (0.29-0.37) | — | 0.073 \pm 0.001 | (0.066-0.082) | — | 1.31 \pm 0.046 | (1.11-1.58) | — |
| <i>X. obesus</i> | 34 ^b | 0.533 \pm 0.003 | (0.49-0.57) | — | 0.354 \pm 0.003 | (0.33-0.39) | — | 0.060 \pm 0.001 | (0.054-0.069) | — | 0.93 \pm 0.010 | (0.84-1.04) | — |
| <i>X. ocellatus</i> | 9 ^c | 0.332 \pm 0.013 | (0.28-0.38) | — | 0.357 \pm 0.003 | (0.33-0.39) | — | 0.080 \pm 0.002 | (0.071-0.088) | — | 1.02 \pm 0.035 | (0.87-1.11) | — |
| <i>X. ophiodon</i> | 1 | 0.49 | — | — | 0.34 | — | — | 0.11 | — | — | 0.90 | — | — |
| <i>X. rostratus</i> | 4 | 0.349 | — | — | — | — | — | 0.062 | — | — | 1.31 | — | — |
| North Coast | 60 | 0.264 \pm 0.002 | (0.23-0.33) | — | 0.362 \pm 0.002 | (0.32-0.39) | — | 0.074 \pm 0.001 | (0.064-0.084) | — | 1.27 \pm 0.011 | (1.00-1.47) | — |
| Huon Peninsula | 29 | 0.283 \pm 0.003 | (0.23-0.32) | — | — | — | — | 0.063 \pm 0.001 | (0.050-0.071) | — | 1.08 \pm 0.012 | (0.95-1.22) | — |
| Western Highlands | 21 | 0.248 \pm 0.002 | (0.23-0.27) | — | — | — | — | 0.058 \pm 0.001 | (0.054-0.063) | — | 1.04 \pm 0.012 | (0.95-1.16) | — |
| Eastern Highlands | | | | | | | | | | | | | |

^aOne specimen from Weyland Ranges excluded; see text.

^bN = 34 for TL/S-V only; HW/S-V, 33; Eye/S-V, 27; E-N/IN, 32.

^cFor Eye/S-V only, N = 8.

rarely that high in *Xenobatrachus*); parasphenoid anteriorly less than half width of frontoparietals in *Phrynomantis*, wider in *Xenobatrachus*).

CONTENT: I recognize eight species: *X. bidens* (van Kampen); *X. giganteus* (van Kampen); *X. macrops* (van Kampen); *X. mehelyi* (Boulenger); *X. obesus* Zweifel; *X. ocellatus* (van Kampen); *X. ophiodon* Peters and Doria, and *X. rostratus* (Méhely). In addition to these, I discuss specimens that may represent undescribed species.

DESCRIPTION: Frogs of this genus show a wide range of adult sizes, from a snout to vent length of 29 to 30 mm. in *bidens* and *ophiodon* to 90 mm. in *giganteus*. The morphology is much the same in all: body stout to quite rotund; head relatively narrow; eyes small (Eye/S-V, 0.09 or less in all but one species); toes with small terminal discs; finger tips not or scarcely expanded; subarticular, palmar, and plantar tubercles virtually absent, but a weak inner metatarsal elevation present; a serrate palatal ridge preceded in some instances by a smooth ridge or tubercle.

Parker (1934, p. 54) characterized the skeletal features of the genus: "Maxillae forming a median suture in front of the premaxillae, and dentaries in front of the mento-meckelian bones; prevomer large, undivided, in contact with its fellow mesially, the post-choanal portion overlying the palatine region and bearing one or two very large steeply-shaped odontoids. . . . Clavicles, procoracoids and omosternum absent; sternum cartilaginous. Vertebral column diplasiocoelous. Terminal phalanges T-shaped or simple."

I have examined cleaned or cleared and stained skulls of two species (*X. obesus* and *X. rostratus*) and add the following observations to Parker's quoted above: vomers expanded anteriorly as well as posteriorly along the midline of the palate, contacting or closely approaching a mesially directed extension of the maxillary shelf (fig. 31); parasphenoid broad anteriorly, almost as broad as frontoparietals (fig. 69), anterior arm of squamosal not contacting maxilla; arch of bone over prootic region lacking; nasals not fused; no frontoparietal crest; roofing bones not rugose.

DISTRIBUTION: *Xenobatrachus* is found over much of New Guinea, at elevations from sea level to perhaps 9500 ft. (2900 m.). No specimens are known from islands fringing New Guinea, and there are none from the extreme eastern "tail" of the island.

KEY TO THE SPECIES OF *Xenobatrachus*

1. Two spikes behind each internal naris 2
One spike behind each internal naris 4
2. Size large, S-V up to 90 mm.; legs relatively short, TL/S-V *ca.* 0.34 *giganteus*
Size small, S-V, 30, perhaps 42 mm.; legs long, TL/S-V greater than 0.40 3
3. Eye-naris distance less than internarial distance (E-N/IN=0.90 in one specimen) . . . *ophiodon*
Eye-naris distance greater than internarial distance (E-N/IN=1.29 and 1.46 in two specimens) *bidens*
4. Size large, up to 73 mm. S-V; ventral surfaces pale, immaculate; legs long, TL/S-V, 0.49 or greater *obesus*
Maximum size *ca.* 55 mm. S-V or less; usually some dark markings on chin or other ventral surfaces; maximum TL/S-V, 0.47. 5
5. Ventral surfaces entirely dark; often dark and light mottling or an irregular "eyespot" in the groin *ocellatus*
Ventral surfaces usually not wholly dark; if wholly dark, then no mottling or eyespot in groin 6
6. Size larger, adults to 55 mm. S-V; distance from eye to naris usually less than length of orbit *macrops*
Size smaller, maximum S-V 47 mm., most individuals less than 40 mm.; distance from eye to naris usually greater than length of orbit 7
7. Legs shorter, maximum TL/S-V, 0.38, mean 0.35 or less *rostratus*
Legs longer, minimum TL/S-V, 0.37, mean 0.40 *mehelyi*

Xenobatrachus bidens (van Kampen)

Xenorhina bidens VAN KAMPEN, 1909, p. 39 (type locality, Digul River, West Irian; holotype, ZMA 5705, obtained by J. W. R. Koch in 1904 or 1905).
Xenobatrachus bidens: VAN KAMPEN, 1919, p. 54.

DIAGNOSIS: This species differs from all other *Xenobatrachus* except *X. giganteus* and *X. ophiodon* in having two spikes behind each internal naris rather than one. The large size of *giganteus*, up to 90 mm. snout to vent length, distinguishes it from *bidens* which is adult at about 30 mm. *Xenobatrachus ophiodon* is of the same size as *X. bidens*, but differs in having relatively larger eyes, and a shorter snout with the nostrils more widely spaced. The ratio Eye/S-V is 0.11 in the single specimen of *ophiodon* and is 0.07 in three *bidens*. The internarial distance is slightly greater than the distance from eye to naris in *ophiodon*.

(E-N/IN=0.90) but is distinctly less in three *bidens* (1.10–1.46).

DESCRIPTION OF TYPE-SPECIMEN: The following description is based on those given by van Kampen (1909, 1923) and Parker (1934), supplemented by my own examination of the holotype.

The body is stout, the head is moderately narrow (HW/S-V, 0.27) and broader than long. The hind legs are long (TL/S-V, 0.42). The eyes are small (Eye/S-V, 0.069), with the interorbital space twice the width of an upper eyelid. The snout is pointed and projecting, about one and one-half times the length of the eye, with the nostrils set relatively close together (E-N/IN=1.29). The tip of the snout is slightly warty. The canthus rostralis is rounded and the loreal region is oblique. The tympanum is equal in diameter to the eye. The skin is smooth except for the aforementioned warts on the nose.

The relative lengths of the fingers are $3 > 4 = 2 > 1$ and of the toes $4 > 3 > 5 > 2 > 1$. I noted scarcely any disc development, but van Kampen (1923, p. 129) stated: "Fingers with slightly swollen tips, toes with small discs . . .," and Parker (1934, p. 57) observed, "Fingers not dilated distally . . . Toes slightly dilated terminally. . . ."

There are two spikes behind each internal naris.

Van Kampen (1923, p. 129) described the color pattern as "Light brown above, uniform or with a few small black dots; a dark band along the canthus rostralis and some dark spots on the lips and the limbs sometimes present; white beneath, finely marbled with brown."

The type-specimen is an adult female. It contained no large ova when I examined it (although the oviducts were enlarged), but Parker's comment "Ovarian eggs large (3.5 mm.)" probably referred to the type, as he identified it as a female and listed the other specimen only as adult.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 29.1; TL, 12.2; HW, 7.9; Eye, 2.0; E-N, 2.2; IN, 1.7; EAR, 2.0.

VARIATION: I have examined two specimens in addition to the holotype; neither of these was available to van Kampen or Parker. Proportions are similar to those of the holotype (see table 8). The holotype is the largest specimen (S-V, 29). Both new specimens have paired vomerine spikes on each side. The fingers bear small terminal

discs, grooved but scarcely broader than the penultimate phalanges. The discs of the toes are distinctly broader.

The specimens are brown above with little in the way of pattern—a few darker markings on the back and legs, some mottling on the upper lip, and a light vertebral hairline in one specimen. The ventral surfaces are mottled with dark and light brown. In one specimen the chin is considerably darker than the abdomen.

COMPARISON WITH OTHER SPECIES: If the presence of paired vomerine spikes is a constant character and not individually variable, as I assume to be the case, then *X. bidens* must be compared only with the other two species having this character: *X. giganteus* and *X. ophiodon*.

Xenobatrachus giganteus, the only two specimens of which are approximately 81 and 90 mm. in length, is so much larger than *X. bidens* (29 mm.) that this difference alone should serve to distinguish the two forms. Juveniles of *giganteus* might be difficult to identify if their immaturity were not apparent. Extrapolation of proportions from adults to juveniles is not always advisable, but the ratio of eye to naris distance to internarial distance seems to change relatively little with growth. Three specimens of *bidens* have the ratio E-N/IN ranging from 1.10 to 1.46, whereas two *giganteus* show ratios of 0.97 and 1.02. Thus, this ratio might be a useful criterion in differentiating adults of *bidens* from juveniles of *giganteus*. In addition, differences in head width and leg length may be useful in distinguishing the species (see table 8).

I have examined only one specimen of *Xenobatrachus ophiodon* and can add nothing to the characters mentioned in the diagnosis.

Two additional specimens with paired spikes that I am unable to assign to species are discussed in a following section under "*Xenobatrachus* spp."

ECOLOGICAL NOTES: Van Kampen (1913, p. 460) remarked of the second specimen of this species, "The stomach contains ants."

DISTRIBUTION AND SPECIMENS EXAMINED: *Xenobatrachus bidens* is known from two definite localities in West Irian and one in the Territory of Papua (fig. 61). The localities on the Lorentz River and at Katau (=Katow) are in coastal lowlands and the type-specimen may also have come from a low elevation, although the data accompanying the specimen are not specific.

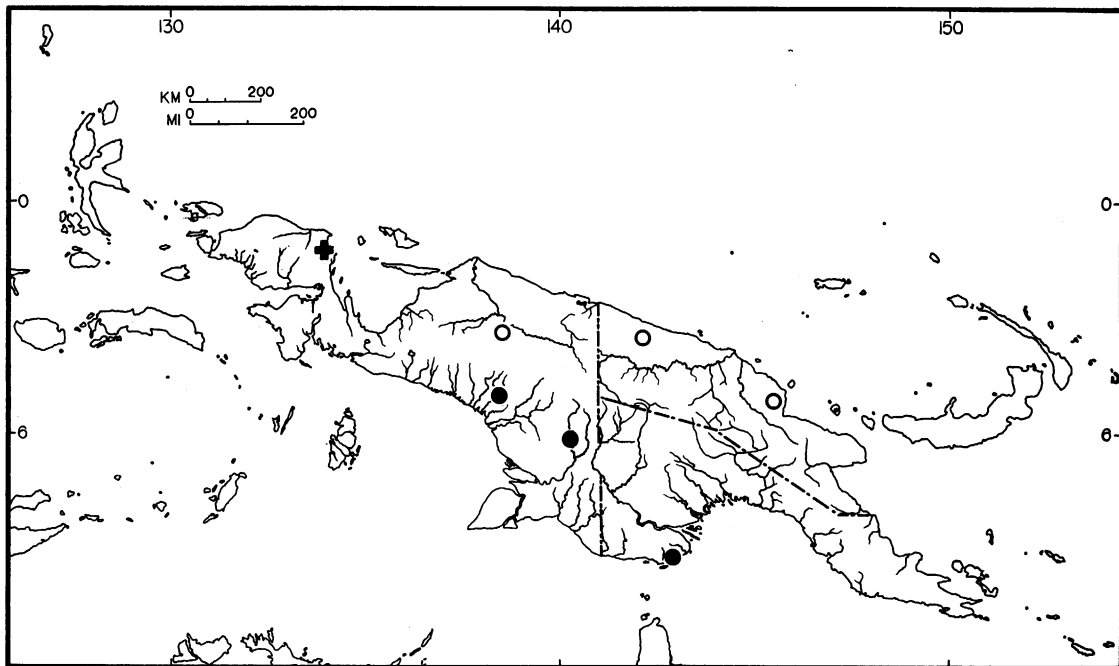


FIG. 61. Distribution of three species of *Xenobatrachus*. Closed circles, *X. bidens*; open circles, *X. obesus*; cross, *X. ophiodon*.

Two of the specimens from West Irian have previously been reported in the literature. The one from Katau was collected by D'Albertis and had not previously been identified or reported.

West Irian: Digul River (ZMA 5705, holotype); Tanah Merah (RMNH 16665); Lorentz River at Bivak Island (van Kampen, 1913, p. 460). Territory of Papua: Western District: Katau (MSNG 41719).

Xenobatrachus giganteus (van Kampen)

Xenorhina gigantea VAN KAMPEN, 1915, p. 40 (type locality, "Bijenkorfbiwak" near the Lorentz River at an elevation of 1700 m. in the Snow Mountains, West Irian; lectotype ZMA 5702, designated by Daan and Hillenius [1966, p. 126], obtained by G. M. Versteeg on January 13, 1913).

Xenobatrachus giganteus: VAN KAMPEN, 1919, p. 54.

DIAGNOSIS: *Xenobatrachus giganteus* is unique within its genus in being the only large species (snout-vent length approximately 90 mm.) with two spikes behind each internal naris. The only species that approaches *giganteus* in size is *X. obesus* (73 mm.), which has single spikes and a distinctive color pattern. The other species with

paired spikes, *X. ophiodon* and *X. bidens*, are adult at a length of 30 mm., and a specimen of uncertain identity is 42 mm. in length (see account of *X. bidens*).

DESCRIPTION: The following description is based on those published by van Kampen (1915, p. 40; 1923, pp. 130–131) and Parker (1934, p. 57), supplemented by my examination of the lectotype and paralectotype. Measurements and proportions of the lectotype are given first, followed by those of the paralectotype.

This is a heavy-bodied frog with a moderately broad head (HW/S-V, 0.40, 0.38), short hind limbs (TL/S-V, 0.34, 0.33) and small eyes (Eye/S-V, 0.067, 0.062). The snout is truncate and slightly longer than the eye, and bears three horizontal rows of small warts. The nostrils are close to the tip of the snout, with the internarial and eye-to-naris distances approximately equal (E-N/IN, 0.97, 1.02). The canthus rostralis is rounded, and the loreal region is oblique and slightly concave. Van Kampen (1923, p. 131) stated that the tympanum was "as large as the eye," and Parker (1934, p. 57) qualified this to "about as large as the eye." My measurements

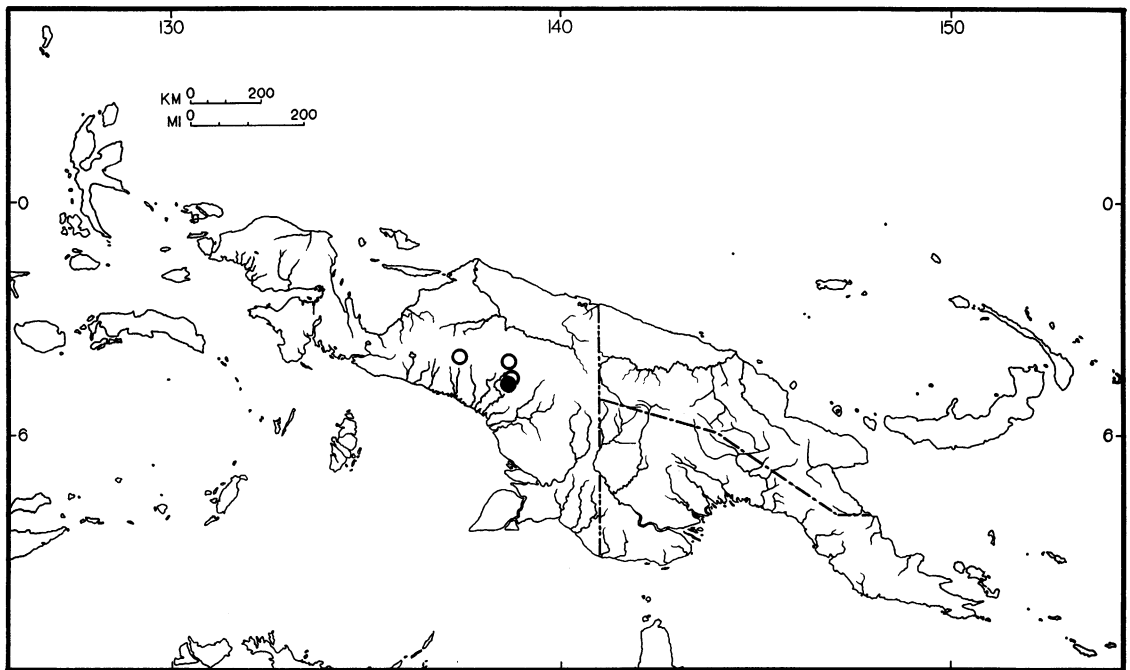


FIG. 62. Distribution of *Xenobatrachus giganteus* (closed circle) and *X. ocellatus* (open circles).

are in closer agreement with Parker's: Eye/EAR, 0.87, 0.78. The tympanum is distinct externally and there is a slight supratympanic skin fold.

The finger tips are scarcely enlarged and the toes bear small discs. The relative lengths of the fingers are $3 > 2 > 4 > 1$ in the lectotype and $3 > 4 > 2 > 1$ in the lectoparatype. The toes in both are $4 > 3 > 5 > 2 > 1$. There is a weak inner metatarsal tubercle and no outer one.

The dorsal color is brown with faint darker maculations. The venter is yellowish brown with darker marbling or spotting. There is no sharp line of demarcation between dorsal and ventral ground colors.

There is a tubercle-like anterior palatal ridge. Vomerine spikes are paired, and the maxillae are symphygnathine.

MEASUREMENTS OF LECTOTYPE AND PARALLECTOTYPE SPECIMENS: S-V, 90.2, 80.8 (86 and 80, according to van Kampen, 1915, p. 40); TL, 31.0, 26.9; HW, 35.7, 30.4; Eye, 6.0, 5.0; EAR, 5.2, 3.9; IN, 5.9, 4.9; E-N, 5.7, 5.0.

The lectotype is a female with ovarian eggs 6 mm. in diameter; the lectoparatype male has a vocal sac (Parker, 1934, p. 57).

COMPARISON WITH OTHER SPECIES: Compari-

sons other than those made in the Diagnosis (above) and in the account of *X. bidens* are unnecessary, as this species is amply distinct from all others of its genus.

DISTRIBUTION AND SPECIMENS EXAMINED: This species is known only from the two type-specimens. The type locality (fig. 62) is near the southern edge of the main mountain mass of New Guinea, south of Mt. Wilhelmina. West Irian: Bijenkorfbiwak near the Lorentz River, Snow Mountains, 1700 m. (5600 ft.) (ZMA 5702, lectotype, 5703, paralectotype).

Xenobatrachus macrops (van Kampen)

Xenorhina rostrata: VAN KAMPEN, 1909, p. 39 (non Méhely).

Xenorhina macrops VAN KAMPEN, 1913, p. 460 (type locality, "peak in Hellwig Mountains, West New Guinea, altitude 2200 m. (coll. H. A. Lorentz, 4.IX.1907)" [Daan and Hillenius, 1966, p. 126]; lectotype ZMA 5725, a male, designated by Daan and Hillenius [*loc. cit.*]).

Xenobatrachus macrops: VAN KAMPEN, 1919, p. 54.

DIAGNOSIS: Among the five species of *Xenobatrachus* with one spike behind each internal naris,

X. macrops is distinguished by eye size, body size, color pattern, and leg length.

The ventral surfaces of *macrops* are light with dark spots or are reticulated in contrast to the uniformly dark venter of *ocellatus* and uniformly pale undersides of *obesus*. The large size of *obesus* (maximum body length 73 mm. in contrast to 55 mm. for *macrops*) also distinguishes that form from *macrops*.

Xenobatrachus macrops typically has longer hind legs than those of *X. rostratus* (TL/S-V averages 0.44 in *macrops*, compared with a maximum in *rostratus* of 0.37), larger body size (to 55 mm. S-V in *macrops*, 44 mm. in *rostratus*), and the distance from eye to naris less than the length of the orbit (eye-naris distance usually larger in *rostratus*).

Xenobatrachus mehelyi is a smaller species than

X. macrops (maximum snout-vent length 33 mm., compared to 55 mm.) with a higher E-N/IN ratio (mean in *macrops* 1.07, maximum 1.15; mean in *mehelyi* 1.33, minimum 1.13).

DESCRIPTION OF SYNTYPES: The four syntypes of *Xenobatrachus macrops* range in length from snout to vent from 47.8 to 55.4 mm. The body is stout, with moderately long hind legs (TL/S-V mean 0.45). The head is rather narrow for a *Xenobatrachus* (HW/S-V mean 0.32), with the bluntly pointed snout slightly to markedly pustulose. The eyes are relatively large (Eye/S-V mean 0.08), and the diameter of the orbit is distinctly greater than the distance from eye to naris (Eye/E-N mean 1.24). The canthus rostralis is rounded, and the loreal region is oblique and slightly concave.

There is a weak supratympanic fold and in

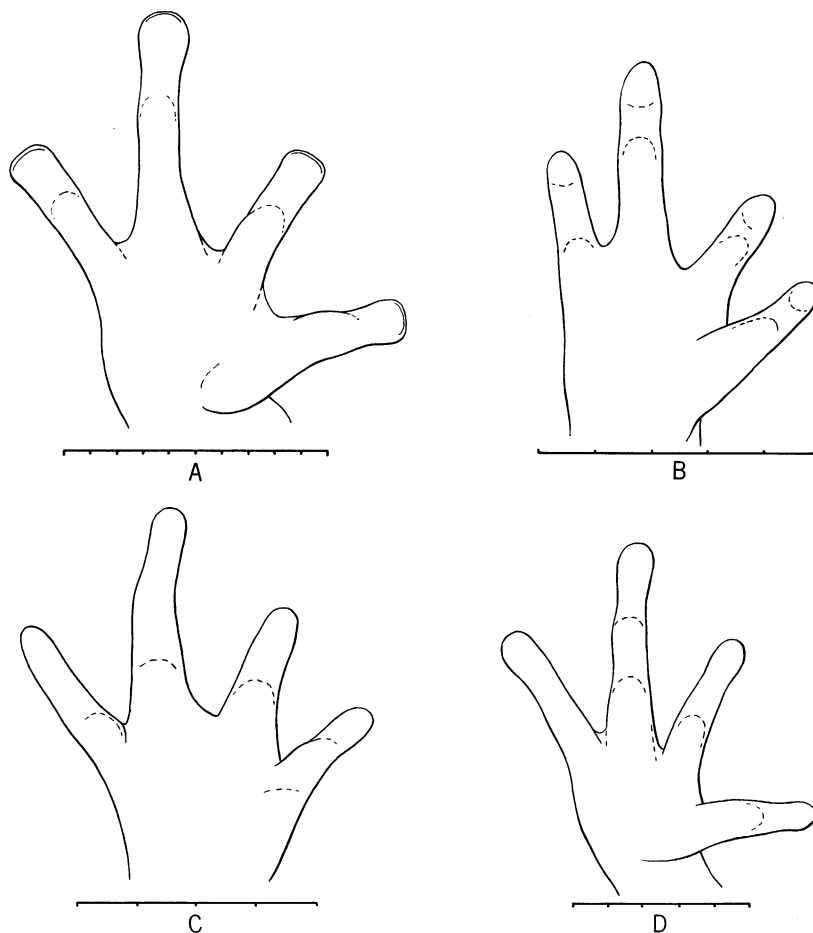


FIG. 63. Hands of *Xenobatrachus* in palmar view. A. *X. obesus*. B. *X. rostratus*. C. *X. ocellatus*. D. *X. macrops*. Scale lines subdivided in millimeters.

one specimen a strong skin fold between the eyes. The tympanum is scarcely distinguishable externally. The skin of the body is smooth above and below.

The relative lengths of the fingers are $3 > 4 > 2 > 1$, and of the toes, $4 > 3 > 5 > 2 > 1$. The tips of the fingers are slightly broadened (fig. 63D, not a syntype), whereas the toes bear small but distinct discs. An indistinct inner metatarsal tubercle is present.

Van Kampen (1923, p. 129) described the coloration: "Brownish violet (in spirit); lips and lower surface, except the throat, marbled with lighter; vent bordered with black."

VARIATION: Variation in proportions is summarized in table 8. I have examined six other specimens that I assign to *macrops*: one from the Weyland Range south of Geelvinck Bay, one from Zanepa in the central mountains, two from mountains south of the Idenburg River, and two from localities that I have been unable to place (Bedawo and Enatadi).

Parker (1934, p. 56) assigned the specimen from the Weyland Range (there are no more specific locality data) to *X. rostratus*, but he also included two syntypes of *macrops* in *rostratus*. Although I am not confident of the allocation of this specimen to *macrops*, I think it even less likely that it represents *rostratus*. This male specimen is almost as large (S-V length, 44.6 mm.) as the largest of all *rostratus* examined (48 mm.). Compared with a *rostratus* of the same size, the eye of the Weyland specimen is distinctly larger (3.3 in contrast to 2.7 mm.), and the internarial distance is greater (3.1 vs. 2.5 mm.). The shape of the body is not readily expressed quantitatively, but the Weyland frog does not have the rotund, corpulent appearance of *rostratus*.

The Weyland specimen resembles the syntypes of *macrops* in body size and ventral pigmentation. The eye size (Eye/S-V=0.074) is insignificantly smaller than the minimum seen in syntypes of *macrops* (0.075), and the ratio E-N/IN is slightly higher (1.13 vs. maximum of 1.07 in the syntypes). The major difference is in leg length: the TL/S-V ratio is only 0.33 in the Weyland specimen, in contrast to the minimum of 0.42 in the syntypes of *macrops* and 0.40 in other *macrops*. I think it best to regard this specimen as a representative of a short-legged, western population of *macrops*, but I have excluded it from the table of variation (table 8).

One specimen comes from the camp of the

1938-1939 Archbold Expedition that was situated at an elevation of 1800 m. (5900 ft.) south of the Idenburg River. It is a juvenile (S-V, 22.5 mm.) with the ventral color pattern and long legs (TL/S-V=0.42) of *macrops*. The eye is quite large (Eye/S-V=0.111), but this is to be expected in a juvenile. I previously assigned this specimen to *macrops* (Zweifel, 1956, p. 3); others from the same general area that I called *macrops* I have now redetermined as *ocellatus* (see account of that species). Van Kampen (1923, p. 129) recorded a specimen of *macrops* (which I have not examined) from "near Idenburg riv., 2400 m."

The other specimen from immediately south of the Idenburg River is MZB 151, collected on September 29, 1920 by W. C. van Heurn at an elevation of 800 m. on the Doorman River. It has a length of 27 mm., and the typically large eyes of a juvenile (Eye/S-V, 0.10); the heavily mottled ventral pattern and relatively long legs (TL/S-V, 0.41) ally it with *macrops*.

The fourth non-syntypic specimen is MZB 1485 from Zanepa. It is a gravid female 43 mm. in length. The ventral surfaces are pale tan with indistinct fine darker mottling. In this respect the specimen resembles the syntypes of *X. macrops* more closely than it does *X. ocellatus*. The leg length (TL/S-V, 0.40) is midway between the maximum in *ocellatus* (0.38) and the minimum in the syntype series of *macrops* (0.42). Across the lumbar region of this specimen there are several large (ca. 2 to 4 mm.), clear yellow spots, asymmetrically placed. Nothing like this color pattern is present in any other *Xenobatrachus* I have examined. The remaining specimens (from Bedawo and Enatadi) are typical of *macrops* in both color pattern and proportions.

COMPARISONS WITH OTHER SPECIES: *Xenobatrachus macrops* is abundantly distinct from the species with paired vomerine spikes (*bidens*, *giganteus*, and *ophiodon*), differing not only in the possession of single spikes but also in being intermediate in size between the two small species and the aptly named *giganteus*. For comparisons with *ocellatus* and *rostratus*, see the accounts of those species. Comparison with *obesus* additional to that in the foregoing diagnosis is unnecessary.

DISTRIBUTION AND SPECIMENS EXAMINED: The known localities for this species are at moderate to high elevations in the mountains of West Irian (fig. 65). Zanepa, 2300 m. (7550 ft.)

(MZB 1485); Hellwig Mountains, 2200 m. (7220 ft.) (ZMA 5725, lectotype; 5726, syntype); Hellwig Mountains, 2500–2600 m. (8200–8530 ft.) (ZMA 5727, 5728, syntypes), Weyland Ranges (BMNH 1921.11.11.15); Idenburg River, 15 km. SW Bernhard Camp, 1800 m. (5900 ft.) (AMNH 49638); Doorman River, 800 m. (2620 ft.) (MZB 151); N Enatadi, ca. 8000 ft. (2440 m.) (BBM 3691); near Bedawo (BBM 3692).

Xenobatrachus mehelyi (Boulenger),
new combination

Figure 64

Choanacantha mehelyi BOULENGER, 1898a, p. 709 (type locality, "Vikaiku," St. Joseph River [Angabunga River], Territory of Papua; holotype, MSNG 29112, collected by Lamberto Loria in 1892).

Xenorhina rostrata: MÉHELÏ, 1901, p. 233.

Xenobatrachus rostratus: VAN KAMPEN, 1919, p. 54.

DIAGNOSIS: This is a small species of *Xenobatrachus* (maximum known snout-vent length, 33 mm.) with a single spike on each vomer and with long hind legs (TL/S-V minimum 0.37, mean 0.40). The most similar species is *X. rostratus*, which has shorter legs (maximum TL/S-V, 0.38) and, in populations closest geographically to *mehelyi*, a lower ratio E-N/IN (see following section on comparison).

DESCRIPTION OF TYPE-SPECIMEN: The body is rotund, with the head conspicuously narrower than the body. The snout is pointed, projecting, and pustulose. The canthus is rounded, the loreal region oblique and flat. The eyes are

small (Eye/S-V, 0.066), with the horizontal diameter less than the distance from eye to naris. The internarial distance is less than the distance from eye to naris (E-N/IN, 1.26). Except for the pustulosity of the snout, the skin is smooth.

The relative lengths of the fingers are $3 > 4 > 2 > 1$ (the second almost equal to the fourth), of the toes $4 > 3 > 5 > 2 > 1$. The fingers are without discs (Boulenger, 1898a, p. 709, described them as "pointed"), but small, grooved discs are present on the toes. The subarticular and inner metatarsal tubercles are low and rounded. There is no webbing between the toes.

Boulenger (*loc. cit.*) described the tongue as "large, free only at sides"; and noted the vomerine spikes as "a large tooth-like process on each side of the palate behind the choanae."

I have little to add to Boulenger's (*loc. cit.*) original description of color and pattern: "Brown above; a dark blotch below the eye; a fine light line from between the eyes to the vent and from the latter along the back of the thighs and the inner side of the legs; hinder side of thighs dark brown; dirty white beneath, marbled with brown." I noted that the holotype has mottling on the chin but not on the rest of the venter. Perhaps the pattern has partly faded.

The holotype has not been sexed.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 28.6; TL, 11.6; HW, 10.5; Eye, 1.9; E-N, 2.4; IN, 1.9.

VARIATION: The 11 specimens referred to this species come from a wide range, with a linear distance of more than 400 miles separating the most distant localities sampled, but there is remarkably little variation in the diagnostic proportional characters (table 8). The finger tips may be without visible expansions, as in the holotype, or may be very slightly broadened into scarcely perceptible discs with faint grooves.

Dorsal color and pattern are much the same in all specimens. The ground color is medium brown in two from Omati, darker grayish brown in the others. Only one specimen in addition to the holotype possesses a vertebral hairline. One of the specimens from Omati has tiny black dots on the dorsum, each centered with white. Black spotting or mottling shows faintly against the dark dorsal ground color of some but not all other individuals, and one has faint, large lumbar ocelli. Variation in ventral pattern includes the following: virtually immaculate except for the border of the chin, and, to a very slight

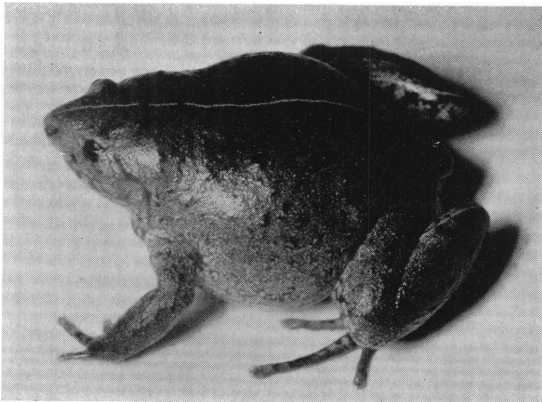


FIG. 64. *Xenobatrachus mehelyi* (MCZ 53099).
Photo by Fred Parker.

extent, the chest (four individuals); chest heavily mottled, remainder of venter clear (one individual); all ventral surfaces, including legs, heavily and coarsely mottled (one individual); numerous small, irregular light spots on a dark background, nearly forming a reticulum over the entire ventral surface (4 specimens).

COMPARISON WITH OTHER SPECIES: In the original description, Boulenger (1898a) compared *mehelyi* with *rostratus*, described in the same year by M  hely  , and differentiated the two on the basis of the longer hind legs and distinguishable tympanum of *mehelyi*. M  hely   (1901) placed *mehelyi* in the synonymy of *rostratus* on the grounds that the distinctness of the tympanum was subject to variation according to the state of preservation (with which I agree fully), and because specimens of *rostratus* taken subsequent to the original description had significantly longer legs than the syntypes.

Xenobatrachus rostratus as I presently understand it consists of three groups, each well distinguished both morphologically and geographically. *Xenobatrachus mehelyi* is most distinct from the *X. rostratus* geographically closest (the two highlands groups). The ratios TL/S-V (maximum in *rostratus* 0.32; minimum in *mehelyi*

0.37) and E-N/IN (mean in *rostratus* 1.04–1.08; mean in *mehelyi* 1.31) serve to distinguish the 11 specimens of *mehelyi* from specimens of *rostratus* in the Eastern and Western highlands.

The sample of *X. rostratus* from the north coast of New Guinea, geographically remote from the range of *mehelyi* on the south coast, resembles *mehelyi* closely in the E-N/IN ratio. There is almost complete separation in leg length, but the difference is less than between *mehelyi* and other *rostratus* (TL/S-V maximum in north coast *rostratus* 0.38). Apparently *rostratus* of the north coast reaches a larger size than *mehelyi* (48 mm. snout to vent, compared with 36 mm.).

Leg length also serves to distinguish *mehelyi* from the large sample (60 specimens) of *rostratus* from the Huon Peninsula, with a maximum TL/S-V ratio of 0.33. As is the case with the sample from the north coast there is no significant difference in the ratio E-N/IN. Evidently these *rostratus* and *mehelyi* are also similar in size.

The specimens that I group under the name *mehelyi* form a natural geographic unit and are virtually 100 per cent distinguishable from those referred to *X. rostratus*. I grant the possibility that *mehelyi* may be only a geographic variant of *rostratus*, but, in my view, the greater

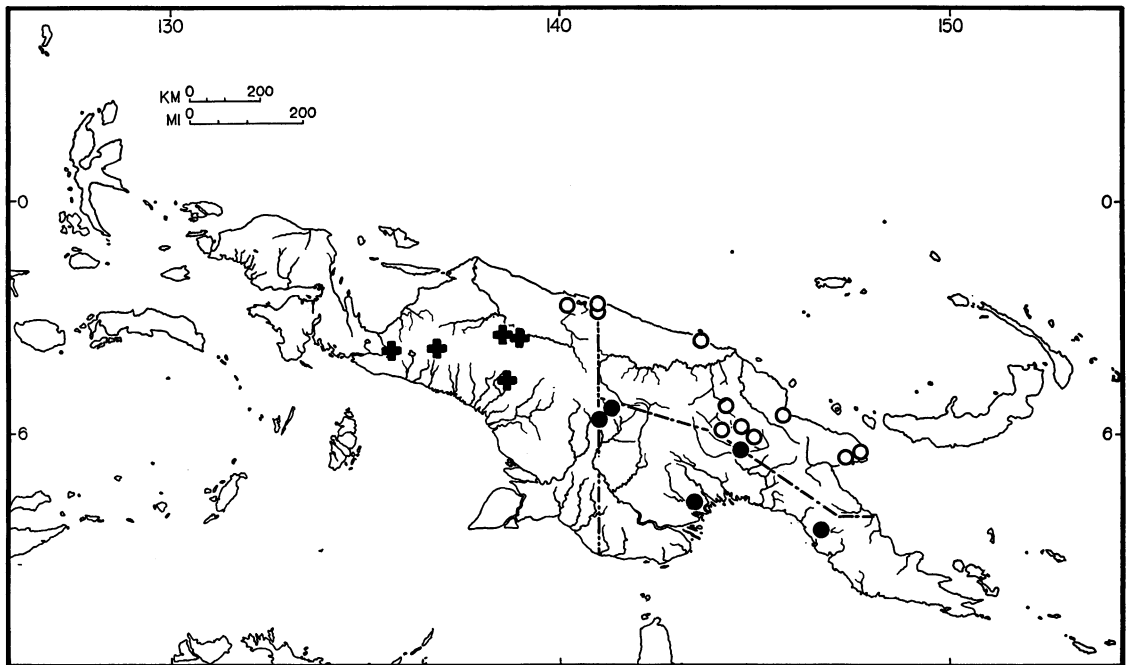


FIG. 65. Distribution of three species of *Xenobatrachus*. Crosses, *X. macrops*; open circles, *X. rostratus*; closed circles, *X. mehelyi*.

distinctness of populations of *rostratus* closest geographically to those of *mehelyi* argues in favor of a specific relationship.

No species other than *Xenobatrachus rostratus* is likely to be confused with *X. mehelyi*. Leg length is similar in *X. macrops* and *X. mehelyi*, but the former is a much larger species (to 55 mm. snout-vent length) with a lower E-N/IN ratio (maximum 1.15). The paired vomerine spikes of *X. bidens* should distinguish it from *mehelyi*, but the two are closely similar in size and proportions.

DISTRIBUTION AND SPECIMENS EXAMINED: *Xenobatrachus mehelyi* occurs at moderately low elevations in the southeastern part of New Guinea draining into the Gulf of Papua (fig. 65). The westernmost record is near the border of West Irian, and the easternmost is north of Port Moresby. Territory of Papua: Western District: Derongo (AMNH 82291; MCZ 81673, 81674); Imigabip, 4200 ft. (1270 m.) (MCZ 80502, 81675, 81676; AMNH 84544). Gulf District: Omati (MCZ 28203, 28204). Central District: Vikaiku (MSNG 29112, holotype). Territory of New Guinea: Chimbu District: Bomai (MCZ 53099).

Xenobatrachus obesus Zweifel

Figure 66

Xenobatrachus obesus ZWEIFEL, 1960, p. 1 (type locality, "Maratambu, Adelbert Mountains, Northeast New Guinea [Madang District, Territory of New Guinea], elevation 2300 feet"; holotype, AMNH 64247, taken on March 29, 1959, by Margaret and E. Thomas Gilliard).

DIAGNOSIS: *Xenobatrachus obesus* differs from the other species of its genus in the following unique combination of characters: a single toothlike vomerine spike behind each internal naris; eye small, snout about twice the length of the eye; size large, up to 73 mm. snout to vent length; ventral surfaces pale and immaculate.

DESCRIPTION OF TYPE-SPECIMEN (quoted from Zweifel, 1960, pp. 1-3): "Adult female, with the following measurements (in millimeters): snout to vent length, 72.3; tibia length, 37.0; head width, 26.0; length of orbit, 4.3; horizontal diameter of tympanum, 3.4; length of snout (anterior corner of eye to tip of snout), 8.3; internarial distance, 5.4; distance from eye to naris, 5.0.

"The head is relatively narrow and tapers

sharply to the rounded snout. The nostrils are closer to the tip of the snout than to the eye. The tympanum is indistinct and is larger in area than the eye, though slightly shorter in length. There is a serrated palatal ridge preceded by three low protuberances. There are no teeth. The tongue is oval, with a median furrow, and is little freer behind than at the sides. The fingers, in order of decreasing length, are $3 > 4 > 2 > 1$. The tip of each finger is flattened into a disc very slightly wider than the penultimate segment [fig. 63A]. A narrow dermal fringe is present on each finger, best developed on the third. There is a low, rounded tubercle at the base of the first finger, and very low elevations in the place of subarticular tubercles. The toes are free of any trace of webbing; their relative lengths are $4 > 3 > 5 > 2 > 1$. The discs of the toes are larger than those of the fingers; the disc of the fourth toe is slightly less than twice as broad as the penultimate phalanx. Very low, rounded, subarticular tubercles, the strongest being the one of the first toe, and a low, rounded, inner, metatarsal tubercle are present. The skin of both dorsal and ventral surfaces is quite smooth.

"The type specimen possesses the typical skeletal features of the genus *Xenobatrachus*: symphagnathine upper jaw and pectoral girdle lacking clavicle and procoracoid.

"The dorsal surface of head, body, and limbs is pale brown faintly speckled with darker brown. A light vertebral line, bordered by dark brown, passes from the tip of the snout to the rear of the body, where it bifurcates and passes along the top of the thigh to terminate behind the knee. There is a short dark bar that commences



FIG. 66. *Xenobatrachus obesus* (AMNH 83081).

behind the eye and passes over the tympanum. A broad, dark stripe begins at the tip of the chin and, involving also the upper lip, passes along the anterior side of the forearm onto the third finger. The stripe is broken opposite the elbow, but reappears on the back of the wrist and, except for a slight break at the axilla, is continuous along the side of the body and anterior side of the hind limb to the fourth toe. There is a conspicuous dorsal extension of the stripe in the groin. The sole of the foot is dark brown, and this color merges with a dark stripe running on the back of the leg to the cloacal opening. This stripe is continuous on the foot and tibia but is interrupted on the rear of the thigh. With the exception of the dark border of the lower jaw, the ventral surfaces are unmarked. Mrs. E. Thomas Gilliard, who saw the specimen while it was alive, recalls (personal communication) that the dorsal surfaces were tan, the lateral stripes and borders of the dorsal stripe rich chocolate brown, and the dorsal stripe and ventral surfaces yellow."

VARIATION: Since I described this species on the basis of three specimens, Jared Diamond collected 34 more individuals at two localities in the Torricelli Mountains about 250 miles west-northwest of the type locality. The color and pattern of these specimens are essentially the same as those described for the holotype. The dorsal surface of the body may be slightly more or less speckled (or mottled) than in the type and the dark lateral stripe may be variously broken or complete, just as noted for the type and paratypes (Zweifel, 1960, p. 4). Diamond stated (*in litt.*) that "In life it is tan above and a colorful yellow below." A living individual from the Adelbert Mountains (fig. 66) examined by me was also tan above and bright yellow beneath. Thus, the colors of the frogs from the Torricelli Mountains are similar or perhaps identical to those from the Adelbert Mountains.

Proportions are summarized in table 8. Frogs from the two regions do not differ significantly in proportions, so data are pooled in the table. *Xenobatrachus obesus* is notable for its unusually long hind legs and small eyes.

The eggs of this species are large; ovarian eggs of four females ranging from 67–73 mm. in length are 4.4–5.5 mm. in diameter.

COMPARISON WITH OTHER SPECIES: *Xenobatrachus obesus* is markedly distinct from its congeners. It exceeds all except *X. giganteus* in

size, and differs from that species in several ways, the most obvious of which are the single vomerine spikes (double in *giganteus*) and characteristic color pattern.

I have considered the possibility that *Xenobatrachus obesus* is a synonym of *X. rostratus*, for the type localities are in the same region of New Guinea and there are similarities of color pattern. However, the differences between the two are too great for them to represent the same taxon. Parker (1934, p. 56) referred to the cotypes of *rostratus* as adults, and one of these was only 39 mm. in body length, juvenile size for *obesus*. The prominent black groin marking of *obesus* is not mentioned for *rostratus*, and Méhely (1898, p. 176) described *rostratus* as dotted with slate-gray beneath, whereas *obesus* is immaculate.

ECOLOGICAL NOTES: The localities where this species was collected in the Adelbert Mountains lie at about 2300 to 2900 feet above sea level. Diamond (*in litt.*) commented that "*Xenobatrachus* was fairly common around 3000' in forest in the Torricellis, where natives call it the 'so.' " Zweifel (1960, p. 6) noted that the holotype had eaten an earthworm. Nothing else is on record of the ecology of this species.

DISTRIBUTION AND SPECIMENS EXAMINED: *Xenobatrachus obesus* has been found in the coastal Adelbert and Torricelli mountains in the northern part of the Territory of New Guinea, and in the northern foothills of the Nassau Mountains far to the west (fig. 61). The coastal ranges are separated by the lower reaches of the Sepik and Ramu rivers, and if the species is limited to uplands, these two populations may be disjunct by as much as 100 miles. The localities in the Territory of New Guinea known at present are about 250 miles apart, and the locality in West Irian is 250 miles farther to the west.

Territory of New Guinea: Madang District: Maratambu, Adelbert Mountains, 2300 ft. (700 m.) (AMNH 64247 [holotype], 64248 [paratype]); Dawa, Adelbert Mountains (AMNH 64251 [paratype]); Yabsau, Adelbert Mountains, 2900 ft. (880 m.) (AMNH 83081). Sepik District: Mt. Somoro, Torricelli Mountains, 7 mi. NE Lumi (AMNH 78187–78189); Mt. Nibo, Torricelli Mountains, 12 mi. NE Lumi (AMNH 84446, 78190–78207 + 12 untagged specimens). West Irian: Doorman River, 800 m. (2600 ft.) (MZB 150).

Xenobatrachus ocellatus (van Kampen)

Xenorhina ocellata VAN KAMPEN, 1913, p. 461 (type locality, "Hellwig Mountains (± 2500 m.)," West New Guinea; syntypes, ZMA 5815 and 5816, and FMNH 100100, the last formerly in the Edward H. Taylor collection, all collected by H. A. Lorentz in November, 1909 [Daan and Hillenius, 1966, p. 127]).

Xenobatrachus ocellatus: VAN KAMPEN, 1919, p. 54.

DIAGNOSIS: Among the species of *Xenobatrachus* that resemble it in having single rather than paired vomerine spikes, *X. ocellatus* is distinguished by having relatively short legs (TL/S-V ranges from 0.28 to 0.38), body of moderate size (up to 43 mm. snout to vent), ventral surfaces entirely dark (except for midventral and interbrachial light lines in some individuals), and often a light-bordered, irregular dark spot deep in the groin.

DESCRIPTION: This is a fat-bodied, short-legged frog (TL/S-V mean 0.33) of moderate size, with a relatively broad head (HW/S-V mean 0.36). The eyes are small (Eye/S-V mean 0.08) and the interorbital distance is equal to twice the width of an upper eyelid. The snout is bluntly pointed and slightly longer than the eye; the canthus is rounded and the loreal region is gently sloping and shallowly concave. The internarial distance averages virtually the same as the distance from eye to naris (E-N/IN mean 1.02). There is a single vomerine spike behind each internal naris.

The tympanum is generally visible, although not notably distinct, and there is a supratympanic fold that is well marked in some individuals, scarcely visible in others. The snout may be pustulose or virtually smooth. The dorsal and ventral surfaces of the body are smooth, but the flanks and hind limbs are slightly granular.

The relative lengths of the fingers are $3 > 4 \geq 2 > 1$, of the toes $4 > 3 > 5 > 2 > 1$. The tips of neither the fingers nor toes are expanded into discs, but the toe tips of some specimens bear faint terminal grooves (fig. 63C). The fingers and toes lack any trace of webs or fringes. The tubercles of the hands and feet are present only as low, indistinct, rounded elevations.

The dorsal surface of the body is light brown. A few small, dark spots may be present dorsally, the supratympanic fold is accented by a dark line, and there is a diffuse dark mark beneath the eye. Some specimens have a light vertebral

hairline that divides and passes onto the posterior sides of the thighs. The chin, chest, and abdomen are dark brown, with light flecking apparent only on close inspection. Some individuals possess a narrow midventral light line crossed by a similar interbrachial line. Most specimens have dark and light mottling deep within the groin. This may take the form of an irregular dark spot with a light border, a light spot with a dark border, or merely mottling with no definite pattern. The groin may be dark with little or no light marking at all (two of eight specimens). The anterior and posterior surfaces of the thighs and undersurfaces of the lower legs are mottled.

The largest of the three syntypes, ZMA 5815, has the following measurements: S-V, 43.3; TL, 16.6; HW, 14.5; Eye, 3.1; E-N, 2.8; IN, 3.1; EAR, 2.9. This specimen and ZMA 5816 are adult females. Another with a length from snout to vent of 36 mm. (AMNH 43759) is gravid.

COMPARISON WITH OTHER SPECIES: *Xenobatrachus macrops* is the species most similar to *X. ocellatus*; in a former publication (Zweifel, 1956), I confused the two. The differences between the forms seem relatively trivial in light of variation seen in other *Xenobatrachus*, but the constant association of short legs with dark belly in *ocellatus* (usually longer legs and mottled belly in *macrops*) together with the presence of the two forms in one region (they may be sympatric) argues for specific rank. Additional differences that may prove to be diagnostic include larger size of *macrops* (the four syntypes are larger than any *ocellatus*) and slightly broader head, on the average, in *ocellatus*.

Xenobatrachus obesus is readily distinguished from *ocellatus* by its much larger size (73 as opposed to 43 mm. S-V), light belly and other aspects of color pattern.

Xenobatrachus mehelyi differs from *X. ocellatus* in ventral color (not entirely dark), relatively narrower spacing of nostrils (E-N/IN minimum in *mehelyi* 1.13; maximum in *ocellatus* 1.11), and relatively longer leg length (TL/S-V, 0.37–0.43 in *mehelyi*, 0.28–0.38 in *ocellatus*). For comparison with *X. rostratus*, see the account of that species.

The three species of *Xenobatrachus* with paired vomerine spikes are easily distinguished from *ocellatus* by that characteristic and differ in several other ways as well.

ECOLOGICAL NOTES: Known localities for this species lie between 2200 and 2800 m. (7000–

9200 ft.) above sea level. Referring to the area 18 km. south of Lake Habbema (2200 m.), Archbold, Rand, and Brass (1942, p. 260) stated that the "forests were composed of three species of *Nothofagus*, all forming great straight-stemmed rough-barked trees over forty meters high and up to a meter and one-half in diameter." The authors also mentioned that "under optimum conditions, the dominants and the subsidiary trees combined to form a fairly close deep canopy." No specific information on the habits of the frog is available, although presumably it dwells in humus.

DISTRIBUTION AND SPECIMENS EXAMINED: This species is known only from four localities in West Irian (fig. 62): Usasigo, 2000 m. (6560 ft.) (MZB 1487); Hellwig Mountains, 2500–2600 m. (8200–8530 ft.) (ZMA 5815, 5816; FMNH 100100; syntypes); Bele River, 2200 m. (7000 ft.), 18 km. N Lake Habbema (AMNH 43690, 43728, 43759; FMNH 121909); 9 km. N Lake Habbema, 2800 m. (9200 ft.) (AMNH 43724). The Hellwig and Lake Habbema area are only about 35 miles apart, but are on opposite sides of one of the highest mountains in the Nassau Range, Wilhelmina Top (ca. 4700 m. [15,500 ft.]).

Xenobatrachus ophiodon Peters and Doria

Xenobatrachus ophiodon PETERS AND DORIA, 1878, p. 432 (type locality, "Hatam, Arfak Mountains," Vogelkop Peninsula, West Irian; lectotype, MSNG 29129, designated by Capocaccia [1957, p. 219], collected by Odoardo Beccari in 1875. There were two syntypes, but one is missing [Capocaccia, *loc. cit.*]).

DIAGNOSIS: This is one of three species of *Xenobatrachus* that possesses two rather than a single spike behind each internal naris. *Xenobatrachus giganteus* reaches a length of 90 mm., and so is much larger than *ophiodon* which is adult at about 30 mm. The other species with paired vomerine spikes, *X. bidens*, is of the same size as *ophiodon* but has relatively smaller eyes (Eye/S-V = 0.07, compared with 0.11 in *ophiodon*) and a longer snout with the nostrils more closely spaced (E-N/IN = 0.90 in *ophiodon*, 1.29–1.46 in *bidens*).

DESCRIPTION OF TYPE-SPECIMEN: The following description is composite, being based on the original description and that of Parker (1934), who examined a syntype, as well as on my own

examination of the remaining type-specimen, which is in soft condition. I did not determine the sex.

The head is small. The snout is slightly longer than the eye. I noted that there were no pustules on the snout, but Parker (1934, p. 58) recorded it as "slightly pustulose anteriorly." The canthus rostralis is rounded and the loreal region is oblique and slightly concave. The external nares are near the tip of the snout. The interorbital space is broader than an upper eyelid, and the eyes are relatively large (Eye/S-V, 0.111). The tympanum is indistinct and about two-thirds of the diameter of the eye (my measurement agrees with Parker's, rather than with the figure of one-half given in the original description). The skin is smooth on all body surfaces.

The relative lengths of the fingers are $3 > 4 > 2 > 1$, of the toes $4 > 3 > 5 > 2 > 1$. Subarticular tubercles are only faintly evident. An inner metatarsal tubercle is present. The fingers and toes bear small, grooved discs, with the discs of the toes slightly larger than those of the fingers; toes and fingers are unwebbed.

There are two recurved spikes behind each internal naris. Peters and Doria (1878, p. 432) found the sternal apparatus "entirely the same" as that of *Kaloula* and *Microhyla*, both of which resemble *Xenobatrachus* in lacking clavicles and procoracoids.

"The upper parts are dark brown, irregularly spotted and marbled with darker. The under parts are whitish, reticulated with brown upon the throat and chest" (Peters and Doria, 1878, p. 433).

MEASUREMENTS OF SYNTYPE SPECIMEN: S-V, 27.0; TL, 13.3; HW, 9.1; Eye, 3.0; E-N, 1.9; IN, 2.1; EAR, 2.0. Both Peters and Doria (1878, p. 432) and Parker (1934, p. 58) gave the total length as 30 mm. Whether the difference between their measurements and mine results from measuring different specimens or from some other cause, I cannot say.

COMPARISON WITH OTHER SPECIES: The comparisons made in the diagnosis should serve to distinguish *Xenobatrachus ophiodon* from its two congeners with paired vomerine spikes. A characteristic of *ophiodon* not stressed above but probably of use in defining the species is the relatively great length of the hind legs: TL/S-V = 0.49. Presumably, a juvenile *X. giganteus* (of the size of an adult *ophiodon*) would have much

shorter legs, for the adults have ratios of 0.33 and 0.34. See a following section, "*Xenobatrachus* spp.," for a discussion of two additional, unidentified specimens with paired vomerine spikes.

DISTRIBUTION AND SPECIMENS EXAMINED: I have examined only the lectotype, MSNG 29129, from Hatam, Arfak Mountains, Vogelkop Peninsula, West Irian (fig. 61). No other specimens are known to exist.

Xenobatrachus rostratus (Méhely)

Figures 67, 68

Choanacantha rostrata MÉHELÝ 1898, p. 175 (type locality, Erima, Astrolabe Bay [Madang District], Territory of New Guinea. In the original description, Méhely [p. 175] referred to a "single female specimen from Erima" collected by Lewis Biró. Later [1901, p. 233] he referred to "des ersten (Erima)-Exemplares," and Parker [1934, p. 56] listed two adult syntypes in the Hungarian Museum, numbers 2414/6. The syntypes have been destroyed [I. Szabo, *in litt.*]).

Xenorhina rostrata: MÉHELÝ, 1901, p. 233.

Xenobatrachus rostratus: VAN KAMPEN, 1919, p. 54.

DIAGNOSIS: The presence of paired vomerine spikes behind each naris (only one in *X. rostra-*

tus) immediately distinguishes *Xenobatrachus bidens*, *X. giganteus*, and *X. ophiodon* from *X. rostratus*. Among the species with single spikes, *X. obesus* differs in its much larger maximum size (73 mm. as opposed to 44 mm.), distinctive color pattern and longer hind legs (TL/S-V minimum 0.49 in *obesus*, 0.37 maximum in *rostratus*).

Xenobatrachus macrops evidently is a larger frog than *rostratus*, reaching 55 mm. body length in contrast to 48 mm. The snout is longer in many *rostratus*, E-N/IN averages 1.2 or greater in contrast to less than 1.1 in *macrops*. In the short-snouted highlands populations of *rostratus*, the hind legs are shorter than in *macrops* (maximum TL/S-V is 0.32 in highlands *rostratus*, minimum 0.33 in *macrops*).

Xenobatrachus ocellatus differs from the long-snouted populations of *rostratus* (E-N/IN=1.2 or greater) in its shorter snout (E-N/IN less than 1.1). The highlands populations of *rostratus* are similar to *ocellatus* in snout length but have, on the average, slightly shorter hind legs. The average of TL/S-V is 0.25 and 0.28 for two samples of *rostratus*, 0.33 for *ocellatus*. The wholly dark belly of *ocellatus* and usual presence of a dark mark in the groin may also be diagnostic.

DESCRIPTION: Populations of *Xenobatrachus rostratus* vary notably in maximum size and color pattern (see Variation, below), but the frogs can generally be characterized as small (up to 48 mm. body length), short-legged, fat-bodied animals with small eyes and head much narrower than the body.

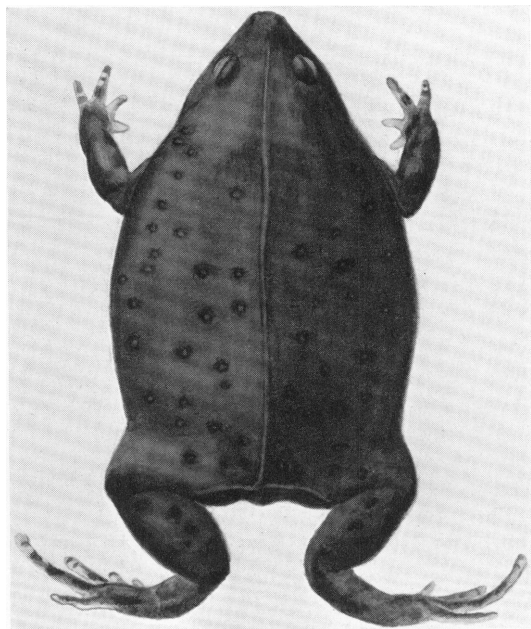


FIG. 67. *Xenobatrachus rostratus* (AMNH 76087), dorsal view. $\times 2$.

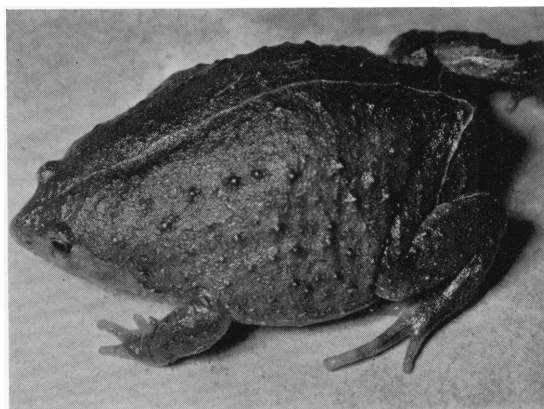


FIG. 68. *Xenobatrachus rostratus* (MCZ X7026 [field no.]), Igindi, Territory of New Guinea. Photo by Fred Parker.

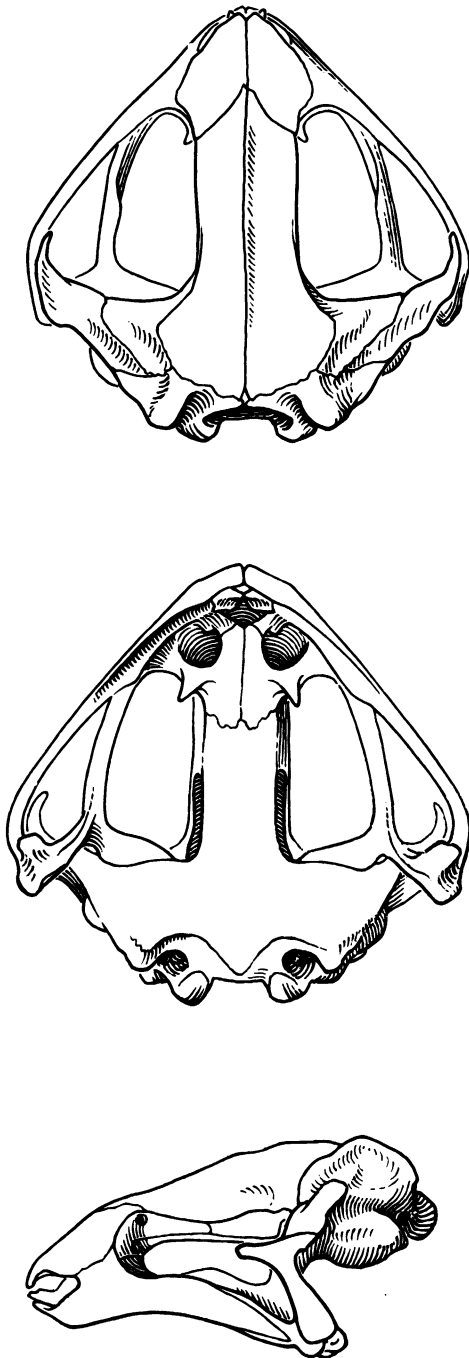


FIG. 69. Skull of *Xenobatrachus rostratus* (AMNH 76070) in dorsal (upper), ventral (middle), and lateral (lower) views. $\times 5.6$.

The snout is bluntly pointed and protrudes slightly, although I have seen no specimens with the snout developed to the extent illustrated by M  hely   for the type-specimen (1898, pl. 12, figs. 1, 3). The nostrils are much closer to the tip of the snout than to the eye. The canthal area is rounded (well-defined canthus rostralis lacking), and the loreal region is a gentle slope that is at the most only slightly concave. The upper surface of the snout may be pustulose or smooth. The interorbital space is about three times the width of an upper eyelid.

There is a weak skin fold above and behind the tympanum and in some a few scattered warts are present on the dorsal surface of the body and warty ridges on the hind limbs. Individuals may be quite smooth both above and below, however.

The fingers are bluntly pointed and without discs or grooves (fig. 63B). Their relative lengths are $3 > 4 > 2 > 1$. Scarcely discernible low, rounded elevations represent the subarticular and palmar tubercles. The toes have terminal grooves and discs that are barely wider than the penultimate phalanges. The relative lengths of the toes are $4 > 3 > 5 > 2 > 1$. There is a fairly distinct inner metatarsal tubercle, but the others are no better developed than on the front feet.

VARIATION: The specimens of *Xenobatrachus rostratus* that I have examined may be arranged into three groups, each of which has both geographic and morphological unity. The geographic units are the Huon Peninsula, the north coast, and the highlands (see table 8).

Members of the Seventh Archbold Expedition collected a large number of *Xenobatrachus* on the Huon Peninsula at elevations between 4400 and 7100 ft. above sea level. The largest of 60 specimens is 42 mm. in length from snout to vent. These are extremely short-legged frogs (TL/S-V mean 0.26) with relatively long snouts (E-N/IN mean 1.27). The eyes are small as in all *Xenobatrachus*, but are larger than in some other populations assigned to *X. rostratus* discussed below.

The dorsal pattern (in preservative) varies slightly from uniform brown to a somewhat mottled or blotchy pattern, occasionally with a trace of lumbar ocelli. The ventral pattern is extremely variable, ranging from virtually immaculate to heavily mottled or spotted (fig. 71, upper).

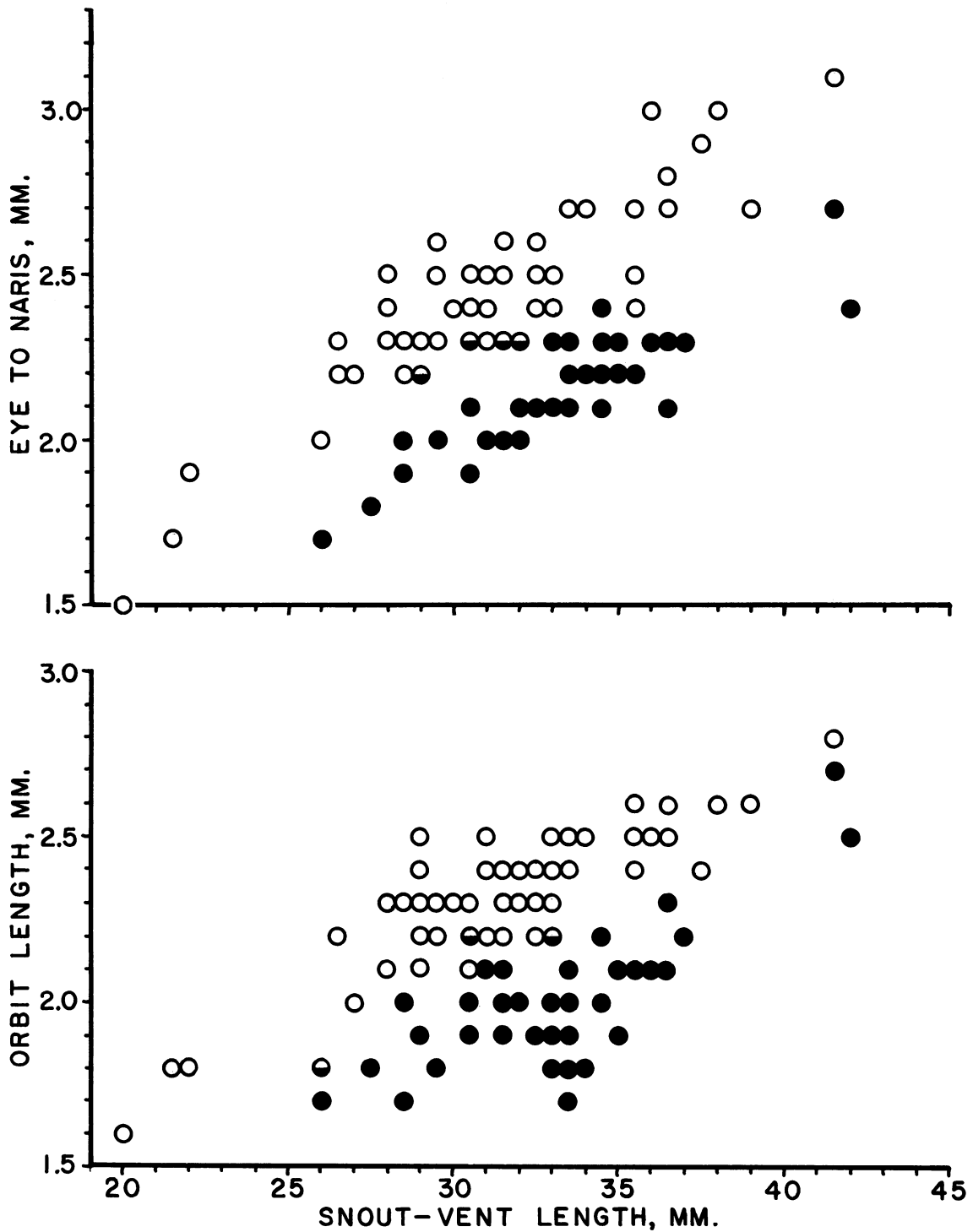


FIG. 70. Relationships of distance from eye to naris and of orbit length to snout-vent length in two samples of *Xenobatrachus rostratus*. Open circles represent specimens from the Huon Peninsula; closed circles indicate specimens from the Eastern and Western highlands; half-filled circles indicate individuals of both samples with identical measurements. Each symbol represents from one to five individual specimens.

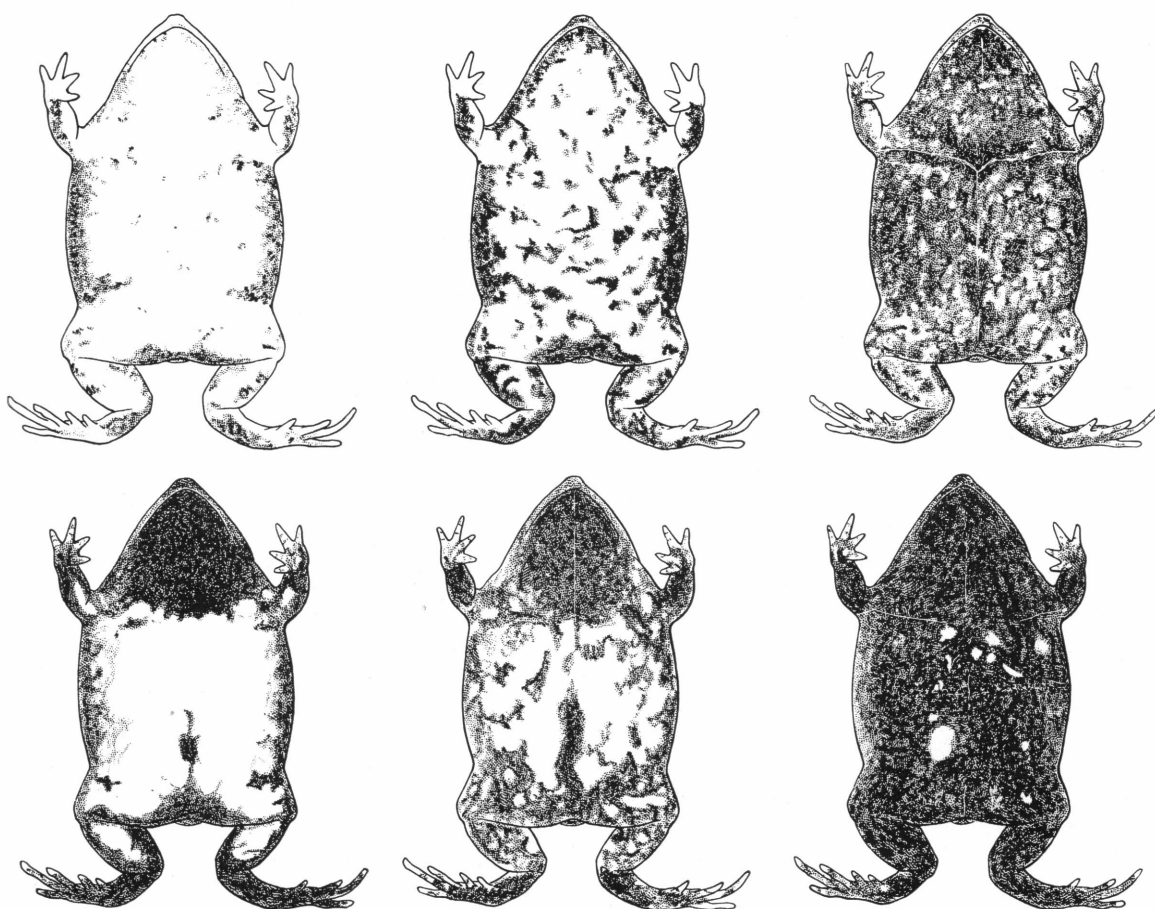


FIG. 71. Variation in ventral patterns of *Xenobatrachus rostratus*. Upper: Individuals from Huon Peninsula, Morobe District. Lower: Individuals from Kaironk Valley, Western Highlands District.

The next largest samples of *X. rostratus* are from mountainous areas in the Eastern Highlands and Western Highlands, 150 to 250 miles west of the localities on the Huon Peninsula. Fifty-three specimens from the Suai Ranges, Wahgi-Sepik Divide, and Schrader Mountains are sufficiently similar to be considered together. These frogs resemble those from the Huon Peninsula in maximum size (42 mm.) and in being short-legged (TL/S-V mean 0.27) but differ in relative snout length, eye size, and color pattern.

The average difference in eye size seems small (Eye/S-V mean 0.061 for highlands frog, 0.074 for those from the Huon Peninsula), but when the measurements are displayed graphically the

almost complete separation of the two samples is seen (fig. 70, lower).

The difference in snout length is evident in the scatter diagram (fig. 70, upper) and in the ratio E-N/IN: highlands mean 1.07; Huon mean 1.27. In some instances a difference in this ratio can be attributed to the difference in eye size, for a larger eye reduces the distance from eye to naris if other proportions do not change, but here just the opposite is seen: the frogs with larger eyes also have longer snouts.

Frogs from both the highlands and the Huon Peninsula show much variation in ventral pattern, but in those from the Schrader Mountains the chin typically is dark even in light-bellied individuals (fig. 71, lower). Tyler (1963,

pp. 13–14) described living specimens from the Wahgi-Sepik Divide as having uniform slate or dull orange dorsal and lateral surfaces, ventral surfaces creamy yellow marbled with slate, palmar surfaces orange with gray patches, and back of thighs and anal region black.

I have examined four specimens from the north coast: two from the Sermowai River, one from Mt. Nomo (both localities in the general region of Humboldt Bay), and one from Wewak. These localities are at low elevations, the maximum being about 180 m. (600 ft.). These specimens have relatively long legs (TL/S-V, 0.33–0.38), eyes of intermediate size for the species (Eye/S-V, 0.056–0.068), and rather long snouts (E-N/IN, 1.23–1.42). Three are notable for their large size: approximately 44 mm. (twice) and 48 mm. snout to vent.

These coastal frogs are distinctly different from those from the Huon Peninsula and the highlands in size and leg length. Among 115 specimens from the last two regions, only two (one from each area) measure longer than 40 mm., compared with three out of four from the coastal region. The greatest ratio of tibia length to snout-vent length among 110 frogs from the highlands and the Huon Peninsula is 0.33, whereas this is the minimum ratio in the small coastal sample.

There is evidence that this “coastal” influence extends well inland, south of the coastal ranges. Through the courtesy of James Menzies, I have examined four specimens from near the junction of the Kaironk and Jimi rivers, elevation approximately 4400 ft. These are large (41–43, S-V) and have long legs (TL/S-V, 0.32–0.36). The size and proportions are in marked contrast to the situation in a sample of 29 specimens from Fungoi at an elevation of 5500 ft. in the Kaironk Valley, no more than 15 miles (airline) away. In this sample, only one specimen (at 42 mm.) is greater than 37 mm. in length, and the mean TL/S-V ratio is 0.28 (range, 0.23–0.32).

The ventral color pattern of frogs from the north coast resembles that of the frogs from the Huon Peninsula in uniformity of spotting or mottling without the dark chin of the highlands specimens. Van Kampen (1914, p. 373) described a specimen from the Sermowai River as (in life) “Back gray, with white or rose-colored median line; abdomen fire-red with black spots.” The specimen from Wewak, which I

examined a few days after it was preserved, was also bright red beneath.

COMPARISON WITH OTHER SPECIES: The species with paired vomerine spikes and one species with single spikes, *X. obesus*, are sufficiently distinct from *rostratus* that further comparisons are not necessary (see Diagnosis). *Xenobatrachus mehelyi* and *X. rostratus* are compared in the account of the former species. Comparisons with the remaining two species, *macrops* and *ocellatus*, are hampered by the inadequacy of material of those species.

Greater average size, longer hind legs and larger eyes differentiate *X. macrops* from *rostratus*. All four type-specimens of *macrops* are larger than almost all *rostratus* (48–55 mm., S-V, in contrast to a maximum of 48), and another specimen tentatively assigned to *macrops* is almost as large as the types (45 mm.). The minimum ratio of tibia length to snout-vent length is greater in the types of *macrops* (0.45) than the maximum recorded for *rostratus* (0.38), but the tentatively assigned specimen from the Weyland Ranges has a ratio (0.33) within the range of *rostratus* although at the upper limit recorded for *rostratus* from high elevations. The relative size of the eye, as measured by the ratio, Eye/S-V, appears to be larger in *macrops* than in most *rostratus* (see table 8), but the difference is too slight and too subject to ontogenetic variation to be of much use in identification.

The color pattern of *X. ocellatus* provides the best means of distinguishing this species from *rostratus*. The uniformly dark ventral surfaces and light-bordered spot (or coarse mottling) in the groin are not duplicated in *rostratus*, though some individuals have the venter all dark. In comparison with *rostratus* from the Eastern and Western highlands, *ocellatus* has longer hind legs and larger eyes (table 8), but these differences are not consistent when all samples of *rostratus* are considered.

TAXONOMIC NOTES: A case could be made for dividing *X. rostratus* into three geographically discrete taxonomic units characterized by differences in maximum size, relative proportions of eyes, snout, and legs and in color pattern. I am not yet ready to propose recognition of more than one form because of the paucity of material from critical areas. With which population to associate the name *rostratus* is the fundamental problem. The type-specimens have been destroyed. The type locality is at sea level, and the

specimen from the closest locality on the north coast at a similar elevation comes from 200 miles away. The localities on the Huon Peninsula are 120 miles from the type locality and at a minimum elevation of 4400 ft. Probably *rostratus* is the proper name for the coastal population, but I think it best to refrain from adding taxonomic complications until the collection of new material from the vicinity of the type locality establishes the status of the population with greater certainty.

A comment must be made here on Parker's (1934, pp. 55-56) treatment of *X. rostratus*. He examined six specimens that he assigned to this species. Two were the syntypes of *rostratus* and one was an adult in the Amsterdam Museum from the Sermowai River, probably the same one I examined. A specimen from the Weyland Range (BMNH 1921.11.11.5) I have tentatively assigned to *X. macrops*. The remaining two specimens, a male and female in the Amsterdam Museum from the "Hellwig Mts., 2,200 m.," probably are the lectotype and a paratype (Daan and Hillenius, 1966, p. 126) of *X. macrops*. Van Kampen (1909, p. 39) originally assigned these specimens to *Xenorhina rostrata* and later referred them to *Xenorhina macrops* (1913, pp. 460-461).

ECOLOGICAL NOTES: Published information on the ecology of *X. rostratus* is limited. Tyler (1963, p. 14) stated, "All specimens were found beneath moss on 20.5.60 at the summit of a pass north of Banz (16 road-miles west of Nondugl), at an altitude of 9,000-9,500 feet upon the Wahgi-Sepik Divide. The pass was covered by low cloud, and the ground saturated with water." Cogger (1965, p. 6) noted: "It is very common in old garden areas, where it burrows among the grass roots. It is heard calling throughout the day, though the local inhabitants maintain that its call is really that of an earthworm."

Natives clearing primary forest for an Archbold Expeditions camp at Gang Creek, 4400 ft., on the Huon Peninsula, uncovered two *Xenobatrachus* in the leaf litter. On the same expedition to the Huon Peninsula, Hobart M. Van Deusen and Stanley Grierson collected several individuals that were calling from within the humus during gentle daytime rains.

DISTRIBUTION AND SPECIMENS EXAMINED: Present information indicates a wide distribution for this species throughout the northeastern part of New Guinea, from the vicinity of Djayapura (Hollandia) to the Huon Peninsula and from

close to sea level to perhaps 9500 ft. (2900 m.) on the Wahgi-Sepik Divide (fig. 65). I have not included here a record by van Kampen (1923, p. 128) for "near Idenburg riv., $\pm 800-1000$ m." because I have not examined the specimen.

West Irian: Mt. Nomo, 600 ft. (180 m.), SSW Mt. Bougainville (BMNH 1938.6.5.80); Sermowai River, ± 70 m. (230 ft.) (ZMA, no number; MZB 148); mouth of Tami River (Vogt, 1911a, p. 420).

Territory of New Guinea: "German New Guinea" (no exact data, AMNH 23584). Madang District: Erima, Astrolabe Bay (type locality, Méhely, 1898, p. 175). Morobe District: Sattelberg (Méhely, 1901, p. 233); Gang Creek, Mt. Rawlinson, 4400 ft. (1340 m.) (AMNH 76048, 76049); divide between Ogeramang and Tobou, 6000-6500 ft. (1830-1980 m.) (AMNH 76050-76052); head of Kua River Valley, NW Avengu, 5300-7100 ft. (1600-2160 m.) (AMNH 76053-76098+5 untagged, 84447, 84448); Indagen, north slope of Mt. Kiren (AMNH 76099); near Indum (AMNH 76100). Chimbu District: Igindi, Suai Ranges (MCZ 59702-59715, 59717; AMNH 76590, 76591); Dumun, Porol Ranges (MCZ 59716). Western Highlands District: Wahgi-Sepik Dividing Range, N Banz, 9000-9500 ft. (2740-2900 m.) (BMNH 1961.877, 1961.878; AMNH 67609); confluence of Kaironk and Jimi rivers, 4500 ft. (1370 m.) (UPNG 1062, 1063, AMNH 83843, 83844); Fungoi, Kaironk Valley (AM 22775-22777, 22779, 22781, 22783, 22785, 22789-22792, 22796, 22798, 22806, 22810, 22812, 22814, 22828-22840); Tomba, 8200 ft. (2500 m.) (MCZ 81672, 64805).

Xenobatrachus spp.

I have examined four specimens that I am unwilling to assign to known or new species.

The first individual, SAM 6408, was obtained by B. Craig at Busilmin (latitude $4^{\circ} 55' S.$, longitude $141^{\circ} 06' E.$) in the Star Mountains of the West Sepik District, Territory of New Guinea, on May 7, 1965. The locality is in the midst of a montane area from which few other specimens of *Xenobatrachus* have been taken. *Xenobatrachus mehelyi* occurs about 35 mi. to the southeast at Imigabip (4200 ft.), and an unidentified form occurs about 40 mi. to the west (see below).

The specimen has the following measurements: S-V, 20.0; TL, 8.2; HW, 6.6; Eye, 1.8;

E-N, 1.4; IN, 1.4. The hind legs are long (TL/S-V, 0.43) and the eyes moderately large (Eye/S-V, 0.09). There is nothing particularly distinctive about the head width (HW/S-V, 0.33) or snout length (E-N/IN, 1.00). The tympanum is indistinct. The tips of the fingers are slightly pointed and disclike, but not expanded. The toes bear small discs. The vomerine spikes are single.

The dorsal surfaces are brown with some irregular darker mottling, but no distinct pattern. The chin and chest are mottled with dark brown, but the rest of the venter is pale and unmarked.

The specimen is a female with the largest ova less than 1 mm. in diameter. Despite their small size, I infer that the frog was approaching adulthood because several of the ova are clearly enlarged, in contrast to the other minute ova.

The ventral color of this specimen resembles that of lightly pigmented individuals of *rostratus* from the Eastern and Western highlands. It differs from these montane *rostratus*, however, in its much longer hind legs and in that the distance from eye to naris is much less than the length of the orbit.

If the specimen were a juvenile *macrops*, it would be expected to have larger eyes. A *macrops* of almost the same size (22 mm. S-V) has an orbit length of 2.5 mm., compared to 1.8 mm. in the Busilmin specimen. The ventral pattern of the questionable specimen is not that of *macrops* and, if the inference about approaching adulthood is correct, it is a smaller species than *macrops*.

The specimen closely resembles *X. mehelyi* in leg length, but has larger eyes and a lower E-N/IN ratio than is recorded for that species; for the present I prefer to leave it unassigned to species.

A second puzzling specimen from the Star Mountains is RMNH 16619 from Tenmasigin, 6 km. N Mabilabol, West Irian. This is a small individual with small, single vomerine spikes and the following measurements and proportions: S-V, 17.0; TL, 5.5; HW, 5.8; Eye, 1.4; E-N, 1.5; IN, 1.2; TL/S-V, 0.32; HW/S-V, 0.34; E-N/IN, 1.25; Eye S-V, 0.08. It differs from the Busilmin specimen in having relatively shorter hind legs and a much higher E-N/IN ratio; it is unlikely that the two represent the same species. The specimen from Tenmasigin does not correspond well with either *mehelyi* or *rostratus* (highlands populations), and cannot be

accommodated easily in the species known from montane areas farther west (*ocellatus* and *macrops*). It is best left unassigned to species.

I have examined two specimens of *Xenobatrachus* with paired vomerine spikes in addition to the six of *X. bidens*, *X. giganteus*, and *X. ophiodon*. These are RMNH 1194 and 1191, collected at Paniai, Wissel Lakes, West Irian, on October 2, 1939. They are, respectively, 42 and 32 mm. in length from snout to vent and have the following proportions: TL/S-V, 0.45, 0.48; HW/S-V, 0.35, 0.38; E-N/IN, 1.24, 1.09; Eye/S-V, 0.081, 0.091; EAR/Eye, 0.79, 0.86. In size, these frogs resemble *ophiodon* and *bidens* rather than *giganteus*. Tibia length is between that of *ophiodon* (0.49) and *bidens* (0.40–0.44), as is head width. The ratios indicative of eye size and relative placement of nares also are intermediate between those of *ophiodon* and *bidens*. It may be that the two specimens from Paniai are intergrades between the populations recognized as *ophiodon* and *bidens*, but I am reluctant to synonymize *bidens* (the younger name) on such meager evidence. I prefer to let the Paniai specimens stand as unidentified pending acquisition of more adequate material of all forms concerned.

GENUS *XENORHINA* PETERS

Xenorhina PETERS, 1863, p. 82 (type-species by monotypy, *Bombinator oxycephalus* Schlegel).

Callulops BOULENGER, 1888, p. 345 (type-species by monotypy, *Callulops doriae* Boulenger).

Pseudengystoma WITTE 1930a, p. 132 (type-species by monotypy, *Pseudengystoma bouwensi* Witte).

DIAGNOSIS: *Xenorhina* is distinguished by the following combination of characters: (1) maxillary bones in contact in front of the premaxillae; (2) dentary bones in contact in front of and fused with the mento-meckelian bones; (3) vomerine bones expanded anteriorly and posteriorly on their median line of contact, but lacking toothlike spikes; (4) parasphenoid bone almost as broad as the frontoparietals; (5) no secondary arch of bone over the prootic region; (6) roofing bones of skull smooth; (7) nasal bones not fused; (8) eyes relatively small, ratio Eye/S-V averaging less than 0.090 in all species.

Xenobatrachus differs from *Xenorhina* only in possessing one or two prominent, toothlike spikes on each vomer. *Phrynomantis* resembles *Xenorhina* in the first and second characters listed

TABLE 9
BODY PROPORTIONS IN SIX SPECIES OF THE GENUS *Xenorhina*

| Species | N | TL/S-V | | | HW/S-V | | | Eye/S-V | | | E-N/IN | | |
|----------------------|-----------------|-------------------|---------------|-------|-------------------|---------------|-------|-------------------|---------------|-------|-------------------|---------------|-------|
| | | Mean | $\pm\sigma_m$ | Range | Mean | $\pm\sigma_m$ | Range | Mean | $\pm\sigma_m$ | Range | Mean | $\pm\sigma_m$ | Range |
| <i>X. bouvensi</i> | 17 | 0.392 \pm 0.003 | (0.37–0.41) | | 0.343 \pm 0.004 | (0.31–0.39) | | 0.084 \pm 0.001 | (0.080–0.091) | | 1.19 \pm 0.024 | (0.93–1.38) | |
| <i>X. doriae</i> | 27 | 0.342 \pm 0.003 | (0.31–0.36) | | 0.357 \pm 0.003 | (0.32–0.38) | | 0.075 \pm 0.012 | (0.063–0.097) | | 1.06 \pm 0.014 | (0.94–1.21) | |
| <i>X. minima</i> | 1 | 0.29 | — | | 0.34 | — | | 0.081 | — | | 0.83 ^a | (0.81–0.86) | |
| <i>X. oxycephala</i> | 11 | 0.423 \pm 0.004 | (0.40–0.45) | | 0.336 \pm 0.005 | (0.31–0.37) | | 0.064 \pm 0.001 | (0.060–0.067) | | 1.49 \pm 0.044 | (1.30–1.79) | |
| <i>X. parkerorum</i> | 8 | 0.410 \pm 0.011 | (0.37–0.46) | | 0.350 \pm 0.008 | (0.32–0.39) | | 0.065 \pm 0.004 | (0.054–0.083) | | 1.00 \pm 0.044 | (0.81–1.18) | |
| <i>X. similis</i> | 16 ^b | 0.329 \pm 0.006 | (0.28–0.36) | | 0.345 \pm 0.003 | (0.32–0.37) | | 0.065 \pm 0.001 | (0.058–0.072) | | 1.14 \pm 0.012 | (1.04–1.22) | |

^aFor E-N/IN only, N = 2.

^bFor TL/S-V only, N = 13; all proportions given are for the type series.

above and in lacking vomerine spikes, but the vomers show little or no mesial expansion, the parasphenoid is little more than one-half the width of the frontoparietals, and the eyes are relatively large (Eye/S-V mean 0.100 or greater in most species). *Hylophorbus* differs from *Xenorhina* in the same ways as does *Phrynomantis*, and in addition lacks the contact of the maxillae and of the dentaries. *Barygenys* lacks the anterior maxillary contact of *Xenorhina*. The vomers are in broad contact mesially, but the expansion does not take the winglike form of *Xenorhina*. Eye size, dentary contact, and relative breadth of parasphenoid bone are similar in *Barygenys* and *Xenorhina*. *Asterophrys* differs most notably from *Xenorhina* in its frontoparietal crest, fused nasals, and rugosity of skull bones. *Pherohapsis* differs from *Xenorhina* in the last two characters mentioned and in addition has a unique arcade of bone over the prootic region and anterior contact of the maxillary and squamosal bones.

CONTENT: I assign six species, one of them new, to this genus: *X. bouwensi* (Witte); *X. doriae* (Boulenger); *X. minima* (Parker); *X. oxycephala* (Schlegel); *X. parkerorum*, new species; *X. similis* (Zweifel).

DESCRIPTION: The genus *Xenorhina* includes the smallest and largest species of the subfamily Asterophryinae, with adults ranging in maximum size from 24 mm. (*bouwensi*) to 100 mm. (*doriae*) snout to vent length. All *Xenorhina* are heavy-bodied frogs with relatively narrow heads (HW/S-V, 0.31–0.38) and very small eyes (Eye/S-V less than 0.100). Both relatively long-legged (TL/S-V up to 0.46) and short-legged (TL/S-V as low as 0.28) species occur. Subarticular tubercles are poorly developed or virtually absent. The fingers lack terminal discs or have them poorly developed. Disc development is somewhat greater on the toes, but one species (*minima*) entirely lacks toe discs.

I have examined complete skulls of three species: *doriae*, *oxycephala*, and *similis*. These are characterized by extensive development of the nasal bones (fig. 79), broad parasphenoid (almost as wide as the frontoparietal), strong anterior and posterior projections along the mesial edges of the vomers (fig. 3H), and a projection from the anterior end of the maxillary shelf that approaches or touches the vomer. There is no bony encrustation of the dorsal surface of the skull. The anterior arm of the squamosal does not reach the maxilla. The

anterior ends of the maxillae contact in front of the premaxillae.

Such features of the skull as could readily be examined by reflection of skin were examined in two other species: *bouwensi* and *parkerorum*. These species agree with those mentioned above in the premaxillary contact, form of vomers and parasphenoid, and development of squamosal. I made no examination of the skeleton of *X. minima*, and assign it to *Xenorhina* on the basis of its external characteristics.

DISTRIBUTION: Species of the genus *Xenorhina* are found throughout New Guinea, from the Vogelkop Peninsula to the Louisiade Archipelago, and from virtually sea level to 2800 m. (9200 ft.).

KEY TO THE SPECIES OF *Xenorhina*

1. E-N/IN mean 1.49, minimum 1.30; TL/S-V minimum 0.40 *oxycephala*
E-N/IN mean less than 1.25, maximum rarely as great as 1.30; TL/S-V usually less than 0.40 2
2. Tips of neither fingers nor toes broadened into discs wider than the penultimate phalanges 3
Tips of toes broadened into discs distinctly wider than penultimate phalanges 4
3. E-N/IN greater than 1.00; size larger, up to 51 mm. S-V *similis*
E-N/IN less than 1.00; size smaller, maximum S-V 28 mm. *minima*
4. Size small, maximum S-V length 24 mm.; fingers with little or no development of discs (fig. 75E) *bouwensi*
Size larger, adults greater than 24 mm. S-V; fingers with at least small discs present (fig. 75A–D) 5
5. Size larger (to 100 mm. S-V); dorsal pattern of round brown spots, many centered with white-tipped warts; posterior surfaces of thighs dark with large pale spots or mottling; legs shorter, TL/S-V maximum 0.36 *doriae*
Size smaller (maximum 68 mm. S-V); color pattern not as described; legs longer, minimum TL/S-V, 0.37 *parkerorum*

Xenorhina bouwensi (Witte), new combination

Pseudengystoma bouwensi WITTE, 1930a, p. 132 (type locality Arfak Mountains, 1000 m., Vogelkop Peninsula, West Irian; holotype, IRSNB 9223:III, collected March 8, 1929, by the Duke of Brabant). *Asterophrys bouwensi*: PARKER, 1934, p. 67.

DIAGNOSIS: *Xenorhina bouwensi* differs from most other species of the genus in its small size (maximum length from snout to vent, 24 mm.)

and in having the tips of the toes but not of the fingers enlarged into discs.

Only one other *Xenorhina*, *X. minima*, is of similarly small size. It closely resembles *X. bouwensi* in general appearance, but lacks discs on the toes, is shorter-legged (TL/S-V, 0.29; mean of *bouwensi* 0.39) and has the nostrils relatively more widely spaced (E-N/IN, 0.81; mean of *bouwensi* 1.19).

Other species of *Xenorhina* and *Phrynomantis* that lack finger discs or have them poorly developed (*X. parkerorum*, *X. similis*, *P. stictogaster*, and *P. wilhelmana*) are so much larger than *X. bouwensi* that there is little likelihood of confusion. Species of *Xenobatrachus* and *Barygenys* are superficially similar to *X. bouwensi* but are readily distinguished, the first by the possession of vomerine spikes, the second by vertical ridges on the snout and the eleutheroagnathine condition of the maxillary bones.

DESCRIPTION OF TYPE-SPECIMEN: The type is a squat, chunky frog, with the head much narrower than the body. The snout is bluntly pointed and the canthal region is rounded, without a trace of a canthal angle. The loreal area is oblique, flat, and slightly pustulose. The nostrils are much nearer to the tip of the snout than to the eye. The internarial distance is slightly greater than the distance from eye to naris. The eyes are small, the horizontal diameter being less than the length of the snout. The interorbital space is more than one and one-half times the width of an upper eyelid. The tympanum is indistinct and has a diameter about 80 per cent of that of the eye. There is no supratympanic fold.

The relative lengths of the fingers are $3 > 2 > 4 > 1$. The fingers are short and blunt, without terminal discs or grooves, and with only the faintest trace of subarticular elevations (fig. 75E). The relative lengths of the toes are $4 > 3 > 5 > 2 > 1$. The tips are dilated into grooved discs slightly but distinctly broader than the penultimate phalanges. Low, rounded subarticular tubercles are present, but the outer metatarsal tubercle is virtually absent. The fingers and toes are unwebbed.

The dorsal color is brown, with a pattern of slightly darker spots coinciding with small warts on the hind limbs and posterior part of the body. Dark crossbars are present on the feet and toes, and less distinct ones on the arms. All ventral

surfaces are mottled with brown on a light tan background.

The anterior processes of the maxillary bones are nearly in contact but are not firmly sutured. Clavicles and procoracoids are lacking. The snout of the specimen is damaged and the bones broken, but it is in good enough condition that if vomerine spikes were present they would be visible, which they are not.

The type-specimen is an adult female containing eggs 2 mm. in diameter. Witte (1930a, 1930b) illustrated the type-specimen.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 18.8; TL, 7.4; HW, 6.7; Eye, 1.6; E-N, 1.3; IN, 1.4; EAR, 1.3.

VARIATION: I have examined 18 specimens of this species, including the holotype. All are small frogs; the largest has a snout-vent length of 24 mm. Proportions are rather similar in all (see table 9). In none of the specimens are there well-developed finger discs. In many the rounded tip of the finger is very slightly broader than the width of the penultimate phalange, and the tip of the third finger may be weakly grooved. The internarial distance of the holotype is slightly greater than the distance from eye to naris, whereas the opposite is true of all other specimens. Because the nasal region of the holotype is damaged, I accord no significance to this difference.

No great differences in pigmentation exist among the specimens examined. The dorsal surfaces are dark purplish brown with obscure, darker mottling or spotting present in some instances. A dark, light-edged lumbar ocellus is present in all specimens from the Sibil Valley but not in the holotype. Some specimens possess a light vertebral hairline. A triangular, black "seat patch" is less evident in the holotype than in the others. In the holotype the chin is only slightly more heavily mottled than the abdomen, but in the other specimens the chin and chest are notably darker. Brongersma and Venema (1962, p. 103) referred to these frogs as "almost black."

TAXONOMIC NOTES: Brongersma and Venema (1962, p. 103) referred to frogs from Kigonmedip as *Asterophrys minima*. Direct comparison of the holotype of *A. minima* with specimens from Kigonmedip made evident the differences in leg length, toe discs, and internarial distance that I emphasize in the foregoing diagnosis.

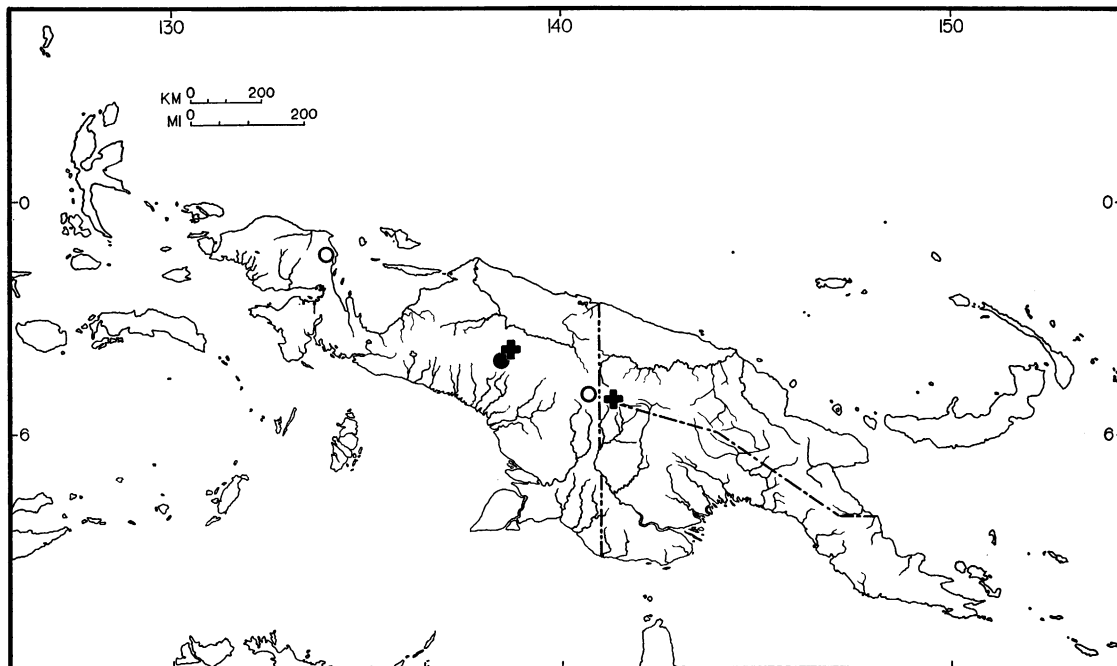


FIG. 72. Distribution of three species of *Xenorhina*. Crosses, *X. similis*; open circles, *X. bouwensii*; closed circle, *X. minima*.

DISTRIBUTION AND SPECIMENS EXAMINED: Specimens collected on the Netherlands Star Mountains Expedition of 1959 extended the known range of this species about 500 miles east-southeast of the only previously known locality, the type locality on the Vogelkop Peninsula (fig. 72). West Irian: Arfak Mountains, 1000 m. (3280 ft.), Vogelkop Peninsula (IRSNB 9223: III, holotype); Mabilabol, Sibil Valley, 1260 m. (4040 ft.) (RMNH 16630, 16640, 16643 [2 specimens]; Sibil Valley 1250 m. (4010 ft.) (BBM 1015); Kigonmedip, Sibil Valley (AMNH 84502; RMNH 16657 [5 specimens], 16658 [5 specimens]); 2 mi. N Dasiga (BBM 3686, locality not found).

Xenorhina doriae (Boulenger),
new combination

Figures 73, 74

Callulops doriae BOULENGER, 1888, p. 345 (type locality, "Milne Gulf" [Milne Bay, Milne Bay District, Territory of Papua]; holotype, BMNH 1947.2.10.99 [formerly 88.3.21.10], collected by H. O. Forbes).

Manthophryne neuhausii VOGT, 1911b, p. 425 (type locality, "Sattelberg," Morobe District, Territory of New Guinea; holotype ZMB 22156, collected by "Herr Prof. Dr. Neuhauss").

Hylophorbus neuhausii: VAN KAMPEN, 1923, p. 144.

Asterophrys doriae: PARKER, 1934, p. 65.

DIAGNOSIS: This species may be distinguished from other *Xenorhina* by the large size it attains (up to 100 mm. snout to vent) and by its dorsal color pattern of brown spots, many with white centers, a pattern seen in no other species.

DESCRIPTION: The body is broad and tapers to the relatively narrow head and slightly truncate snout. The largest specimen I examined measures 89 mm. snout to vent, but Parker (1934, p. 66) recorded a length of 100 mm. The canthus rostralis is rounded and the loreal region oblique but nearly vertical. There is a shallow depression posterior to the nostril, but the rest of the loreal region is slightly convex. The nostrils are closer to the tip of the snout than to the eyes and are lateral but angled slightly forward. The tympanum may be distinct or not, and its horizontal diameter is usually 70 per cent or more (13 of 16 specimens, up to 94 per cent) of

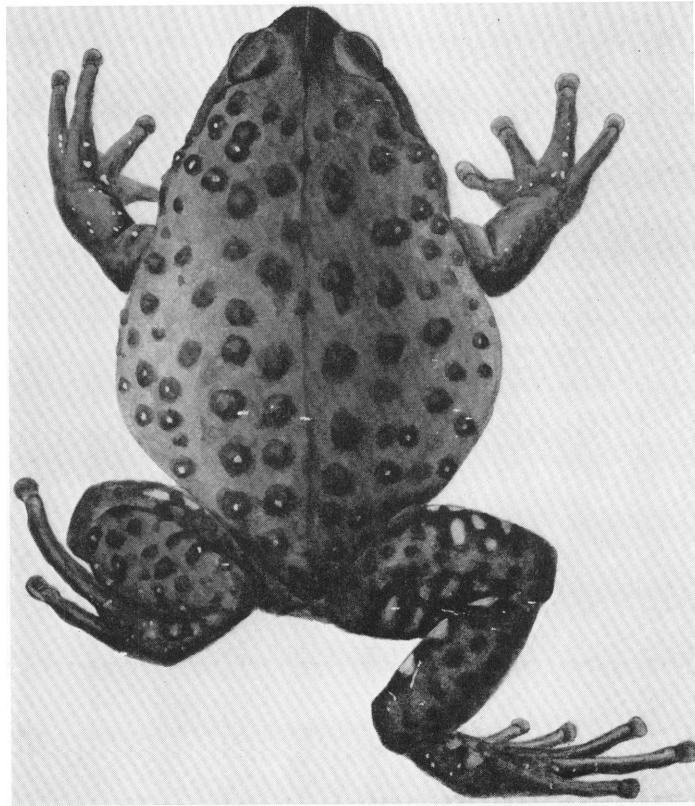


FIG. 73. *Xenorhina doriae* (AMNH 76462), dorsal view. $\times 1$.

the diameter of the eye. The internarial distance is usually only slightly less than the distance from eye to naris.

The skin of the body is smooth middorsally, but the sides, posterior part of the body, and hind limbs are warty, the warts and brown spotting of the color pattern being coincident. An indistinct fold of skin passes from the posterior corner of the eye above the tympanum and then abruptly downward.

The fingers (fig. 75A) and toes are relatively short and blunt-tipped with small discs, those of the toes being slightly the larger. The relative lengths of the fingers are $3 > 4 \geq 2 > 1$, and of the toes, $4 > 3 > 5 > 2 > 1$. There are low, rounded subarticular prominences, but metacarpal and metatarsal tubercles are scarcely indicated.

A specimen from Garaina (fig. 74) had the following colors in life: ground color of dorsal surfaces moderately dark brown; dorsal surfaces with rather evenly spaced warts, each with a bluish white tip and black base; similar light spots present on lower limbs where warts not

present; posterior surfaces of thighs dark brown, almost black, with creamy white mottling; ventral surfaces, including limbs, gray with lighter and darker indistinct spotting and mottling; chin slightly darker than posterior part of abdomen; iris speckled with brownish gold, highly similar to dorsal surfaces of body.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 73.7; TL, 25.7; HW, 26.5; Eye, 5.5; E-N, 4.7; IN, 5.0; EAR, 4.9.

VARIATION: There is relatively little variation in proportions (table 9). In only four of 27 individuals is the internarial distance greater than the distance from eye to naris. *Xenorhina doriae* is almost the largest species of microhylid frog, reaching a maximum length of 100 mm. Evidently its only rivals are *Platyhyla grandis* and *Dyscophus guineti* of Madagascar, for which species Parker (1934, pp. 37 and 25) recorded maximum lengths of, respectively, 95 and 102 mm.

The color pattern described above is rather characteristic of *X. doriae*. The specimen from Sudest Island has a dark brown dorsal color



FIG. 74. *Xenorhina doriae* (AMNH 82886).

without spotting evident. This specimen is considerably wartier than others; even the mid-dorsal region is not smooth. Burt and Burt (1932, p. 485), referring to two specimens from Mt. Lamington, stated, "The back is black . . .," but I would characterize it (at least in the present state of preservation) as dark brown; darker spots are present.

COMPARISON WITH OTHER SPECIES: The only species of *Xenorhina* that might be confused with *X. doriae* are *X. oxycephala* and *X. parkerorum*. The first is much smaller than *doriae* (maximum snout-vent length, 47 mm.), has smooth dorsal skin, lacks the characteristic pattern of light spots or mottling in the groin and on the concealed surfaces of the thighs, and has the nostrils relatively much more closely spaced (E-N/IN minimum 1.30). *Xenorhina parkerorum* is compared with *doriae* in the account of the former species.

TAXONOMIC NOTES: Relatively few specimens of this species have reached collections and the taxonomy has (perhaps as a result) remained relatively simple. Parker (1934, p. 65) assigned *Manthophryne neuhaussi* Vogt with question to the synonymy of *doriae*; he had not examined the type-specimen. Through the courtesy of Dr. Günther Peters I was able to examine the holotype (ZMB 22156), and I confirm its identity with *doriae*.

Two misidentifications in the literature must be mentioned. Kinghorn (1928, p. 289) referred to specimens from Mt. Lamington as "*Hylophorbus* sp." and later (1929, pp. 76–77) discussed these and additional specimens more at length

as "*Hylophorbus robustus*." Parker (1934, p. 65) accepted Kinghorn's identification, but the specimens (which I have examined) are *Xenorhina doriae*. The other misidentification was by Burt and Burt (1932, p. 485), who identified two specimens from Mt. Lamington as *Xenorhina oxycephala* (Zweifel, 1956, p. 4).

ECOLOGICAL NOTES: Nothing has been published with respect to the ecology of this species, but presumably it is an inhabitant of the floor of the rain forest. Records range in elevation from near sea level (Sudest Island) to 6000 ft. (1830 m.) (Mt. Albert Edward). The only living individual I have seen came from hilly rain forest at an elevation of 700 m.

DISTRIBUTION AND SPECIMENS EXAMINED: The few records for this species are scattered through the eastern part of New Guinea, including the Huon Peninsula, both northern and southern watersheds of the Territory of Papua, and as far east as Sudest Island (fig. 76). Collections that notably extend the previously known range of this species were made by the Fifth Archbold Expedition on Sudest Island and by Fred Parker at Bomai.

Territory of New Guinea: Morobe District: Garaina, 2300 ft. (700 m.) (AMNH 82886); Sattelberg (ZMB 22156, holotype of *Manthophryne neuhaussi*). Chimbu District: Bomai (AMNH 76462; MCZ 59898–59901, 60800–60804, X6654, X6655).

Territory of Papua: Northern District: Mt. Lamington (AMNH 35406, 35407; SAM 4256 [4 specimens]; AM 9343, 9602–9606). Central District: Mondo, 5000 ft. (1520 m.) (Parker, 1936, p. 72); Albert Edward Mountains, 6000 ft. (1830 m.) (Parker, 1934, p. 66); Astrolabe Mountains, 4000 ft. (1220 m.) (Parker, 1934, p. 66); Haveri (MSNG 29435). Milne Bay District: Milne Bay (BMNH 1947.2.10.99, holotype of *Callulops doriae*); Rambuso, Sudest Island (AMNH 60035).

Xenorhina minima (Parker),
new combination

Xenorhina ocellata (part): VAN KAMPEN, 1913, p. 461.
Asterophrys minima PARKER, 1934, p. 67 (type locality, "Went. Mts., 1,000–1,360 m.," West Irian; holotype, ZMA 5818, collected on the Netherlands South New Guinea Expedition, October 13, 1909).
Asterophrys pansa minima: LOVERIDGE, 1948, p. 307.

DIAGNOSIS: *Xenorhina minima* is the only small species of its genus (snout to vent length less than

30 mm.) with the tips of both fingers and toes bluntly rounded, lacking terminal discs. The other asterophryine species that lack discs are *X. similis*, *Phrynomantis stictogaster* and *P. wilhelmana*. The maximum known lengths of these three species are, respectively, 51, 80, and 54 mm. Other external differences from *X. minima* include the following: distance from eye to naris greater than internarial distance in *similis*, less than internarial distance in *minima*; a tubercle between eye and nostril in *stictogaster*, but none in *minima*; eye smaller in *minima*, Eye/S-V = 0.08 compared with an average of about 0.10 in *wilhelmana*.

DESCRIPTION OF HOLOTYPE SPECIMEN: My brief examination of the holotype was limited largely to making measurements; hence, I quote Parker's (1934, p. 67) original description: "Anterior palatal ridge reduced to a median tubercle. Snout bluntly rounded, slightly prominent, a little longer than the diameter of the eye; canthus rostralis rounded; loreal region oblique, concave; interorbital space about as broad as the upper eyelid; tympanum very indistinct, a little smaller than the eye. Fingers without discs, the second shorter than the fourth. Toes also without discs, the third longer than the fifth; subarticular and inner metatarsal tubercles very indistinct. Tibio-tarsal articulation reaching the shoulder.

"Skin smooth above and below; a few small, scattered warts on the sides; a supratympanic fold.

"Pale brown above, stippled with darker; a definite triangular marking from the posterior corner of the eye to the angle of the mouth, a smaller spot on the lip in front of the eye and a spot on the tip of the snout, clear white; a fine white line from snout to vent. Lower surfaces dusted with dark brown; a white stripe along the edge of the lower jaw, continued to the shoulder; under surfaces of the limbs, hands and feet also white."

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 28.0; TL, 8.1; HW, 9.4; Eye, 2.3; E-N, 1.7; IN, 2.1.

The type-specimen is a female, according to Parker.

VARIATION: The only specimen other than the holotype, the paratype, was thought by van Kampen (1913, p. 461) to be a juvenile and he referred it with question to *Xenorhina ocellata* (*Xenobatrachus ocellatus*); Parker regarded it as

"apparently fully adult." The specimen is now in too poor a condition for accurate measurement or study of color pattern.

COMPARISON WITH OTHER SPECIES: Sufficient comparisons with species resembling *X. minima* in foot structure have been made in the Diagnosis. The only other species meriting close comparison is *X. bouwensi*, which resembles *minima* in size and general appearance. The presence of grooved discs on the toes of *bouwensi* should immediately distinguish it from *minima*. In addition, *bouwensi* has longer legs (TL/S-V, 0.37–0.41 in 17 specimens, compared with 0.29 in the holotype of *minima*), and more closely spaced nostrils (E-N/IN averages 1.19 in *bouwensi* compared with 0.81 in *minima*). See the account of *X. parkerorum* for a comparison with that species.

TAXONOMIC NOTES: Loveridge (1948, pp. 307, 417–419) confused *Cophixalus pansus*, *Xenorhina minima*, and *Phrynomantis wilhelmana* and arranged the three as subspecies of *Asterophrys pansus*. Zweifel (1956, pp. 41–43) showed that *pansus* is not an asterophryine and placed it in the genus *Cophixalus*, and considered *minima* and *wilhelmana* as different species of *Asterophrys*. Brongersma and Venema (1962, p. 103) referred specimens from the Star Mountains of West Irian to *A. minima*, but I identify them as *X. bouwensi*.

DISTRIBUTION AND SPECIMENS EXAMINED: The only two specimens of this species were captured at moderate to high elevations in the southern (Lorentz River) watershed of the central ranges, S Mt. Wilhelmina (fig. 72). West Irian: Went Mountains, 1000–1360 m. (3280–4460 ft.) (ZMA 5818, holotype); Hellwig Mountains, ca. 2500 m. (8200 ft.) (ZMA 5817, paratype).

Xenorhina oxycephala (Schlegel)

Bombinator oxycephalus SCHLEGEL 1858, p. 58 (type locality, "New Guinea," defined more explicitly as "south coast of the Netherlands part of the Island" by van Kampen [1914, p. 376]. In defining the type locality of *Asterophrys turpicula*, Brongersma [1953, p. 573] noted that all herpetological collections [except for one snake] made by Müller in New Guinea in 1828 came from Triton Bay. Therefore, the true type locality of *oxycephalus* may be defined as Triton Bay, West Irian. Syntypes, RMNH 2280 [two specimens], collected in 1828 by S. Müller).

Xenorhina oxycephala: PETERS, 1863, p. 82.

Xenorhina oxycephalus: VAN KAMPEN, 1919, p. 54.

Xenorhina stresemanni AHL, 1932, p. 897 (type locality, "Jobi (Japen)" [Japen Island] West Irian; holotype, ZMB 34108, missing and probably destroyed; [G. Peters, *in litt.*, 1969], collected by G. Stein on March 10, 1931).

Asterophrys oxycephala: PARKER, 1934, p. 67.

DIAGNOSIS: *Xenorhina oxycephala* differs from all other species of its genus in its relatively narrow internarial distance. The ratio E-N/IN averages 1.49 and has a minimum of 1.30 in 11 specimens. The highest ratios seen in other species are 1.21 to 1.39 (*X. bouwensi*, *X. doriae*, and *X. similis*), and in none is the mean higher than 1.19.

DESCRIPTION: The original description (Schlegel, 1858, p. 58) is simple in the extreme: "In *Bomb. oxycephalus* of New Guinea the discs are very small and the snout is cone-shaped." The

following description is a composite, based on several specimens.

The body is rotund, much wider than the small head, and the legs are relatively long (TL/S-V mean 0.42). The head tapers abruptly to the small, truncate snout with laterally directed nostrils placed very close to the tip. The canthal area is rounded, with the canthus rostralis not at all defined. The loreal region is a gentle slope, flat except for a slight concavity anteriorly behind the nostril. The eyes are very small, much shorter than the snout. The interorbital space is three or more times the width of an upper eyelid. The tympanum is moderately distinct and usually is as large as or larger than the eye. There is a weak supratympanic fold, but the skin is otherwise smooth on both dorsal and ventral surfaces.

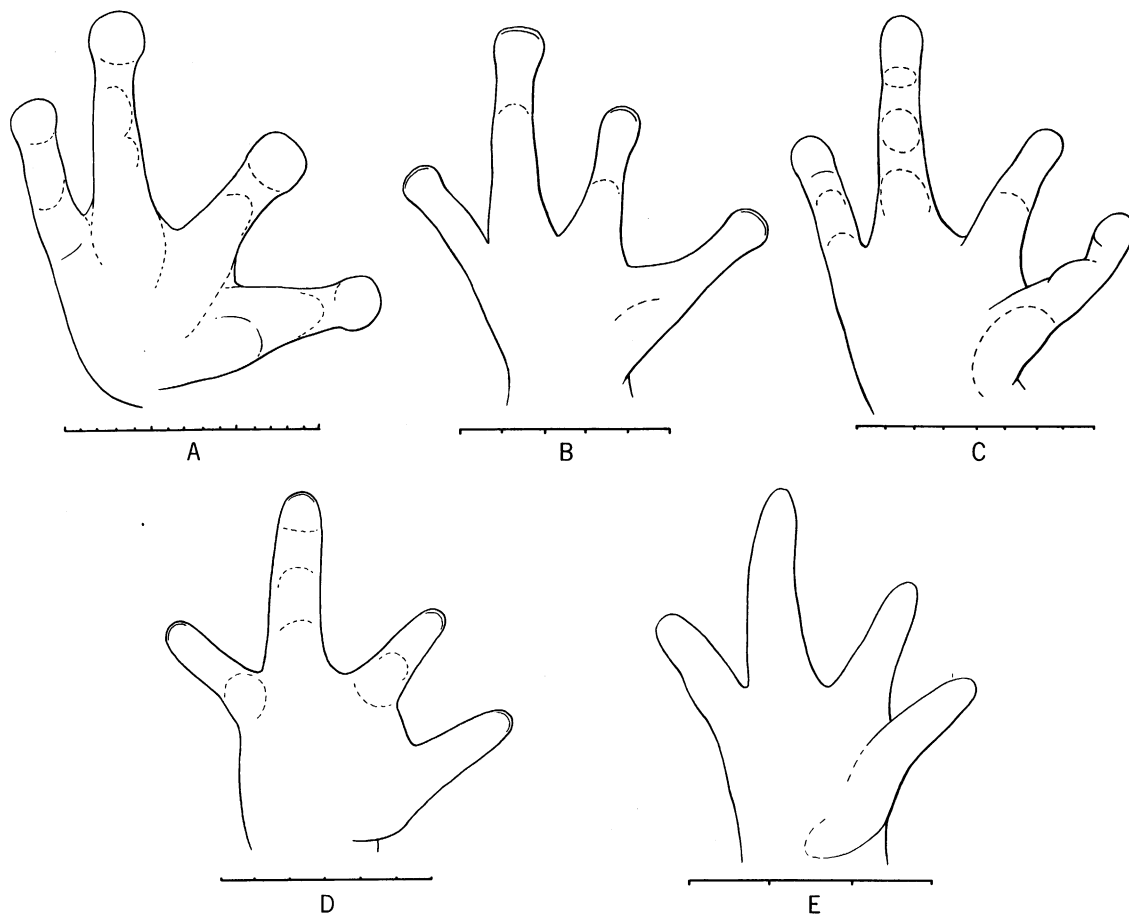


FIG. 75. Hands of *Xenorhina* in palmar view. A. *X. doriae*. B. *X. oxycephala*. C. *X. parkerorum*. D. *X. similis*. E. *X. bouwensi*. Scale lines subdivided in millimeters.

The fingers are short, with relative lengths as follows: $3 > 2 \geq 4 > 1$. They have grooved terminal discs that are scarcely broader than the penultimate phalanges (fig. 75B). The relative lengths of the moderately long toes are $4 > 3 > 5 > 2 > 1$. The grooved terminal discs are larger than the toes, with that on the fourth toe about twice the width of the penultimate phalange. There are no subarticular tubercles on the fingers, and only low, indistinct swellings on the toes. The inner metacarpal tubercle is present only as a faint swelling, and the inner metatarsal tubercle is similarly indistinct.

The body is brown above with lighter mottling and a light vertebral hairline. The chin is gray, the chest and belly paler, and the undersides of the hind legs heavily mottled. Dark brown of the posterior surfaces of the thighs is in a triangular patch, with the apex at the cloacal opening. The upper surfaces of the limbs are the same brown as the body.

Van Kampen (1914, p. 375) gave the following description of colors in life: "Both examples from the vicinity of Humboldt Bay had back and throat gray-violet, abdomen and undersides of the thighs brick red; in the case of the

specimen from the Mosso the back was lake-red, the abdomen orange colored, the sides white; the adult specimen from the Sermowai River had . . . the back brown, the abdomen bright gray."

MEASUREMENTS OF SYNTYPE SPECIMEN: S-V, 40.1; TL, 17.2; HW, 14.0; Eye, 2.7; E-N, 3.7; IN, 2.6; EAR, 3.3. The second syntype lacks its skull and was not measured.

VARIATION: See table 9 for variation in proportions. There are too few specimens from too large an area to permit any meaningful discussion of variation. The largest of 11 specimens is a female 47 mm. in length from snout to vent.

COMPARISON WITH OTHER SPECIES: As is indicated in the Diagnosis, this species is unique among *Xenorhina* in the high value of the E-N/IN ratio. The species most similar to *X. oxycephala* is *X. similis*, but this short-legged, montane form could not easily be confused with the long-legged, lowland *oxycephala*.

TAXONOMIC NOTES: *Xenorhina oxycephala* was the second microhylid frog to be described from New Guinea (preceded by *Asterophrys turpicula* in 1837), but perhaps because of its distinctiveness and rarity in collections, its taxonomic history is

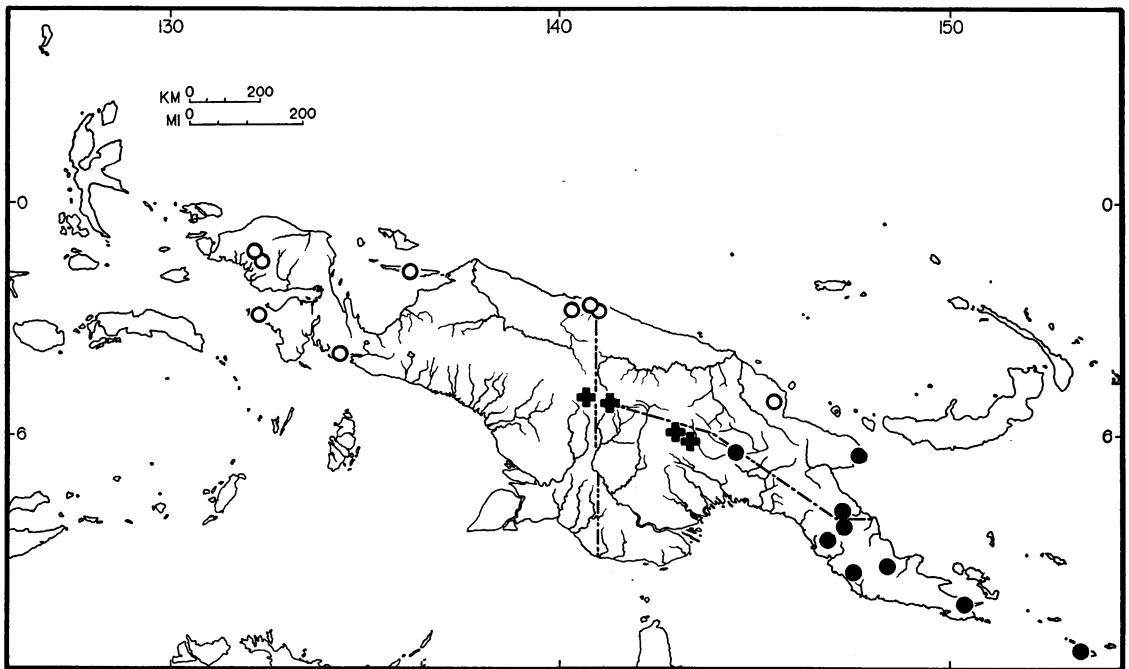


FIG. 76. Distribution of three species of *Xenorhina*. Crosses, *X. parkerorum*; open circles, *X. oxycephala*; closed circles, *X. doriae*.

simple. Only one synonym has been created, *Xenorhina stresemanni* Ahl, 1932. I have not examined the type-specimen of *stresemanni* (which probably was destroyed in World War II), but Ahl's description and illustration leave me no doubt that it and *oxycephala* are the same species. The only difference cited, "underside smooth" in *oxycephala* and "underside granular and transversely wrinkled" in *stresemanni* could easily be the result of individual variation or conditions of preservation.

Van Kampen (1918, p. 54; 1923, p. 132) confused *X. oxycephala* with *Barygenys atra*, and was followed in this error by Nieden (1926, p. 55). Before van Kampen, Méhely (1901, p. 236) had with question referred *atra* to the synonymy of *oxycephala*. Burt and Burt (1932, p. 485) misidentified *X. doriae* from the Northern District of Papua as *X. oxycephala*.

ECOLOGICAL NOTES: *Xenorhina oxycephala* is undoubtedly an inhabitant of the forest floor (Brongersma, 1954, p. 158), but almost nothing is known of its ecology. Brongersma (*loc. cit.*) and Zweifel (1960, p. 6) examined specimens that had fed on earthworms.

DISTRIBUTION AND SPECIMENS EXAMINED: *Xenorhina oxycephala* is known on the north coast of New Guinea from the Adelbert Mountains in the Territory of New Guinea (Zweifel, 1960) to Japen Island and the Vogelkop Peninsula (fig. 76). The type locality is the only record for the south coast. West Irian: Ajamaroe, Vogelkop Peninsula (RMNH, 2 unnumbered specimens); Komara, Vogelkop Peninsula (RMNH, no number); Kamboeaja, Vogelkop Peninsula (RMNH, 2 unnumbered specimens); Triton Bay (RMNH 2280, 2 syntypes); south coast of Humboldt Bay (RMNH 5032; MCZ 7610); Sermowai River at 70 and 400 m. (230, 1310 ft.) (van Kampen, 1914, p. 374); Mosso River (ZMA, no number); Japen Island (Ahl, 1932, type locality of *Xenorhina stresemanni*); Fak Fak (RMNH 17017). Territory of New Guinea: Maratambu, Adelbert Mountains, 2300 ft. (700 m.) (AMNH 64249, 64250).

***Xenorhina parkerorum*, new species**

Figures 77, 78

HOLOTYPE: MCZ 81678, collected by Fred Parker at Imigabip, 4200 ft. (1280 m.), ca. 11 mi. S, 9 mi. W Telefomin, Western District, Territory of Papua, December 11, 1969.

PARATYPES: AMNH 84589 from the type locality; MCZ 80509 (Tifalmin, 4300 ft. [1310 m.], ca. 11 mi. W, 2 mi. N Telefomin, collected by Fred Parker); SAM 6404, 6405 (Okfekaman, near Telefomin, West Sepik District, Territory of New Guinea, collected by Barry Craig); RMNH 16666 (Tigibi, Huria River, 1600 m. [5250 ft.], Southern Highlands District, Territory of Papua, collected by W. Vink); AMNH 84555 (Nipa, 5000 ft. [1520 m.], Southern Highlands District, Territory of Papua); RMNH 16619 (Tenmasigin, 6 km. N Mabilabol, West Irian, collected on the Netherlands Star Mountains Expedition; another specimen with the same number is *Xenobatrachus* sp.).

DIAGNOSIS: *Xenorhina parkerorum* differs from the other species of the genus in the following diagnostic ways: from *oxycephala* in relatively wider spacing of the nostrils (E-N/IN maximum in *parkerorum*, 1.18; minimum in *oxycephala*, 1.30); from *similis* in having distinct discs on the toes and longer hind legs (TL/S-V maximum in

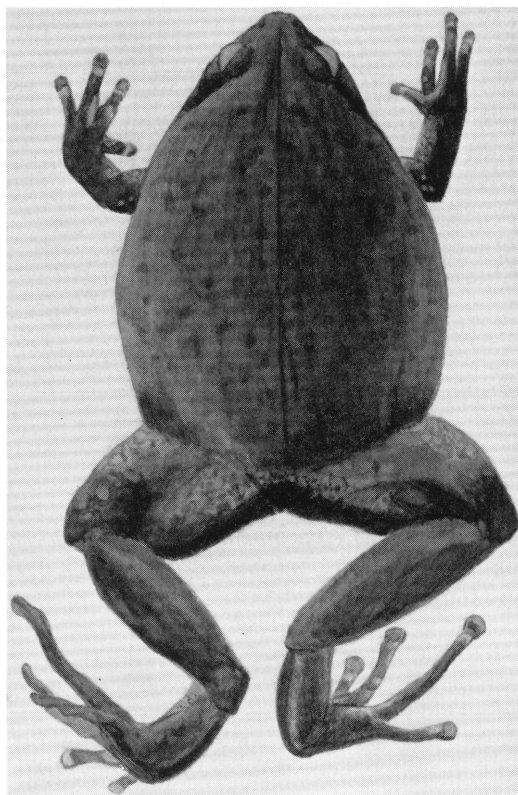


FIG. 77. *Xenorhina parkerorum* (SAM 6404), dorsal view. $\times 2$.

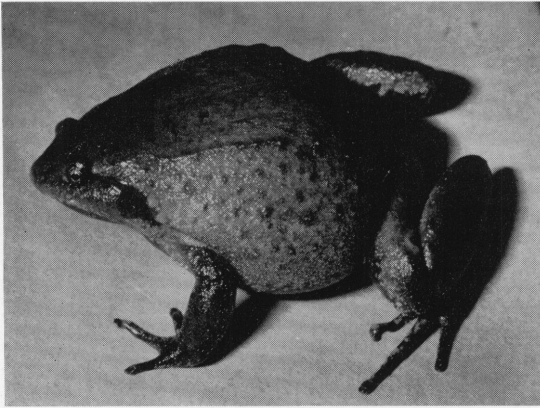


FIG. 78. *Xenorhina parkerorum* (MCZ 81678, holotype). Photo by Fred Parker.

similis, 0.36; minimum in *parkerorum*, 0.37); from *doriae* in smaller size (68 mm. compared to 100 mm. maximum length), longer hind legs (same relative ratios as in *similis*), and color pattern; from *bouwensi* and *minima* in size (maximum in these, less than 30 mm.), and from the latter also in its lack of discs on the toes.

DESCRIPTION OF TYPE-SPECIMEN: The broad body tapers to a relatively narrow head with pointed snout. The snout is about 1.8 times the length of the eye, with the internarial distance less than that from eye to naris. The top of the head and snout are rounded in cross section; the loreal region is oblique and shallowly concave, without a canthal angle. The eyes are small, with the interorbital distance about 2.5 times the width of an upper eyelid. The tympanum is indistinct.

The anterior surface of the snout is slightly pustulose. There is a heavy supratympanic and posttympanic skin fold, and a low dorsolateral fold commences slightly posterior and mesiad to the tympanum, becoming indistinct in the sacral region. Low pustules are present on the back and sides, more prominent in the lateral area.

The relative lengths of the fingers are $3 > 4 > 2 > 1$, of the toes $4 > 3 > 5 > 2 > 1$. The finger tips are rounded, not or scarcely broader than the penultimate phalanges, and very faintly grooved (fig. 75C). The tips of the toes bear distinct although only slightly enlarged discs, all with distinct terminal grooves. Subarticular tubercles on hands and feet are low and rounded. The

inner metatarsal tubercle is low and rounded; there is no outer tubercle. The fingers and toes are unwebbed.

The maxillary bones are symphygnathine. The vomers bear tiny odontoids but lack enlarged spikes and have well-developed posterior extensions. The anterior projection of the squamosal is weak and does not reach the maxilla. There is a smooth anterior palatal fold followed by a short serrate fold consisting of only four major tubercles.

The dorsal color is brown, noticeably darker on the top and sides of the head and tympanum. The sides of the head are flecked with white and the tip of the snout is lighter than the rest of the head. The dorsolateral folds are darker brown than the ground color, as are the low pustules of the back and sides. The groin is dark brown. The anterior and posterior surfaces of the thighs are also dark brown but speckled with a lighter shade. The ground color of the ventral surfaces is brown with faint lighter mottling and spotting. The throat is darker than the abdomen.

The holotype is a male with vocal slits in the floor of the mouth lateral to the tongue. The single vocal sac is subgular.

MEASUREMENTS OF HOLOTYPE SPECIMEN: S-V, 61.0; TL, 24.0; HW, 21.2; E-N, 4.5; IN, 3.8; Eye, 3.5; tip of third finger, 1.4; disc of fourth toe, 1.9. Proportions are as follows: TL/S-V, 0.393; HW/S-V, 0.347; Eye/S-V, 0.057; E-N/IN, 1.18.

VARIATION IN THE TYPE SERIES: The largest of the eight specimens, MCZ 81677, is a male measuring 68 mm. snout to vent. Variation in proportions is given in table 9. The smaller specimens (27, 32, and 34 mm., S-V) are relatively longer-legged, with relatively larger eyes and (in consequence) lower E-N/IN ratios. The slight dorsolateral folds seen in the two largest frogs (61 and 68 mm. S-V) are lacking in the others (27–57 mm.). Judged from the tiny size of its ova, a specimen measuring 42 mm. had not yet reached maturity.

Color pattern is essentially the same in all specimens. The palest individuals show a distinct postocular, supratympanic dark stripe that is less conspicuous in the other darker specimens. The throat area is dark and virtually unspotted in all specimens. The belly is notably spotted or mottled in five paratypes, but two have almost uniformly dark venters, with only faint light flecking.

COMPARISON WITH OTHER SPECIES: *Xenorhina parkerorum* bears a close resemblance to the dwarf species *X. bouwensi* and *X. minima*. The proportions of these two are much like those of *parkerorum* but in that they are less than 30 mm. in snout-vent length, adults are not likely to be confused with *parkerorum*. The Eye/S-V ratios in *bouwensi* and *minima* (ca. 0.08) are larger than in adult *parkerorum* (0.06), but a juvenile *parkerorum* in the size range of the two small species has relatively large eyes. The lack of toe discs should distinguish *minima* from *parkerorum* of similar size, but it may be necessary to establish the state of sexual maturity to distinguish between small *parkerorum* and *bouwensi*.

Xenorhina doriae is clearly the species most similar to the new form. Proportions are much alike in the two, but the distinctive color pattern of *doriae*, together with its better developed finger discs and larger size, should make it difficult to confuse with *parkerorum*.

DISTRIBUTION AND SPECIMENS EXAMINED: *Xenorhina parkerorum* is known only from the type and paratypes (localities given above). The localities, in the extreme western parts of New Guinea and Papua and eastern West Irian, are at moderate elevation on both sides of the central divide (fig. 76).

ETYMOLOGY: This species is named for two disparate Parkers: the late H. W. Parker of the British Museum (Natural History) whose "Monograph of the frogs of the Family Microhylidae" (1934) remains an indispensable work almost four decades after its publication; and Fred Parker, whose extraordinary collecting activities have vastly enriched our knowledge of the herpetofauna of New Guinea.

Xenorhina similis (Zweifel),
new combination

Asterophrys similis ZWEIFEL, 1956, p. 5 (type locality, "9 kilometers northeast of Lake Habbema, 2800 meters, Netherlands New Guinea [West Irian]"; holotype, AMNH 43722, collected by W. B. Richardson on October 31, 1938).

DIAGNOSIS: *Xenorhina similis* differs from all species of *Xenorhina* except *X. minima* in that the tips of the fingers and toes are not expanded into discs. Other species have the tips of the toes or fingers and toes broadened into discs that are distinctly wider than the penultimate phalanges. The finger tips of *similis* are bluntly rounded,

and the toe tips somewhat disclike but not expanded.

Xenorhina minima is a smaller species than *A. similis*; the largest of two *minima*, a gravid female measures 28 mm. snout to vent, whereas *similis* reaches a length of 51 mm. The internarial distance is greater than the distance from eye to naris in *minima* (E-N/IN, 0.81 and 0.86), but usually is less in *similis* (minimum 0.96).

Three species of *Phrynomantis* superficially resemble *X. similis* owing to their lack of digital discs. *Phrynomantis stictogaster* is much larger than *similis* (to 80 mm.) and has a distinctive tubercle situated between the eye and the nostril that is lacking in *similis*. *Phrynomantis wilhelmana* is essentially the same size as *similis* and is similar

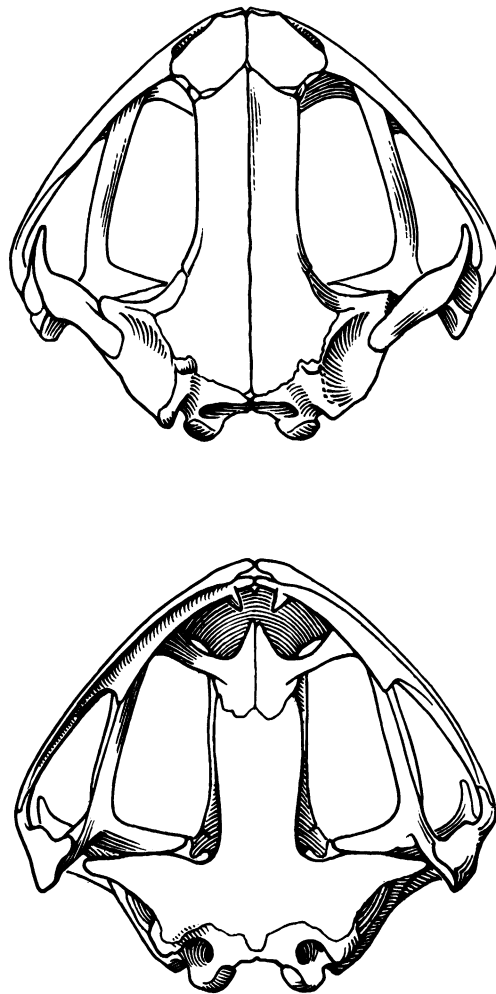


FIG. 79. Skull of *Xenorhina similis* (AMNH 43749) in dorsal (upper) and ventral (lower) views. $\times 2.8$.

in hind leg length, but has much larger eyes. The maximum recorded ratio Eye/S-V for *similis* is 0.072 (mean 0.065), whereas the minimum in *wilhelmana* is 0.088 (average greater than 0.10; see table 9). Also, the digital tips of *wilhelmana* lack grooves, but tips of *similis* are weakly grooved. *P. glandulosa* differs from *X. similis* in the same ways as does *P. wilhelmana*, and in addition has a well-developed supratympanic gland.

DESCRIPTION OF TYPE-SPECIMEN: The specimen is an adult female with ova more than 3 mm. in diameter. The head is relatively narrow (HW/S-V, 0.34) and is narrower than the chunky body. The snout is bluntly pointed and slightly pustulose. The canthal region is rounded and the loreal area flat and oblique. The nostrils are much closer to the tip of the snout than to the eye and are directed more forward than upward. The internarial distance is slightly less than the distance from eye to naris (E-N/IN, 1.15). The eyes are quite small (Eye/S-V, 0.066), with their horizontal diameter being much less than the length of the snout. The tympanum is indistinct and has a horizontal diameter approximately equal to that of the eye. A strong fold of skin passes from the posterior corner of the eye across the upper edge of the tympanum and then downward diagonally to the arm. Except for some slight pustulosity at the posterior end of the abdomen and for a transverse dorsal fold anterior to the vent, the skin is essentially smooth.

The relative lengths of the fingers are $3 > 2 > 4 > 1$, of the toes $4 > 3 > 5 > 2 > 1$. The finger tips are grooved and bluntly rounded, without expansions (fig. 75D). The tips of the toes are grooved and slightly flattened, but are not broader than the penultimate phalanges. Sub-articular tubercles on hands and feet are represented only by very low, rounded elevations. The inner metacarpal and inner metatarsal tubercles are even less distinct. The fingers and toes are unwebbed.

The tongue is scarcely free at the margins and has a slight median groove that passes into a pit posteriorly. The anterior palatal fold is low and indistinct; the posterior fold has seven serrations.

There are no teeth. The maxillae meet in front of the premaxillae. Procoracoids, clavicles, and omosternum are lacking. The terminal phalanges are T-shaped.

The dorsal ground color is uniform light tan. A dark band follows the supratympanic fold,

and a triangular dark patch with its apex at the vent covers part of the posterior and lower surfaces of the thighs. The ventral surfaces are mottled with dark brown on a tan background, with the dark pigment most abundant on the abdomen.

MEASUREMENT OF HOLOTYPE SPECIMEN: S-V, 48.3; TL, 16.6; HW, 17.8; Eye, 2.8; E-N, 2.8; IN, 2.5; EAR, 2.5.

VARIATION: Variation in proportions in the type series is summarized in table 9. The largest specimen is a female that measures 51.4 mm. snout to vent. Males have a median, subgular vocal sac. The dorsal color and pattern are virtually invariable. The gular area and chest are darkly mottled in all specimens. In some the entire abdominal region is dark brown, whereas in others light mottling is present.

The single specimen from the Territory of Papua differs slightly in proportions in having a slightly lower E-N/IN ratio (0.96) than is seen in the type series. The color pattern is virtually identical to that seen in other specimens except that the soles are dark brown, rather than light brown. Notice must be given of a mistake in the original description, where it was stated, "length of orbit 1.3 times the snout length," and "length of the orbit averages 1.35 times the snout length . . ." (Zweifel, 1956, p. 7). The words "snout" and "orbit" were transposed; the snout is longer than the eye.

COMPARISON WITH OTHER SPECIES: The species that bear the greatest similarity to *Xenorhina similis* and presumably are most closely related to it are *X. minima* and *X. oxycephala*. Comparison with the first is made in the diagnosis. *Xenorhina oxycephala* resembles *X. similis* in general appearance and size, but has a much higher E-N/IN ratio (minimum 1.30, compared with a maximum of 1.22 in *similis*), longer legs (TL/S-V mean 0.423 in *oxycephala*, 0.345 in *similis*), and discs on fingers and toes. Comparison of *X. similis* and *X. parkerorum* is made in the account of the latter.

ECOLOGICAL NOTES: Nothing has been published with particular reference to these frogs, but Archbold, Rand, and Brass (1942, pp. 258-266) described two of the localities from which the species is known in some detail. The area is heavily forested, with species of southern beech (*Nothofagus*) dominant.

DISTRIBUTION AND SPECIMENS EXAMINED: *Xenorhina similis* was known from two localities

in the drainage of the Baliem River in the central mountainous region of West Irian, but recently Fred Parker obtained one individual about 200 mi. to the east-southeast in the north-western part of the Territory of Papua (fig. 72). West Irian: 9 km. NE Lake Habbema, 2800 m. (9190 ft.) (AMNH 43721, 43722 [holotype],

43723); Bele River, 18 km. N Lake Habbema, 2200 m. (7220 ft.) (AMNH 43725, 43726, 43730, 43749–43756, 43760; MCZ, 28501). Territory of Papua: Western District: Mt. Fugilil, 8000 ft. (2440 m.), ca. 18 mi. W Telefomin (MCZ 80504). All specimens cited from West Irian (other than the holotype) are paratypes.

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