OCCASIONAL PAPERS of the NATURAL HISTORY MUSEUM OF STANFORD UNIVERSITY

NO. 5
A REVIEW OF THE NEOTROPICAL TREE-FROGS
OF THE GENUS PHYLLOMEDUSA

By Anne Funkhouser



NATURAL HISTORY MUSEUM OF STANFORD UNIVERSITY Stanford, California, U.S.A.

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INTRODUCTION

The tropical American hylid frogs referred to the genera *Phyllomedusa* and *Agalychnis*, which are here treated as a single genus, have interested zoologists because of the possession by some species of an "opposable thumb" and by reason of their unusual breeding habits. The last complete systematic revision of the group was done by Boulenger (1882a). Nieden's (1923) treatment was mainly a repetition of Boulenger's work with addition of the species described since 1882. Subsequent to 1923 a number of new species have been added, and although some workers have placed *Agalychnis* in the synonymy of *Phyllomedusa*, no one has thoroughly justified this change.

The genus Phyllomedusa is of special evolutionary interest. It has undoubtedly arisen from the genus Hyla, and the species of the genus present an almost unbroken continuum from Hyla-like forms to some of the most bizarre and highly specialized frogs in the world.

The objects of this work have been primarily to redefine the limits of the genus *Phyllomedusa*, and as far as possible to evaluate the probable phylogenetic relationships within this genus. An attempt has also been made to show the geographic range of the genus and its species and to include drawings of those forms which have not been illustrated previously.

Sufficient collecting has been done at this time to justify an attempt to show the geographic limits of the genus. By a compilation of published data, spot maps can be drawn to show the general outlines of each species range and that of the genus as a whole. (Maps 1-4, pp. 10-13.)

 $^{^1}$ The breeding habits have been described by several authors. See Noble (1931, p. 69), Boulenger (1882c and 1913), Budgett (1899), Agar (1901), Bles (1905) and Musshoff (1906). Budgett (1899) and Bles (1907) have described the embryology.

NOTES ON CHARACTERS USED

As an aid in comparison of species, characters are described in the same order for each species, and are divided by paragraphs into characteristics of the head, limbs and body (Fig. 1). Some of these key characters and measurements are described below.

Tongue.—Most of the descriptions begin with some reference to the shape of the tongue. In this genus it is usually somewhat heart-shaped (= cordiform), more pointed anteriorly, free behind and notched on the broader posterior edge. Unfortunately this has little value when working with preserved material because such a soft structure is so easily injured or pushed out of shape. The shape of the tongue apparently does not vary significantly within the genus.

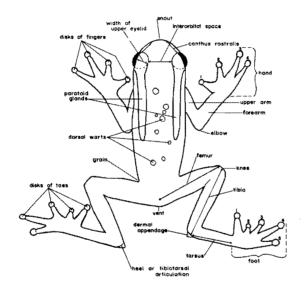


Fig. 1. Hypothetical Phyllomedusa showing characters defined and used.

Vomerine teeth.—In forms possessing vomerine teeth, the teeth are located in the roof of the mouth, mediad to the choanae, and variously slanted in relation to the choanae. When teeth are present, their position is fairly uniform within species, but shows little more variation between species, making it of small value as a key character. In this group of frogs the presence or absence of vomerine teeth is not constant within species, but seems to vary more in some species than in others. Like the shape of the tongue, the inclusion of vomerine teeth in the descriptions is purely conventional.

Choanae. - Internal openings of the nares.

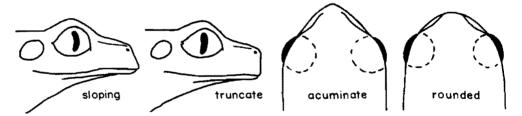
Canthus rostralis.—The canthus rostralis, a more or less angular ridge from the anterior corner of the eye to the nostril, is of some value in the definition of species. In some forms (aspera, dacnicolor, etc.) it is rounded and does not form a sharply angular ridge (as in bicolor, blombergi, feltoni, etc.). But an occasional specimen of boliviana, for example, will

exhibit a most angular canthus rostralis or a specimen of *edentula* will show no prominent angle. This may be the result of careless preservation, as when too many specimens are crowded together, or it may be natural variation within the species. In general, however, the shape of the canthus rostralis seems fairly constant within species.

Loreal region.—The loreal region (the space between the eye and the nostril, bounded above by the canthus rostralis and below by the upper lip) may be plane (i.e., flat) or concave (i.e., curved inward), and may also slope outward or be perpendicular to the medial plane of the body. The relative shape of the loreal region is fairly constant within species.

Tympanum.—Where measurements of the tympanum relative to another structure are given, the tympanum is always measured along its greatest diameter, unless otherwise noted. When the author has not seen examples of the species, the original wording is retained without comment. The size of the tympanum is relatively constant within species, but in some species, and in some immature specimens, it is inconspicuous or obscured by the skin texture. In this group there is no evident sexual dimorphism in relation to size of the tympanum.

Interorbital distance and width of upper eyelid.—Measurement of the interorbital is the width of the bone between the eye sockets. The width of the upper eyelid is taken from the inner edge of the eye socket to the outer edge of the upper eyelid. This measurement is valid only in well-preserved material, since the eye is so easily misshapen from careless preservation. With few exceptions these relative measurements show too little variation between species to give them much value as diagnostic characters.



Figs. 2-5. Hypothetical *Phyllomedusa* head. 2. Profile, sloping snout. 3. Profile, truncate snout. 4. Dorsal view, acuminate snout-tip. 5. Dorsal view, rounded snout-tip.

Snout.—The shape of the snout, both in profile and when viewed from above, is a most useful character for separating certain groups within this genus. In profile the snout is either truncate or sloping. (The possible significance of this is discussed in the section on Evolution and General Distribution.) When viewed from above the snout may be rounded or somewhat acuminate, and shows various stages between these two conditions. Except when a naturally sloping snout may be pushed in after preservation, the basic shape is not likely to be changed from that of the living creature, is constant within species, and frequently within groups of related species.

Webs.—A significant degree of webbing between the fingers and toes occurs only in the Agalychnis group and intermediate types (Fig. 7). Neiden (1923, pp. 8-9) has excellent illustrations of varying degrees of webbing. Although the degree of webbing varies within species it is still constant enough to afford a useful character. The main difficulty lies in differentiating the multitude of steps between full webs and their complete absence. In those species where differences in the degree of webbing were noticeable, an attempt has been made to include the observed limits in the

descriptions. The degree of webbing, up to a maximum for a given species, may be developed with maturity, as in Hyla vasta (Noble, 1931, pp. 99-100).

Opposability of the fingers and toes.—This character can be judged adequately only from living specimens. However, the lengthening and twisting of the first toe, which results in that toe being opposable to the others (primarily to the three outer ones) is of such importance in the evolutionary development of this group that the author has attempted to comment on it for each species.

In all species the thumb appears to be opposable to the other fingers. The hand has not changed significantly in evolutionary development except

for loss of webs and great reduction in disk size.

The foot, however, has changed considerably during evolution. Among those species in which the first toe is shorter than the second, and which possess extensive webbing, the first toe is quite obviously not twisted or opposable to the others. In the forms which have lost the webs and lengthened the first toe until it is longer than the second, the first toe is twisted in relation to the others and is opposable to them. Between these two extremes there are several species in which the opposability appears to be intermediate. Where there is considerable doubt as to the opposability of the toes, the condition is listed as "may be opposable to the other toes", and in those where there is less doubt it is stated as "probably opposable to the other toes." ("The other toes" in this usage means the three outer toes.)

Fringes.—These are the dermal extensions on either side of the phalanges, giving the digits a broad flat look, and are generally present only in the forms which possess webs.

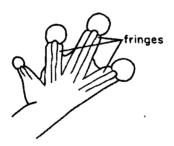


Fig. 6. Hypothetical Phyllomedusa foot. Fringed toes.

Disks.—Except for the digits which are reduced in size in some species (first finger, and second and third toes) the relative size of the disks on the fingers and toes is quite constant within species. Only three specimens were found which differed significantly from the described condition (see under lemur and boliviana). The disks of the fingers are generally slightly larger than those of the toes.

Tiblotarsal articulation.—The point to which the tibiotarsal articulation (the joint between the tibia and tarsus) reaches when the leg is brought forward along the body has been conventionally used in descriptions of these frogs, but the author does not feel that this is of much significance in this group. It is quite constant within species, and does not differ markedly between species. In most preserved material an attempt to actually straighten the leg would tear muscles or break the leg bones. Consequently, this measurement has been made by taking the distance between the knee and tibiotarsal articulation with dividers, and bringing this measurement forward along the body. In those cases where no specimens were

available the original description has been retained without comment.

Parotoid glands.—Evidently parotoid glands have arisen independently in the Phyllomedusa, about half the species of which possess them. Among the species with distinct parotoids there is remarkably little variation in the shape or size of these glands. In most species the glands are long and narrow, extending from the posterior half of the upper eyelid to about the middle of the body. In some species (i.e., craspedopus and lorts) there is a swelling, most prominent above the angle of the jaw, but the tissue does not appear to be glandular. In such cases the structure is referred to as a parotoid swelling.

Unfortunately, the appearance of the parotoid glands is often considerably affected by preservation, and possibly by the condition of the animal before preservation. In the large groups of boliviana and iheringi, there was much variation in the prominence of these glands, with no evident relation to locality or date collected, or to sex. However, the shape and relation to locality or date collected, or to sex.

ative area of the body covered by the glands remained unchanged.

Skin.—As a very general rule the skin of the Agalychnis and intermediate types is smooth while that of the more specialized forms tends to be rougher. It is difficult to find concise terms for a feature as variable as the skin, which may appear smooth and almost translucent (i.e., lemur), or coarse and studded with osteoderms (bicolor). And this genus shows all variations between these extremes. For the purposes of this paper the author has used the following terms for the basic skin texture:

Smooth—no roughness evident to the naked eye. Coarse—unevenly roughened.

Either of these conditions may be modified by:

(a) warts—a protuberence of the skin, usually smooth, much broader than high, and of more sporadic occurrence on the body than (b).

(b) granules—smaller than (a), usually rounded, closely spaced, well-defined grain-like elevations of the skin. The sides and ventral surfaces of most of the frogs in this genus are granular.

(c) tubercles—a rough, contcal protuberance, usually on the sides or

ventral surface.

(d) osteoderms—a bony deposit in the skin of the dorsum. Probably does not occur in smooth-skinned forms. Some species (e.g., feltont) seem to have a bony deposit in the skin, but the author hesitates to conclude that these are definitely osteoderms.

The basic skin texture does not vary greatly among individuals of a species, but the number of warts and tubercles per individual may vary considerably. In general, an immature specimen will have fewer and less conspicuous warts and tubercles than an adult. The size of the osteoderms and extent to which they cover the body probably also varies with age. The author found no evidence that sex or sexual state affects the appearance or condition of the skin.

Color.—Judging from preserved material the basic color patterns in this group of frogs are remarkably constant within species, and often form the easiest way of separating otherwise rather similar species. Were it not for the drastic changes caused by all preserving methods, often resulting in a complete loss of all color, an easily workable key could be written to this genus on the basis of color pattern alone. It is unfortunate that so few workers have had an opportunity to examine their material alive. As a group the members of the genus Phyllomedusa are undoubtedly among the most beautiful of their highly colored family.

However, certain changes evoked by preservation are constant within the group. Thus green usually becomes gray-blue or violet, purple changes to brown or black, while the red, orange and yellow tend to fade out completely. When a "color pattern" is referred to in the key, it means that part

which is left after preservation. Because of these color changes, the author has attempted to restrict the use of color patterns in the key to those instances where morphological differences are too small, or too variable, to be easily measured.

The constant recurrence of such terms as "probable", "generally", "seems to" and the like may be irksome to some, but "Every physical character found in frogs varies to some extent, and some characters vary much more than others. These facts have not been fully realized by some authors. For instance, the position and development of the vomerine teeth, used by Boulenger, Cope, and other herpetologists, are not constant in some species. Key characters must therefore be interpreted rather widely, with the realization that no key will suffice for the identification of every individual in a variable species." (Cochran, 1955, pp. XV-XVI.)

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The author is especially grateful to two of South America's outstanding zoologists, Dr. Gustavo Orcés V., of the Escuela Politécnica Nacional, Quito, Ecuador, and Sr. Antenor Leitão de Carvalho, of the Museu National, Rio de Janeiro, Brazil (recently at Stanford University as a Guggenheim Fellow). Both have contributed numerous specimens for study. Dr. Orcés sent two of the previously undescribed species included here, and Sr. Carvalho was a constant help, especially with the Brazilian forms.

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ABBREVIATIONS OF INSTITUTIONS AND COLLECTIONS

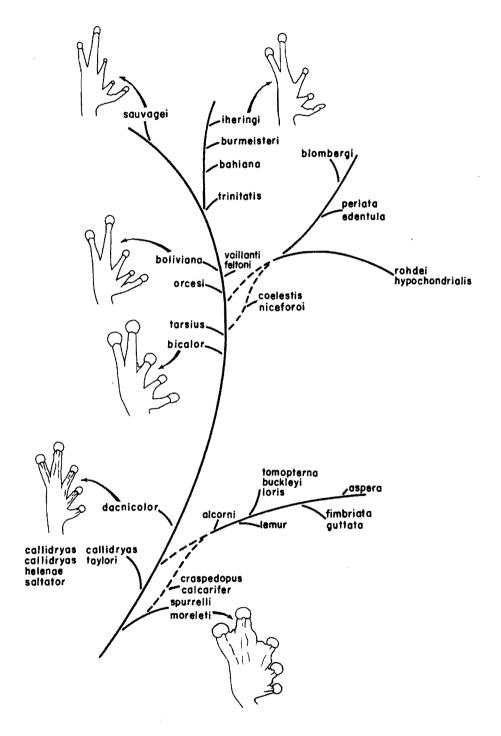


Fig. 7. The genus Phyllomedusa. Proposed phylogenetic arrangement of species.

lection of Edward H. Taylor and Hobart M. Smith (see Smith and Taylor, 1945), specimens now in UKMNH or University of Illinois. EPN - Escuela Politécnica Nacional, Quito, Ecuador. MCZ - Museum of Comparative Zoölogy, Harvard University, Cambridge, Mass. MHNP - Muséum National d'Histoire Naturelle, Paris, France. NRS - Naturhistoriska Riksmuseum, Stockholm, Sweden. OV - Private collection of Dr. Gustave Orcés V., Escuela Politécnica Nacional, Quito, Ecuador. SM - Senckenberg Museum, Frankfurt-am-Main, Germany. SU - Natural History Museum, Stanford University, California. UKMNH - Museum of Natural History, University of Kansas, Lawrence. UMMZ - University of Michigan, Museum of Zoology, Ann Arbor. USNM - United States National Museum, Washington, D. C. ZMB - Zoologisches Museum, Berlin, Germany.

NEW SYSTEMATIC NAMES PROPOSED

Phyllomedusa craspedopus. Ecuador.
Phyllomedusa callidryas taylori. Mexico.
Phyllomedusa blombergi. Ecuador.
Phyllomedusa orcesi. Ecuador.

EVOLUTION AND GENERAL DISTRIBUTION Figure 7; Maps 1-4

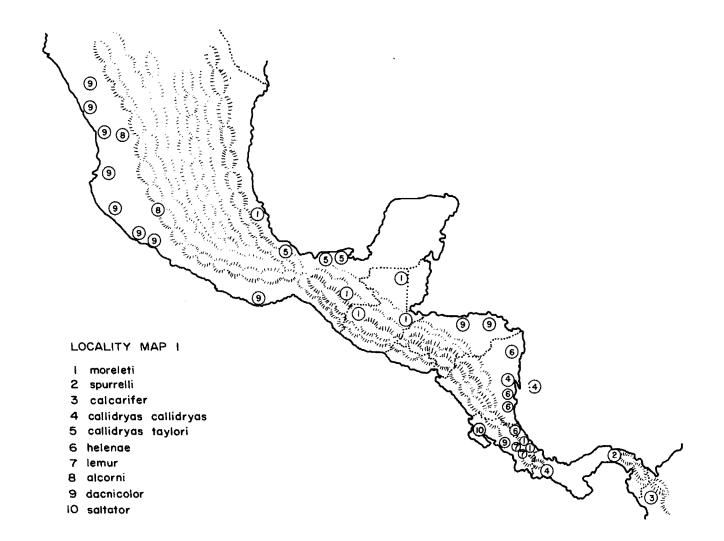
The range of the genus *Phyllomedusa* extends from Mexico through Central America and South America to Argentina. The distribution within this large area is generally confined to a constantly humid environment. Thus, on the western side of the Andes these frogs are stopped by the deserts which begin in southwestern Ecuador, and east of the Andes by the cold and relatively arid conditions of southern Argentina. *Phyllomedusa boliviana* is reported to occur at 2000 meters in Bolivia, probably an extreme of altitude for members of this group. (See Maps 1-4.)

Noble (1931) states that the evolution of this genus from Hyla has been through the Agalychnis types to forms which at present differ most from Hyla (e.g., P. sauvagei, theringi, etc.) by a "reduction in webs, an elongation of the first toe, a shortening of the second, together with a slight twisting of the first until in the most specialized forms it opposes the other toes. The extreme species lose the digital dilation entirely, reduce the intercalary cartilages to thin wafers, and develop large parotoid glands." The tendency toward loss of the omosternum in certain species is probably of secondary importance to the main line of evolution in the genus as a whole. (See p. 16.)

The proposed arrangement of the species in the genus *Phyllomedusa* is shown in Figure 7. The feet and toes are represented diagrammatically.

THE AGALYCHNIS GROUP

The Agalychnis types, which include Phyllomedusa spurrelli, moreleti, craspedopus, calcarifer, callidryas, helenae and saltator, closely resemble the larger species of neotropical Hyla. The foot is unspecialized, with the first toe shorter than the second, and both fingers and toes are more or less strongly webbed, with large flat disks. Associated with the Hyla-like structure of the hands and feet, movement is principally by leaping plus adhesion and friction (comparable to Hyla maxima, rosenbergi, etc.) in contrast to the "walking" and grasping of the more specialized forms. The species of the Agalychnis group have not developed parotoid glands, although





- I calcarifer
- 2 spurrelli
- 3 craspedopus
- 4 guttata
- 5 fimbriata
- 6 aspera
- 7 Ioris
- 8 buckleyi
- 9 tomopterna



LOCALITY MAP 3

- 1 hypochondrialis 2 rohdei
- 3 perlata
- 4 edentula
- 5 blombergi
- 6 bicolor
- 7 tarsius
- 8 niceforoi
- ? (See text page 48)



parotoid swellings may be present. The iris is red in life in all members of this group except calcartfer—in which it is gray—and possibly cras-pedopus upon which there are no data. (The red iris was formerly one of the characteristics used to differentiate the genus Agalychnts.) Vomerine teeth are normally present in the adults.

Most of the species of the Agalychnis group occur in Central America and northern South America. Phyllomedusa calcarifer on the western side of the Ecuadorian Andes and craspedopus on the eastern side, also in Ecuador, represent the presently known southern limits of this group. Phyllomedusa craspedopus seems an isolated example on the eastern side of the Andes, but it is not unlikely that specimens of this or related Agalychnis-type species will be found on the lower eastern slopes of the Colombian Andes.

The evolutionary development of these species has most likely been from forms similar to more leti and spurrelli to ones such as callidryas and helenae. Except for the vertical pupil, more leti could pass for a Hyla, while callidryas and helenae have begun to lose the extensive webbing characteristic of the Agalychnis forms and have developed the distinctive color pattern of the more highly specialized members of the genus. Most of the Agalychnis group possess the long sloping snout shown in most of the more specialized forms. The exceptions, craspedopus and calcarifer, may be an evolutionary link to the following group.

The species of the next "branch" (Phyllomedusa alcornt, lemur, tomopterna, loris, buckleyi, fimbriata, guttata and aspera) all possess a characteristic short, truncate snout, and share the undifferentiated foot structure of the Agalychnis types (first toe shorter than the second with relatively well-developed disks), but show varying degrees of reduction in webbing. Most, if not all, have the typical color pattern of the genus, in which the surfaces concealed in repose are different in color and texture from the always visible surfaces, and—with the possible exception of lemur—the adults possess vomerine teeth. None have parotoid glands, although, like the Agalychnis types, there may be parotoid swellings.

As a whole these species probably represent one phase of an evolutionary "branching away" from the Hyla-like origin of the genus. However, in the author's opinion this alcorni-aspera group has not given rise to more advanced forms, and is perhaps best thought of as a dead end of this particu-

lar phase of evolution.

P. lemur and alcornt are the only members of this group occurring in Central America, but are not necessarily closely related. P. alcornt, the northernmost species, occurs on the west coast of Mexico at low elevations. From Taylor's (1952) description and illustration it would appear to be separated from the Agalychnts types mainly by the truncate snout and lesser degree of webbing, and to be closer to them than is lemur.

According to Dunn (in litt.) *lemur* occurs in a heavily forested, hilly section of Costa Rica which is now being cleared. With the destruction of the forest, Dunn believes, will come the extinction of this frog. The species lacks webs on the fingers, and has only basal ones on the toes. Vomerine teeth are usually absent, but with the variation observed in this character in other members of the genus it is quite likely that some indi-

viduals possess them.

Superficially, P. loris (probably a synonym of buckleyi, see p. 27) and tomopterna most closely resemble the Agalychnis group. In the relatively large disks and reduction of webbing they would fall within the original definition of the genus Phyllomedusa if their questionable parotoid swellings are considered true parotoid glands. Both possess a triangular heel appendage, not as extensive as in craspedopus, but more developed than in guttata and fimbriata. Miss Lutz (1950) places tomopterna in Pithecopus, while loris and bicolor comprise Phyllomedusa—an arrangement which seems quite unsatisfactory considering the many obvious similarities of loris and tomopterna, and the very considerable dissimilarities between loris and bicolor. These two closely related species occur in the northwestern section of the Amazon Basin, loris in Ecuador, and tomopterna from Ecuador to the Upper Amazon of Brazil.

Of the small species in the vicinity of Rio de Janeiro, Brazil, guttata and fimbriata are the least specialized. Both show a reduction in the degree of webbing from the generalized Agalychnis type—guttata much more so than fimbriata. The dermal heel appendage of each is a minute bit of tissue, often barely, if at all, discernible. Although differing considerably in the extent of webbing, these two species are probably more closely related to each other than to other presently existing members of this

intermediate group.

No examples of aspera could be obtained. To the author's knowledge it is known only from the type locality in northeastern Brazil. It has been placed in this group because the first toe is shorter than the second, the snout truncate, and the webbing reduced (often totally absent on the fingers). The dorsal surfaces, described as tuberculate, are in contrast to the smooth skins of the other species of this group.

P. dacnicolor, of Mexico and Central America, agrees with the alcorniaspera group just discussed in general characteristics of the feet and absence of parotoid glands, but seems to be of a slightly different order than the preceding forms. While the other species are small, or, as in tomopterna and loris, slight in build, dacnicolor is a large, heavy-bodied frog, with a prominently sloping snout, resembling in general appearance such forms as boliviana and tarsius. The evolution of the more highly specialized species of Phyllomedusa was most probably through a form such as this. It may be of interest to note that dacnicolor has been shuffled between Agalychnis and Phyllomedusa more than any other single species.

THE PHYLLOMEDUSA GROUP

In all of the remaining species (the *Phyllomedusa* group) of the genus the first toe is longer than the second (with the exception of *bicolor*, in which the first and second toes are sometimes equal), and opposes the others; movement is by grasping and drawing the body up; and the snout is sloping in profile (except rohdet, hypochondrtalis and blombergt). Webs are lacking (except possible basal ones on the toes of bicolor and trinttatis), the disks are reduced, especially on the first finger and the first three toes, the larger forms normally possess vomerine teeth, and most species have parotoid glands. Thus, the more specialized of these forms illustrate Noble's "extreme species", having lost the webs and large disks, evolved the "grasping foot" through reduction of the second toe and twisting of the first, and developed parotoid glands.

A peculiar color characteristic, shared by all the species of the *Phyllomedusa* group except *hypochondrialis*, *rohdei*, *bahiana*, *burmeisteri* and *theringi*, is the presence of one or more prominent, light, usually darkedged spots on the throat or chest and on the lower surface of the thigh on each side of the vent. In the original description such spots are not mentioned beside the vent of *vaillanti*, nor on the chest of *coelestis*. Unforfortunately, no specimens of these two species were available for comparison.

THE BICOLOR-VAILLANTI SUB-GROUP

The species in the "intermediate" group—bicolor, tarsius, orcest, boliviana, niceforoi, coelestis, feltoni and vaillanti—appear to be relatively closely related. These species have been arranged on the phylogenetic tree largely on the basis of their differences in disk size, from the very large disks of bicolor and tarsius to the much smaller ones of boliviana and feltoni. The color pattern of preserved specimens is remarkably similar within this bicolor-vaillanti sub-group. The dorsal surfaces are uniformly dark blue-gray, the venter light, with the previously mentioned spots on the throat and beside the vent, and the dorsal and ventral colors merge on the sides of the body and legs in a broad mottled band—quite different from the sharp color differentiation of the Agalychnis and lower intermediate alcorni-aspera types, or the more specialized species.

Osteoderms in the skin of the dorsal surfaces of bicolor, orcest, vatllanti and feltoni (and possibly niceforoi) are probably of secondary evolutionary importance.

P. bicolor is probably the most primitive of this group. As in the less specialized forms, the disks are large—even on the first finger and first three toes—the second toe is often as long as the first, and there may be rudiments of webs on the toes. However, bicolor, the largest Phyllomedusa, has well-developed parotoid glands (see note p. 39) and an extremely

coarse skin texture which is not found in any of the less specialized forms.

P. tarsius is superficially most similar to bicolor. The disks of tarsius are slightly smaller than those of bicolor, the second toe has been considerably reduced, and there are no webs. The parotoid glands are large, although frequently indistinct, and the skin is coarse in texture, but lacks osteoderms.

At present bicolor is known from Dutch Guiana and the upper Amazon of Peru (and supposedly in the inter-Andean valley of Colombia (Dunn, in litt.), a locality the present author questions), and tarsius is also from

the upper Amazon of Peru.

Only one example of orcest is known, and, although distinct, it is similar to, and probably represents the same general level of specialization as boltviana and feltont. The hands and feet are similar in all of them, there are no very significant differences in size of the disks, the parotoid glands are more or less well developed, and the color pattern and general body form are similar.

Unfortunately, no examples of vaillanti, coelestis, or niceforoi (see Remarks, p. 48) could be obtained. They have been placed in this group on the basis of relative disk size, structure of the hand and foot, skin texture, color pattern, etc. According to the description, the parotoid glands of vaillanti are short but distinct, while coelestis and niceforoi lack them. It is most unlikely that the parotoid glands have been secondarily lost, as is assumed to be the case with hypochondrialis and rohdet, but this feature alone is probably not of great evolutionary significance.

All of these species are from the Amazon basin and its Andean foothills —vaillanti in the lower Amazon from Santarém to the coast, orcest and feltoni in the upper Amazon of Ecuador, along with boliviana, the range of which extends along the eastern Andean foothills to Bolivia, while coelestis is so far known only from the region of Moyabamba, Peru, and niceforoi from Villavicencio, Colombia.

The Omosternum

Miss Lutz (1939) illustrates the sternal apparatus of *rohdei* but does not comment on the obvious lack of an omosternum. The presence or absence of this structure has been used in some groups as a basis for generic separation, but in this genus it seems to indicate only an evolutionary phase of certain species. In any case it is more likely that the singular development of the hand and foot in this genus is of considerably greater evolutionary importance than the loss of the omosternum. But to state positively that there is even a tendency toward loss of the omosternum in certain species would require many more specimens than were available.

In the following table the "omosternum?" column refers to cases in which the structure was so thin, or misshapen or generally difficult to discern as an omosternum (e.g., a small blob of cartilaginous material more or less in the omosternal locus) that its presence or absence could not be definitely determined. See page 17.

THE HYPOCHONDRIALIS-EDENTULA SUB-GROUP

The predecessors of edentula and perlata, and, to an even greater extent, hypochondrialis and rohdet have probably been evolving away from the "main line" for some time, and these forms now represent the end of a line. These four species are the only ones in the above table which the author feels may show some significant trend toward loss of the omosternum.

Species	Specimens examined	Omosternum present	Omosternum ?	Omosternum absent
bicolor tarsius orcest boliviana pniceforoi	1			1 2
feltoni	5			4 2 3 16 20

The specimens listed as ?niceforot are discussed on page 48.

Because of the very few known specimens of edentula and perlata the decision as to whether or not these species have truly lost the omosternum must await further collection. At present they are shown as having been derived from the "intermediate" (bicolor-vaillanti) group in that they share the highly specialized hand and foot, but differ considerably from that group in the distinctive development of the parotoid glands. The long narrow glands form an angular ridge along the side of the body and are defined by a prominent set of tubercles found in no other species except blombergi. In addition edentula presents an oddly warty or tuberculate appearance all over, and the tubercles on the outer edges of the arms and legs of perlata are very much larger in relation to its size than for any other Phullomedusa.

On the basis of external morphology it would seem that divergence from the "main line" has probably not advanced as far in edentula and perlata as in hypochondrialis and rohdet, which, like the preceding, appear quite closely related to each other. However, they differ in their very small size and truncate snouts from all other species (except blombergi) with specialized feet. They lack parotoid glands, and usually do not possess The tendency toward, loss of the omosternum is probably vomerine teeth. more "complete" in these two species than in any others, but it is impossible to say whether or not this is associated with their other differences from the more specialized forms. The development of the hand and foot is fully as specialized as in boliviana, for example, the disks are small, and the walking and grasping movement is that of the most advanced forms. The color pattern of the two is similar, but different and constant enough in each to afford an easy superficial method of separation.

The range of hypochondrialis, which evidently extends throughout the low-lands of eastern South America, from Bolivia to the Guianas and to the eastern tip of Brazil, is the most extensive so far known for a species of this genus. From the specimens examined it would seem that hypochondrialis is remarkably similar in all parts of its range. P. rohdei occurs from the region of Rio de Janeiro, Brazil, to lower Bolivia.

The placement of blombergi on the evolutionary "tree" is frankly arbitrary. The specimen was received just prior to the final typing of this paper, and the intrusion of this beast shows up the arbitrary nature of any such attempt as this to systematize our vague knowledge of the living world. The hands and feet of blombergi are highly specialized, the disks relatively as small as those of sauvagei, and the color pattern is similar to that of the advanced forms. However, the snout is truncate (as in hypochondrialis and rohdei), the parotoid glands are structurally similar to those of perlata and edentula, and are marked by a line of white tubercles (as in perlata).

THE SAUVAGEI SUB-GROUP

Phyllomedusa sauvaget from Argentina, is one of the most highly specialized members of this evolutionary line. It probably arose from a form similar to boliviana. The reduction in size of the disks has been carried to an extreme, the tips of the fingers being no wider than the digits themselves. In preservative the color pattern of this frog differs from most others of the genus in that the whole body, except the belly, turns the characteristic blue-gray color usually restricted to the dorsum. Unfortunately, the author could find no life-color notes on this species.

THE TRINITATIS-BURMEISTERI SUB-GROUP

Some creature such as trinitatis might have given rise to the bahtana-theringi species. The disks of trinitatis are smaller than those of boliviana, not as reduced as those of sauvagei, and are rather long and narrow in contrast to the very round disks of the preceding forms.

The three remaining species of the genus form a very natural little group—with the possible exception of bahtana. Although the author has not seen bahtana, it is included here because Miss Lutz, who is familiar with the species, included it as a member of her "burmetstert Kreis" along with theringi. However, the author does not agree with Miss Lutz's classification of these frogs as subspecies of burmetstert—they are all more than sufficiently distinct to warrant their being given full specific status.

All of these species (with trinitatis) have large parotoid glands (although indistinctly developed in theringi), very small disks, and in contrast to most of the other specialized forms, a rather slender body form, tapering from a wide head to a narrow groin.

These species, occurring on the coast of Brazil from Bahia southward, are tentatively related to *trinitatis* principally on the basis of the structure of the disks, color pattern and body form. Although no examples of *bahiana* were examined, the hands and feet of *burmeisteri* and *theringi* present the same general appearance as those of *trinitatis*.

Genus PHYLLONEDUSA Wagler

Phyllomedusa Wagler, 1830, p. 201 (type species by monotypy Rana bicolor Boddaert).

Agalychnis Cope, 1864, p. 181 (type species by original designation #yla callidryas Cope); 1865, p. 110 (in key).

Pithecopus Cope, 1866, p. 86 (type species by original designation Phyllomedusa azurea Cope- Hyla hypocondrialis Daudin).

Hylomantis Peters, 1872b, p. 772 (type species by monotypy Hylomantis aspera Peters).

Phrynomedusa Miranda-Ribeiro, 1923, p. 3 (two species included, neither designated as type; restricted to Phrynomedusa fimbriata Miranda-Ribeiro by Miranda-Ribeiro, 1926, pp. 105-106; type species hereby designated as Phrynomedusa fimbriata Miranda-Ribeiro).

Bradymedusa Miranda-Ribeiro, 1926, p. 104 (no type species designated; type species hereby designated as Bradymedusa moschata Miranda-Ribeiro-Phyllomedusa rohdet Mertens).

DIAGNOSIS: Pupil vertical; tongue oval, extensively free behind; vomerine teeth usually present in most species; fingers and toes webbed or not;

tips of fingers and toes dilated into regular disks; inner digits more or less opposable; outer metatarsals united; omosternum when present cartilaginous; sternum a cartilaginous plate; diapophyses of sacral vertebrae strongly dilated; visible dorsal surfaces separated in color and texture from those concealed in repose; spawn deposited above water; range, Central and South America.

DISCUSSION: The genus Phyllomedusa, proposed by Wagler (1830) for P. bicolor, was differentiated by him from other neotropical hylids by a vertical pupil, large disks, reduced webs, more or less opposable inner digits, the first toe being shorter than or equal to the second, and the presence of parotoid glands. Cope (1865) described the genus Agalychnis for a less specialized neotropical hylid. The more fully webbed members of the group were put into this genus. They closely resembled their relatives in the genus Hyla except for the vertical pupil and more or less opposable inner digits. Pithecopus Cope (1866) and Hylomantis Peters (1872b) were proposed for forms which did not seem to fit into either of the previously defined genera. The height of splitting was achieved by Miranda-Ribeiro (1926) who, working only with Brazilian forms, set up a subfamily Phyllomedusinae, including the genera Phyllomedusa, Hylomantis, Bradymedusa and Phrynomedusa. This arrangement has not been generally recognized by subsequent workers.

In reviewing the genus Phyllomedusa, Boulenger (1882a) included Pithecopus, Hylomantis, and part of Agalychnis (viz., A. dacnicolor). Many subsequent authors have included the whole of Agalychnis in Phyllomedusa.

Miss Lutz (1950) recognized the naturalness of this group, but was handicapped by lack of material other than some of the Brazilian forms. In her classification, which was based mostly upon a study of the literature, she preferred to retain the old generic names—Agalychnis, Phyllomedusa, Hylomants and Pithecopus—and set up a classification based on the characters originally proposed for each genus. She seemed particularly loath to part with Pithecopus, which she felt should be retained either at full generic status or as a separate section of Phyllomedusa. Unfortunately, this very neat system does not stand up under an examination of most of the species involved. The present author does not feel that these old generic names—particularly Pithecopus—represent natural groups. Though marked divergence is shown within the genus Phyllomedusa the presence of intermediate forms makes it impossible to establish definite breaks of generic magnitude in the sequence at any point. Following the International Rules of Zoological Nomenclature, the oldest available generic name (Phyllomedusa) is accepted.

KEY TO THE SPECIES OF THE GENUS PHYLLOMEDUSA

- 1a. First toe shorter than, or equal to, the second; no distinct parotoid glands (except bicolor), although parotoid swellings may be present; webs may or may not be present.
 - 2a. Snout truncate in profile; vomerine teeth may or may not be present; no parotoids (although parotoid swellings may be present).
 - 3a. Some sort of dermal appendage, at least on the heel.
 - 4a. Extensive dermal folds on the forearm, around margin of lower jaw, and from heel to fifth toe (E. Ecuador)...... craspedopus (p. 23)
 - 4b. Inconspicuous dermal appendage on the heel and/or elbow.
 - 5a. Sides of body below the darker dorsal color with conspicuous dark vertical stripes (see Figures, calcartfer and tomopterna).
 - 6a. Fingers and toes at least one-half webbed; a single triangular heel appendage (Panama to N. W. Ecuador)..... calcartfer (p. 24)
 - 6b. Fingers free, toes free or only basally webbed; two triangular heel appendages, one projecting inward and one outward (upper Amazon Basin)...... tomopterna (p. 25)

5b. Sides of body below the darker dorsal color without conspicuous
dark vertical stripes. 7a. Vomerine teeth usually present in the adult; tympanum quite
distinct. 8a. Rudimentary webs on fingers and toes (E. Ecuador)
8b. Outer fingers and toes one-third to one-half webbed (Costa Rica)
7b. Vomerine teeth usually not present in the adult; tympanum indistinct; adults usually less than 45 mm. in length.
9a. Fingers and toes at least one-third webbed. 10a. Tibiotarsal articulation reaches to or beyond tip of snout (E.
Ecuador)
9b. Fingers not webbed, or only basally so (S. E. Brazil)
3b. No dermal appendages.
lla. Vomerine teeth usually present in the adult. 12a. Fingers and toes free, or with a very small remnant of a web
(Bahia, Brazil) aspera (p. 29)
12b. Fingers and toes at least one-fourth webbed. 13a. Tibiotarsal articulation reaches beyond anterior corner of eye.
14a. Sides with distinct oblique light lines; dorsum without trans-
verse dark markings (Panama to Costa Rica)
14b. Sides without light lines; dorsum with more or less distinct transverse dark markings (Costa Rica) saltator (p. 36)
13b. Tibiotarsal articulation reaches only to tympanum (Mexico)
11b. Vomerine teeth usually not present in the adult.
15a. Fingers free, toes webbed only at base (Costa Rica)
15b. Fingers one-third, toes nearly one-half webbed (upper Amazon of Ecuador)
2b. Snout sloping in profile; vomerine teeth usually present in the adult; no parotoids (except bicolor).
16a. An inconspicuous dermal appendage on heel and/or elbow.
17a. A triangular heel appendage; sides with conspicuous dark vertical bands; dorsum without darker transverse markings (Panama to N. W. Ecuador)
17b. Very small dermal appendage on elbow and heel; sides unmarked; dor-
sum with more or less conspicuous dark transverse markings (Costa Rica) saltator (p. 36)
16b. No dermal appendages; no dark vertical stripes on sides.
18a. Sides of body have pale vertical stripes against a darker background color; fingers and toes at least one-third webbed.
19a. Sides of body with conspicuous dark, semi-rectangular spots, sep-
arated from each other, and from the dorsal color by light stripes (see figure) (southern Mexico to Panama) helenae (p. 32)
19b. Sides without strongly contrasting markings, pale vertical stripes
on a slightly darker background color, the darker interspaces con- nected to the dark dorsal color.
20a. Heels overlap slightly when legs are held at right angles to the
body; tibiotarsal articulation reaches to nostril or beyond tip of spout (Costa Rica to Panama)

- 18b. Sides of body unmarked, or without pale vertical stripes; fingers and toes webbed or not.
- 21a. Fingers and toes not webbed, or only basally so.
 - 22a. Size very large (adults about 100 mm.); osteoderms in skin of dorsum (Amazon and Magdalena basins; Guianas)... bicolor (p. 38)
- 21b. Fingers at least one-half webbed, toes at least two-thirds webbed.
- 23a. Conspicuous white, dark-bordered warts on the back (Panama to Colombia)......spurrelli (p. 39)
- 1b. First toe longer than, or equal to, the second; usually distinct parotoids; no webs, or very small basal ones.
- 24a. Snout truncate in profile; vomerine teeth may or may not be present.25a. Parotoid glands conspicuous; vomerine teeth usually present in the adult.
 - 26a. Parotoid glands marked by a single line of white or light-colored tubercles; other tubercles on the limbs may be present but are not prominent.
 - 27a. Parotoids marked by a single line of white tubercles which contrast strongly with the dorsal color; interorbital distance equals the upper eyelid (E. Ecuador).......................... blombergi (p. 41)
 - 27b. Parotoids marked by a single line of pearly tubercles, not contrasting so sharply with the dorsal color; interorbital distance greater than the upper eyelid (E. Andean foothills of N. Peru; British Guiana) perlata (p. 42)
 - 26b. Parotoid glands marked by several lines of tubercles or by a distinct ridge of glandular roughness resembling tubercles; other tubercles on limbs, especially hind limbs, conspicuous (E. Andean foothills of Ecuador).................................. edentula (p. 43)
- 25b. No parotoid glands; usually no vomerine teeth.
- 28b. Dorsal color does not cover loreal region; disks of fingers about equal to the tympanum; dark network on sides; color of forearm does not extend to hands (Bolivia to Rio de Janeiro)..........
- 29a. Parotoid glands lacking or indistinct.
 - 30a. No parotoid glands.

 - 31b. Interorbital space broader than upper eyelid (E. Colombia).......

 niceforoi (p. 47)
 - 30b. Parotoids indistinct.

 - 32b. Skin of dorsal surfaces smooth; disks oblong, longer than wide.

 - 33b. Sides same color as dorsum with definite white spots (Trinidad Island)...... trinitatis (p. 50)
- 29b. Parotoid glands present, usually quite distinct.

34a. Largest disk of finger distinctly larger than the tympanum.
35a. Osteoderms in skin of dorsum (N. E. Peru, through the Amazon Basin to
the Guianas; Magdalena Basin)bicolor (p. 38)
35b. No osteoderms, although skin of dorsum may be coarse (upper Amazon of
Peru) tarsius (p. 51)
34b. Largest disk of finger smaller than the tympanum.
36a. Osteoderms in skin of dorsum, or dorsal surfaces roughened, giving
the appearance of possessing osteoderms.
37a. Parotoids short, not extending beyond the angle of the jaw; osteo-
derms in skin of dorsum (Santarém, lower Amazon)
37b. Parotoids extending at least to point reached by adpressed elbow;
osteoderms may be present.
38a. Interorbital space much broader than the upper eyelid; osteoderms
in skin of dorsum (N. E. Peru, through the Amazon Basin to the
Guianas; Magdalena Basin) btcolor (p. 38)
38b. Interorbital space about equal to the upper eyelid; skin roughened,
giving the appearance of possessing osteoderms.
39a. Parotoids distinct, frequently forming an angular ridge along the
side of the body; chest and belly light colored (E. Andean foot-
hills of Ecuador) feltoni (p. 52)
39b. Parotoids indistinct; throat and chest dark, belly tinged with
black (E. Ecuador) orcesi (p. 48)
36b. Osteoderms usually not present in skin of dorsum.
40a. Parotoids quite prominent, short, not extending past the axilla. 41a. Osteoderms in skin of dorsum; dorsal surfaces rough, but no dis-
tinct warts (Santarém, lower Amazon)
41b. No osteoderms; dorsal surfaces smooth, flat warts sometimes present
(N. Argentina, S. Brazil, S. Bolivia) sauvagei (p. 54)
40b. Parotoids prominent, reaching to middle of body.
42a. Leg short, tibiotarsal articulation reaches only to axilla (E.
coast of Brazil, N. of Rio de Janeiro to northern Bahia)
bahtana (p. 55)
42b. Leg longer, tibiotarsal articulation reaches at least to tympanum.
43a. Snout acuminate when viewed from above; dorsal surfaces roughened,
either giving the appearance of possessing osteoderms or with
numerous tubercles on the sides and limbs. 44a. Parotoids marked by several lines of tubercles or a distinct
glandular ridge resembling tubercles; other prominent tubercles
on limbs (E. Andean foothills of Ecuador)
edentula (p. 43)
44b. Parotoids distinct, not marked by tubercles; skin of dorsum rough-
ened, but tubercles on sides and limbs rather small (E. Andean
foothills of Ecuador) feltont (p. 52)
43b. Snout rounded when viewed from above; dorsal surfaces smooth.
45a. Disks light, contrasting with remainder of hand and foot; no dis-
tinct light spots on each side of vent (coastal Brazil)
burmeisteri (p. 56)
45b. Disks not sharply defined in color from remainder of hand and
foot; distinct light spots on each side of vent (Ecuador to Bolivia)boliviana (p. 57)
BULLVIE, (p. 31)

SYSTEMATIC ACCOUNT OF THE SPECIES

Phyllomedusa craspedopus, new species Figures 7, 10; Map 2

DIAGNOSIS: A Phyllomedusa of the Agalychnis group, appearing closest to the west Andean P. calcarifer from which it differs in having a sharply truncate snout, narrower lateral bands, the presence of exceptional dermal folds on tibia, tarsus, fifth toe and forearm, and the presence of a dermal fold around margin of lower jaw. The present form differs from all other known members of this genus in the presence of such well-developed dermal folds.

HOLOTYPE: Stanford University 10310, adult male, 55 mm. snout-to-vent, from Chicherota, Río Bobonaza, Napo-Pastaza Province, eastern Ecuador (Lat. 2° 22' S., Long. 76° 38' W.), at an altitude of about 280 meters, collected by Ramón Olalla, 1941.

PARATYPE: Escuela Politécnica Nacional (Quito, Ecuador) 53, adult female, 73 mm. snout-to-vent, from the same locality and by the same collector.

DESCRIPTION OF HOLOTYPE: Vomerine teeth in two short, oblique series between anterior edges of the choanae. Tip of snout bluntly rounded when viewed from above, truncate in profile; canthus rostralis poorly developed, slightly incurved; loreal region oblique, plane. Head slightly broader than long, broader than sacrum. Interorbital distance broader than upper eyelid, about equal to distance from front corner of eye to nostril and to diameter of exposed part of eye. Nostrils closer to tip of snout than to eye; distance between nostrils almost equal to distance from anterior corner of eye to nostril. Tympanum distinct, its vertical diameter equal to exposed part of eye, horizontal diameter three-fourths length of eye. Distinct parotoid swellings (possibly not glandular?), extend from above tympanum to a point just posterior to insertion of forearm, most pronounced directly above insertion of forearm.

Fingers two-thirds webbed. Subarticular tubercles prominent. Disks well developed; disks of second and fourth fingers equal to tympanum, disk of third slightly larger, and of first much reduced, about half the tympanum. Toes three-fourths webbed; first toe shorter than second, not opposable to the others. Subarticular tubercles prominent; an oval outer, a very small round inner metatarsal tubercle. Disks well developed, of fifth toe about equal to tympanum, others progressively decreasing in size to first which is about two-thirds diameter of tympanum. Broad fringes extend to disks of outer fingers and toes. Heels overlap slightly when legs are held at right angles to body. Tibiotarsal articulation reaches between eye and tip of snout.

Dermal folds along both fore and hind border of tibia. The anterior fold or ridge very feeble, continuing around knee and along thigh anteromesad to fade out midway between knee and vent. The posterior fold of the tibia is more pronounced, and extends into an expanded triangular flap on heel, continues along posterior margin of tarsus as an irregular, broadly expanded fold which produces two more irregular spurs, the first about one-third the distance between heel and tarsometatarsal articulation, at which point the second is produced, the broad dermal fold continues to disk of fifth toe. A very small dermal fold or ridge on anterior edge of forearm. A more expanded fold along posterior edge from elbow to disk of fourth finger. A third fold around margin of lower jaw, weakly cleft medially and expanded slightly on either side of cleft for a short distance.

Skin of dorsal and lateral surfaces quite smooth, faintly granular on

abdomen and under surface of thighs.

COLOR IN LIFE: (From adult female paratype. Notes by Dr. Gustavo Orcés V., taken one month after specimen had been preserved.) "Above, a shiny green which was turning to blue; below white, but as I remember, tinged with orange-yellow. Between the pale color of the under parts and the bright green of the upper, there existed a narrow zone of purplish brown, sparsely dotted with white, (the white flecks were found only in the purplish-brown region and not in the green), this hue extending from the region of the tympanum backwards. Of this same purplish-brown color were the narrow vertical lines on the sides, and it seemed so had formerly been colored the transverse stripes over the limbs."

COLOR IN ALCOHOL: Dorsum and exposed surfaces of arms and legs, including fifth toe, dark blue-gray; dark color of dorsum extended in vertical bands on the anterior surface of forearm, sides, anterior and posterior surfaces of thigh and tibia, anterior face of tarsus and fourth toe; venter immaculate; outer or exposed surface of fold around lower lip dark bluegray. The male possesses a conspicuous dark brown nuptial spot on thumb.

VARIATION: The paratype exhibits the following differences from the holotype: The vertical, or longest measurement of tympanum is equal to exposed part of eye; disks of all the fingers except first larger than tympanum; disks of toes decrease in size from the fifth, which is equal to tympanum, to the first, which is about three-fourths the tympanum; dark vertical bands on sides longer and more conspicuous, but have the same distribution as in the male.

Phyllomedusa calcarifer (Boulenger) Figures 7, 11; Maps 1, 2

Agalychnis calcarifer Boulenger, 1902a, p. 52 (type locality: Río Durango, northwest Ecuador; holotype in British Museum, female, length 57 mm.); 1913, p. 1023, pl. 102, figs. 2-2b (life color of type specimen).

—Nieden, 1923, p. 335 (compiled description).—Dunn, 1931, p. 415 (Panama; third known specimen).

Phyllomedusa (Agalychnis) calcarifer Bertha Lutz, 1950, pp. 601 (in Portuguese), 619 (in English).

RANGE: Panama to northwestern Ecuador, west of the Andes.

DISTINGUISHING CHARACTERISTICS: Extensive webbing, large disks; snout sloping in profile; color pattern (see below). Most similar to *craspedopus* and *spurrelli*.

DESCRIPTION: Tongue openly emarginate behind; vomerine teeth in two short, oblique series between the choanae. Head moderately depressed, as long as broad. Snout rounded when viewed from above, not projecting beyond the lower jaw, distinctly sloping in profile. Canthus rostralis feeble; loreal region slightly concave. Interorbital space as broad as upper eyelid. Tympanum close to eye, half or nearly equal to its diameter.

Fingers two-thirds webbed, the disks almost as large as tympanum. Toes rather short; first toe shorter than second, not opposable to the others, three-fourths or entirely webbed, disks a little smaller than those of fingers. Fringes extend to disks of outer fingers and toes. Subarticular tubercles very prominent. Tibiotarsal articulation reaches to eye or tip of snout.

Skin smooth on dorsum, granular on belly and in front of vent. A narrow dermal fold along outer edge of forearm and tarsus. A truncate, rather indistinct dermal flap above vent. Heel with a large triangular dermal flap.

LENGTH: 47-57 mm.

COLOR IN LIFE: Brilliant sage-green above; flanks and upper surface of thighs (with the exception of a narrow green streak) rich orange-yellow with black bars; hands and feet and lower parts orange-yellow; iris gray, bordered with orange-yellow; lower eyelid transparent, edged with turquoise. Based on specimen from Peña Lisa, Condoto, Colombia (Boulenger, 1913).

COLOR IN ALCOHOL: Gray-blue above; venter, sides, and concealed portions of limbs white; black bars as described above; white line on outer

edge of tarsus; foot bordered with brown below.

SPECIMENS EXAMINED: One, MCZ 15610, Barro Colorado Island, Canal Zone.

Phyllomedusa tomopterna (Cope) Figures 7, 12; Map 2

Pithecopus tomopternus Cope, 1868, p. 112 (type locality: below mouth of Río Napo, or Rio Amazonas below mouth of the Río Napo; types: given as Smithsonian Mus. 6651, length 23 lines; probably now in USNM).

Phyllomedusa hypochondrialis (nec Daudin, 1803) Peters, 1871, p. 404.

Phyllomedusa palliata Peters, 1872b, p. 773, footnote (type locality: Ucayali; type in Berlin).—Boulenger, 1882a, p. 426 (description).—Nieden, 1923, p. 342 (compiled description).

Phyllomedusa tomopterna Boulenger, 1882a, p. 430 (compiled description).
—Cope, 1886b, p. 96 (name only).—Nieden, 1923, p. 343 (compiled description).

Phyllomedusa (Pithecopus) tomopternus Bertha Lutz, 1950, pp. 603 (in Portuguese), 621 (in English), map.

RANGE: Upper Amazon of Peru, Ecuador and Brazil.

DISTINGUISHING CHARACTERISTICS: Snout longer than eye; fingers free, toes usually free; sides of body and limbs with distinct dark bands. Most similar to loris.

DESCRIPTION: Tongue indistinctly emarginate. Vomerine teeth in two oblique groups on a level with anterior edge of choanae. Snout longer than diameter of eye, rounded when viewed from above, truncate in profile. Loreal region plane, nearly vertical. Canthus rostralis moderately well defined. Interorbital space broader than upper eyelid. Tympanum half diameter of eye.

Fingers free, first shorter than the second, may be opposable to the others; disks nearly as large as tympanum. No fringes on fingers or toes. Toes free or with a rudiment of a web; first toe equal to or slightly longer than the second; disks of toes slightly smaller than those of fingers. Subarticular tubercles prominent, inner metatarsal tubercle not prominent. The tibiotarsal articulation reaches beyond the eye.

Skin smooth above; granular on belly and under thighs. Parotoid glands indistinct or lacking. A feeble dermal fold on lower arm, strongest at elbow; another fold, also feeble, on tarsus, terminating on heel in two dermal processes, one projecting inward and one outward.

LENGTH: 45-51 mm.

COLOR IN ALCOHOL: Exposed surfaces reddish or gray-blue; belly yellow, or white like remainder of venter, sides, humerus, hand and inner toes; dark purplish brown bands on sides and concealed portion of limbs.

SPECIMENS EXAMINED: Three, as follows: MCZ 4775: one from Pebas, Peru. SU 13066: one from eastern Andean foothills, Ecuador. UMMZ 31744: one from Santiago, De Boia, upper Amazon, Brazil.

Phyllomedusa loris Boulenger Figures 7, 13; Map 2

Phyllomedusa loris Boulenger, 1912, p. 186 (type locality: El Topo, Río Pastaza, eastern Ecuador; type: in British Museum, length 46 mm.).
—Nieden, 1923, p. 344 (compiled description).

Phyllomedusa (Phyllomedusa) loris Bertha Lutz, 1950, pp. 601 (in Portuguese), 619 (in English).

RANGE: Eastern Andean foothills of Ecuador.

DISTINGUISHING CHARACTERISTICS: Snout as long as eye; rudimentary webbing on fingers and toes; sides of body and limbs unmarked. Most similar to tomopterna.

DESCRIPTION: Tongue cordiform, nicked behind. Vomerine teeth in two small groups between the choanae. Snout as long as exposed part of eye, vertically truncate in profile. Canthus rostralis fairly well developed, curved near nostril. Loreal region oblique, plane. Eyes directed obliquely forward. Interorbital space broader than upper eyelid. Tympanum half or less than half diameter of exposed part of eye.

Fingers with a slight rudiment of a web; first finger shorter than the second. Toes webbed at base; first and second toes equal; first toe may be opposable to the others. Disks of fingers as large as, or slightly larger than tympanum, of the toes a little smaller. Narrow fringes extend to disks of outer fingers and toes. Subarticular tubercles moderately prominent; inner metatarsal tubercle small, elliptic. Tibiotarsal articulation reaches to eye or tip of snout. Tibia approximately one-half length of head and body.

Skin smooth above, granular on belly and under thighs. A glandular (?) ridge on superior face of forearm between dorsal and ventral colors. Parotoids (or parotoid swellings) feebly developed. Heel with a small triangular dermal appendage projecting outward; a suggestion of another projecting inward.

LENGTH: 46-52 mm.

COLOR IN ALCOHOL: Lilac above with a few dark spots; humerus, four inner fingers, thigh (except a narrow dorsal lilac streak), inner toes and lower parts yellow or white.

SPECIMENS EXAMINED: One, UMMZ 92102, from Abitagua, Río Bobonaza, eastern Ecuador.

REMARKS: See "Remarks" under P. buckleyt.

Phyllomedusa buckleyi Boulenger Figures 7, 14; Map 2

Phyllomedusa buckleyi Boulenger, 1882a, p. 425, pl. 29, fig. 1 (type locality: Sarayacu, eastern Ecuador; holotype in British Museum, half grown, length 32 mm.).—Nieden, 1923, p. 344 (compiled description).—Bertha Lutz, 1950, pp. 601 (in Portuguese), 619 (in English).

RANGE: Known only from the type locality.

DISTINGUISHING CHARACTERISTICS: No vomerine teeth; snout as long as eye; sides of body and limbs unmarked. Most similar to loris (see Remarks below).

DESCRIPTION: "Tongue small, entire. Vomerine teeth none. Snout a little longer than the diameter of the eye, rounded; loreal region slightly oblique; interorbital space much broader than the upper eyelid; tympanum

hidden. Fingers one-third webbed, toes nearly half webbed; first finger shorter than second, fourth slightly shorter than third; first toe a little shorter than second; disks of fingers and toes moderate, about one-third the diameter of the eye; subarticular tubercles moderately prominent; inner metatarsal tubercle scarcely prominent. The hind limb being carried forwards along the body, the tibio-tarsal articulation reaches a little beyond the tip of the snout. Skin smooth, granulate on the belly; parotoids none. Lilac above, minutely dotted with lighter; humerus, femur, hand, and foot (except outer toe) not colored; beneath whitish, immaculate. From snout to vent 32 millim." (Boulenger, 1882a.)

SPECIMENS EXAMINED: None.

REMARKS: Boulenger's original description is based on a single, half-grown specimen, and to the best of the author's knowledge there have been no other specimens collected. In the detail of finger and toe webbing the description does not coincide with the plate, the description stating "fingers one-third webbed, toes nearly half webbed", while the plate shows no webbing on either fingers or toes. A number of forms of this genus have been described from the eastern Andean foothill region of Ecuador. Boulenger's description is of an immature specimen, probably of a species described later from an adult. If this is so the other form involved is most likely P. loris, with which it agrees in a number of characters. However, since the author has not seen the type of buckleyl and has had an opportunity to examine only one adult specimen of loris, it seems inadvisable to synonymize them at this time.

Phyllomedusa fimbriata (Miranda-Ribeiro) Figures 7, 15; Map 2

Phrynomedusa fimbriata Miranda-Ribeiro, 1923, p. 4 (type locality: Alto da Serra, São Paulo, ?actually Paranapiacaba, near Santos [see Remarks]; holotype: Museu Paulista 316, length 45 mm.); 1926, p. 106, fig. 62 (amplified description).

Phyllomedusa appendiculata Adolpho Lutz, 19250, p. 139 (diagnosis; type locality: Teresópolis, Rio de Janeiro, Brazil; holotype in Adolpho Lutz Collection, Instituto Oswaldo Cruz, male, length 35 mm.); 1926, pp. 8, 15.—A. and B. Lutz, 1939, p. 236, pl. 1, fig. 4, pl. 3, pl. 7, figs. 5-6, pl. 8, fig. 3 (description).—Bertha Lutz, 1950, pp. 601 (in Portuguese), 619 (in English).—Cochran, 1955, pp. 196 (key; description), 203 (note on voice), 379 (table), pl. 18, figs. J-K.

RANGE: Known from Rio de Janeiro to São Bento.

DISTINGUISHING CHARACTERISTICS: Size small; no parotoids; usually no vomerine teeth; single, very small, dermal heel appendage; fingers and toes one-third webbed. Most similar to P. guttata.

DESCRIPTION: Tongue shallowly emarginate. Vomerine teeth usually absent. Eye large, prominent, longer than its distance from nostril. Snout rounded, truncate in profile. Canthus rostralis distinct. Loreal region plane, sloping. Nostrils subterminal, lateral, separated by an interval equal to three-fifths the interorbital space. Tympanum not prominent, its diameter about two-fifths that of eye.

Fingers one-third webbed; first shorter than the second; fourth shorter than the third, whose disk nearly covers tympanic area; toes one-third webbed; first shorter than the second, and may be opposable to the others. No outer metatarsal tubercle. Tibiotarsal articulation reaches to the eye. When placed at right angles to the body the heels overlap. A small triangular heel appendage.

Skin smooth above, slightly granular below. Visible surfaces divided

from those concealed in repose by undulating glandular ridges on forearm and foot.

LENGTH: 32-37 mm.

COLOR IN LIFE: Dorsal surfaces green or brown-violet; concealed surfaces orange to yellow; a longitudinal line of darker dots down the middle of the upper surfaces of thigh; hands and feet paler. Glandular ridges of forearm and foot, outline of upper jaw, tympanic ridge and free edge of upper eyelid light with dark dots. Under side, including median lower thighs and perianal region, white.

COLOR IN ALCOHOL: Dorsum blue-gray; venter pale. According to Lutz (1939) the markings on the glandular ridges persist, but this varies according to the state of preservation. The single specimen examined lacked

markings of any kind.

SPECIMENS EXAMINED: One, USNM 96447, and several almost transformed

tadpoles, USNM 96448, Teresópolis, Rio de Janeiro.

REMARKS: Because *Phrynomedusa fimbriata* had been placed in the synonymy of both *appendiculata* and *guttata* by different workers, the author asked Sr. Antenor L. de Carvalho to examine the types in question. Due to Sr. Carvalho's preparations for an expedition, Werner C. A. Bokerman very kindly answered the author's request as follows: "Miranda Ribeiro describes in 1923 (Bol. Museu Nacional) a species under the name of *Phrynomedusa fimbriata* (gen & spec. nov.) from Alto da Serra, actually Paranapiacaba, in the mountains near Santos. In 1926 the species was re-described by Miranda Ribeiro in his general work on Brazilian batrachians (Arq. Museu Nacional).

"Lutz described the same species as *Phyllomedusa appendiculata* in 1925. I have examined cotypes of Lutz's *appendiculata* and I am of the opinion that really it is a synonym of *fimbriata*. This species is characterized by a

small dermal appendage on the heels.

"Cochran in her paper "Frogs of Southeastern Brazil" uses the name appendiculata Lutz, but does not give any explication for this preference, although she cites Miranda Ribeiro's 1923 paper in her bibliography."

Assuming Sr. Bokerman's observations are correct, the priority of the

name fimbriata requires that it be used for this species.

Phyllomedusa guttata Adolpho Lutz Figures 7, 16; Map 2

Phyllomedusa guttata Adolpho Lutz, 1925a, p. 241 (diagnosis) (type locality: Carioca Mountain at Tijuca, Rio de Janeiro, Brazil; holotype in Adolpho Lutz Collection, Instituto Oswaldo Cruz, male, length 35 mm.); Lutz 1926, pp. 8, 14.—Adolpho and Bertha Lutz, 1939, pp. 219, 225, pls. 1, 2, 7, 8 (description; life color; behavior; skeleton; tadpoles; Rio de Janeiro, Brazil).—Myers, 1946, p. 14 (Portuguese), p. 32 (English) (Tijuca above Cascatinha; Bom Retiro; tadpoles).—Cochran, 1955, pp. 196 (key), 201 (description; tadpoles; Districto Federal, Rio de Janeiro, Brazil), pl. 19, figs. C-D.

Phyllomedusa (Hylomantis) guttata Bertha Lutz, 1950, pp. 601 (in Portu-

guese), 619 (in English).

Phrynomedusa fimbriata Miranda-Ribeiro, 1926, p. 106, fig. 62 (diagnosis; type locality: Alto da Serra, São Paulo; holotype Museu Paulista 316, 45 mm. in length).

RANGE: Southern coastal Brazil: region of Rio de Janeiro to São Paulo. DISTINGUISHING CHARACTERISTICS: Size small; no parotoid glands; usually no vomerine teeth; single small heel appendage; tympanum usually not visible; fingers free, outer three toes basally webbed. Most similar to fimbriata.

Tongue slightly notched behind. Vomerine teeth usually Snout very short, openly triangular, slightly projecting not present. beyond the lower jaw, and truncate in profile. Eye directed partly forward, large and extremely prominent. Canthus rostralis sharp, angular. *Loreal region slightly concave, nearly vertical. Tympanum covered by skin, not or barely visible.

Fingers free; first shorter than second, fourth slightly shorter than Rudimentary web at base of third, fourth and fifth toes; first toe shorter than second, and may be opposable to the other, fifth much shorter than fourth. Subarticular palmar and plantar tubercle well developed.

Tibiotarsal articulation reaches to anterior corner of eye.

Body somewhat tapering, width of head contained just under three times in snout-to-vent length. Skin smooth above; slightly granular below. No distinct parotoids, but granular upper eyelids, and a slightly overhanging ridge running from posterior edge of upper eyelid to shoulder, sometimes outlining upper edge of tympanum. The always visible surfaces separated from those concealed in repose by glandular ridges which are especially well developed on forearm and foot, forming a very small horn-like appendage on heel, and a lesser one on elbow (except for heel appendage these glandular ridges are often difficult to distinguish in preserved material).

LENGTH: 35 to 46 mm.

COLOR IN LIFE: Dorsum green, shading to brown according to substratum and amount of light; glandular ridges with longitudinal lines of black dots, also found on light edge of upper lip; concealed surfaces vivid orange; violet spots on sides, hands, feet and thighs; throat and belly white; iris gold: nictitating membrane green.

COLOR IN ALCOHOL: Dorsum pale violet to deep reddish brown with darker spots on sides and often on dorsum, forming no particular pattern; venter

immaculate.

SPECIMENS EXAMINED: Seventeen adults and 33 tadpoles, all from Brazil. as follows: UMMZ 68764: one from Rio de Janeiro; USNM 81147-48: two; 96224-25: two; 96226-27: five (tadpoles); 118996: one; 118997: three (tadpoles) from Rio de Janeiro; 96548-56: nine; 96642-43: 20 (tadpoles) from SU 12722: five (tadpoles), Tijuca above Alto da Boa Vista, Distrito Federal; 13064: one, Baixada do Barro Branco, Estado do Rio de Janeiro; 13065: one, Bom Retiro, Tijuca, Distrito Federal.

The life-color notes above were taken from A. and B. Lutz REMARKS: (1939), who present very detailed life-color observations, skeletal features, behavior characteristics, and a description of the tadpoles. latter are characterized by a large membranous peristome around the dorsally placed mouth opening, evidently associated with their montane habitat. Miss Cochran (1955) describes the tadpole mouth parts in detail.

Phyllomedusa aspera (Peters) Figures 7, 17; Map 2

Hylomantis aspera Peters, 1872b, p. 772, pl. 1, figs. 2-2a (type locality: Bahia, Brazil, (probably Caravellas); holotype in Zool. Museum, Berlin, length 54 mm.). -- Miranda-Ribeiro, 1926, p. 101, fig. 59 (translation into Portuguese of Peters' description).

Phyllomedusa aspera Boulenger, 1882a, p. 425 (compiled description). - Nieden, 1923, p. 339 (compiled description).

Phyllomedusa (Hylomantis) aspera Bertha Lutz, 1950, pp. 601 (in Portuguese), 619 (in English).

?Known only from the type locality. DISTINGUISHING CHARACTERISTICS: No parotoid glands; upper surfaces apparently covered with tubercles.

DESCRIPTION: Tongue doubly cleft in front, shallowly emarginate behind. Vomerine teeth in two small, oblique groups between anterior borders of the choanae. Snout rounded when viewed from above, truncate in profile, no longer than the very prominent eye. Canthus rostralis rounded. Loreal region sloping. Tympanum covered with skin, rather indistinct, about one-third diameter of eye.

Fingers quite free, only a rudiment of a web between the third and fourth; first finger shortest, third longest and second a little shorter than the fourth. Rudiment of a web on toes; first shorter than second. Disks on fingers and toes as large as tympanum. Subarticular tubercles well developed.

Upper surfaces appear tubercular in illustration of type [no mention is made of this in the original description]. No parotoids.

COLOR (? IN ALCOHOL): Dorsum, including forearm from elbow to fourth finger, femur, tibia and tarsus to fifth toe violet or grayish violet, with or without rust-colored or whitish, dark-edged spots. Sides and venter yellowish. (From Peters' description.)

SPECIMENS EXAMINED: None.

REMARKS: Although this species seems to be known only from the type description, the following combination of characters distinguish it very clearly from other species in the genus: lack of parotoids; evidently tubercular upper surfaces; presence (in some examples) of light, dark-edged spots on the dorsum.

Phyllomedusa alcorni (Taylor) Figures 7, 18; Map 1

Agalychnis alcorni Taylor, 1952a, p. 31, pl. 1, figs. 1-2, 3c (type locality: south bank of Río de Tepalcatepec, 17 miles south of Apatzingán, Michoacán, Mexico; holotype: Univ. of Kansas Mus. Nat. Hist. 29763, female. length 48 mm.).

RANGE: Only the type locality and the locality of the paratype are known.

DISTINGUUSHING CHARACTERISTICS: No parotoid glands; snout truncate in profile; tibiotarsal articulation reaches only to tympanum.

DESCRIPTION: Tongue emarginate posteriorly. Vomerine teeth in two small, narrow, transverse series, separated from each other by a distance equal to transverse length of one series. Width of head a little greater than length. Length of eye approximately equal to axial length of snout. Canthus rostralis rounded. Loreal region not concave, sloping abruptly to lip. Lateral profile of snout angular at nostrils, sloping abruptly [i.e., truncate]. Width of upper eyelid about two-thirds interorbital space. Tympanum vertically oval; a thin fold from back of eye runs above and curves down behind it, in contact with posterior border [outlining a parotoid swelling?]; vertical diameter of tympanum about one-half horizontal eye measurement.

Fingers about one-fourth webbed with fringes, more or less distinct, extending to disks. Two inner toes about one-fourth webbed, three outer ones nearly one-half webbed; first toe shorter than second, not opposable; fringes on toes reaching to disks. Disks small, only slightly wider than digits, including fringes. Leg short, the tibiotarsal articulation reaching not quite to tympanum.

Skin smooth above; no parotoid glands, chin and breast indistinctly granular. A slight fold or ridge on outer surface of arm extending to elbow; a distinct tarsal fold. Venter and entire under surface of thigh cov-

ered with distinct small granules. Posterior surface of thigh with upper part bearing much larger granules.

LENGTH: 38-48 mm.

COLOR IN LIFE: Green above, including most of sides, upper part of forearm and outer finger, a narrow stripe on dorsal surface of femur, tibia, tarsus and part of two outer toes; tympanum lavender; iris black; transparent lower eyelid black edged; chin and breast paper white; venter, under surface of thigh and concealed parts of limbs yellow to orange-yellow; a few small white flecks border lateral green color, and the area about the vent is frosted with white; a cream white line borders the green of the forearm to elbow, and outer edge of tarsus across heel; a few irregularly placed white dots on back. (From E. H. Taylor's description.)

SPECIMENS EXAMINED: None.

REMARKS: "This species occurs on the west coast (of Mexico) at low elevations in the same general regions in which Agalychnis dacnicolor is to be found. The most significant differences in specimens of dacnicolor of equal snout-to-vent length are a very much longer, more attenuated snout; heel reaches to middle of eye; vent carried to below level of thigh, the area about the opening swollen, protuberant." (Taylor, 1952a.) Known from the holotype (see above in synonymy) and one paratype. The latter, UKMNH 28100, 38 mm., from one-half mile east of San Blas, Nayarit, Mexico.

Phyllomedusa lemur Boulenger Figures 7, 19; Map 1

Phyllomedusa lemur Boulenger, 1882a, p. 425 (type locality: Costa Rica; holotype in British Museum, female, length 43 mm.).—Nieden, 1923, pp. 344-345 (compiled description; Costa Rica).—Taylor, 1952b, pp. 809-811, fig. 41 (description: Costa Rica: Volcán Poás, 2500 ft.; Isla Bonita, 5500 ft.)

Agalychnts lemur Cope, 1887, p. 15 (check list).—Günther, 1901, pp. 291-292 (description; Costa Rica).

Phyllomedusa (Agalychnis) lemur Bertha Lutz, 1950, pp. 601 (in Portuguese), 619 (in English).

RANGE: Mountains of Costa Rica.

DISTINGUISHING CHARACTERISTICS: Size small to medium; fingers and toes free; disks small; range.

DESCRIPTION: Tongue variably emarginate, usually only slightly so. No vomerine teeth. Length of snout equal to, or slightly longer than, diameter of eye, truncate in profile, rounded when viewed from above. Loreal region plane, nearly vertical. Eyes very prominent, directed obliquely forward. Interorbital space broader than upper eyelid. Tympanum very indistinct, less than one-third diameter of eye.

Fingers free; first shorter than second; thin, round in cross-section; disks smaller than tympanum. Toes free or very slightly webbed at base; first slightly shorter than second, not opposable to the others; disks slightly smaller than those of fingers, usually no fringes on fingers or toes (two specimens, UMMZ 7921, adult female, and USNM 75066, have broad fringes extending to the disks of the outer fingers and toes, and the disks of the fingers are considerably larger than the tympanum). Tibiotarsal articulation reaches from between eye and tip of snout to beyond snout. Subarticular tubercles moderately prominent. Inner metatarsal tubercle very indistinct.

Skin smooth above. No parotoids, but indistinct parotoid swellings. Slightly granulate on the belly; a group of coarse granules on under side of thighs on each side of vent.

LENGTH: 28-48 mm.

COLOR IN LIFE: "At night bright lemon yellow or yellow green. In daylight usually with some bronze marbling, fine blackish spots or reddish brown marks. Concealed parts of hands and feet, front and back of thighs, yellow. Chin whitish, belly cream." (E. H. Taylor field notes.)

COLOR IN ALCOHOL: Light lilac or terra cotta above, lightly speckled with darker; inner fingers and toes, upper arm, thighs (except for a narrow

band along upper side) and lower surfaces yellowish white.

SPECIMENS EXAMINED: Twenty-seven, all from Costa Rica, as follows: UMMZ 7921-22: two from La Palma; 7966: one from Cariblanco. USNM 75066: one from La Palma. UKMNH (field nos.) 31700-19: 20; 31721: one; 31774: one; 31876: one from Moravia de Chirripó.

Phyllomedusa helenae (Cope) Figures 7, 20; Map 1

Agalychnis helenae Cope, 1885, p. 182 (type locality: Nicaragua; holotype: USNM 13737); 1886a, p. 274 (another specimen, color note; Nicaragua). —Peracca, 1896, p. 12 (paper not seen).—Günther, 1901, p. 290 (description; Mexico: Teapa, Tabasco; Nicaragua, Hacienda Rosa de Jericho, 3250 ft.; Costa Rica, San Carlos; Panama, Darién, Rio Sabaná). —Nieden, 1923, p. 334 (compiled description; Mexico, Nicaragua, Costa Rica, Panama).—Taylor, 1952b, pp. 802 (key), 805 (description; Costa Rica).

Phyllomedusa (Agalychnis) helenae Bertha Lutz, 1950, pp. 601 (in Portuguese), 619 (in English).

RANGE: Southern Mexico to Panama.

DISTINGUISHING CHARACTERISTICS: Fingers and toes about two-thirds webbed; series of large quandrangular black spots on sides, separated from each other and from dorsal color by light lines. Most similar to callidryas (see Remarks below).

DESCRIPTION: Tongue large and broad, distinctly emarginate behind. Vomerine teeth in two short rows, converging posteriorly, between the choanae. Head large and broad. Snout sloping in profile. Length of eye equal to its distance from tip of snout. Canthus rostralis distinct, curved. Loreal region nearly vertical. Tympanum indistinct, about two-thirds length of eye.

Outer fingers two-thirds webbed, inner fingers one-fourth or less. Toes two-thirds webbed. First toe shorter than second, not opposable to the others. Disks almost as large as tympanum. Fringes extend to disks of outer fingers and toes. Tibiotarsal articulation reaches beyond eye, usually to tip of snout. Heels overlap when held at right angles to body.

Skin of dorsum smooth; strongly granulate below. Dermal folds (sometimes quite indistinct) on outer edge of forearm, tibia and foot; no parotoid glands.

LENGTH: 30-70 mm.

COLOR IN LIFE: Upper parts, including upper surface of forearm, tibia, tarsus, outer finger and toe, and narrow band on upper surface of femur brilliant green; a single linear series of large quadrangular plack spots on sides, which are separated from the upper parts by an uninterrupted yellow border, and from one another by narrow oblique yellow stripes; humerus together with concealed surfaces of limbs dark purplish blue; forearm, hand, tarsus and foot margined with white; lower lip and chin cream; toes and remainder of concealed surfaces cream to yellow or red-orange; iris red.

COLOR IN ALCOHOL: Gray-blue above; black spots on sides as above; venter and concealed surfaces of limbs cream to pale yellow.

SPECIMENS EXAMINED: Fourteen, as follows: USNM 14186: one; 16146: one, from Nicaragua; 20699: one from Escondito River, Nicaragua; 29959-60: two from San Carlos, Costa Rica. UKMNH (field nos.) 8045-50: six; 8317: one; 8722: one, from 2 mi. SW of Turrialba, Costa Rica; 9368: one from Tunnel Camp near Peralta, Costa Rica.

REMARKS: The Costa Rican specimens differ from the Nicaraguan ones in a number of minor characteristics—most notably in size—and it is probable that there is more than one geographic race of this species. However, the author feels that the specimens available are inadequate for separating these forms.

Phyllomedusa callidryas callidryas (Cope) Figures 7, 21; Map 1

Hyla callidryas Cope, 1862, p. 359, footnote (type locality: Panama; holotype presented to the Academy of Natural Sciences, length 1 inch and 9 lines).

Agalychnis callidryas Cope, 1864, p. 181 (named type species); 1865, p. 110, footnote (name only); 1887, p. 15 (check list; in part; specimens from Panama only; others from Córdoba, Veracruz, probably belong to P. callidryas taylori).—Boulenger, 1882a, p. 423 (compiled description).—Günther, 1901, p. 290 (compiled description).—Nieden, 1923, p. 334 (compiled description; Panama to Mexico).—Barbour and Loveridge, 1929, p. 145 (Corn Islands off mainland of Nicaragua; San Pablo, Republica de Panama).—Dunn, 1931, p. 414 (Barro Colorado Island, Canal Zone).—Schmidt, 1941, p. 487 (in check list; Valentin, British Honduras).—Breder, 1946, p. 417, fig. 20, pl. 54 (life history notes at Darién, Panama).—Stuart, 1948, p. 35 (Alta Verapaz, Guatemala).—Taylor, 1952b, pp. 802 (key), 807 (description from that of type; specimens from Tierra Colorado, Veracruz; differences from Panama callidryas noted).

Phyllomedusa (Agalychnis) callidryas Bertha Lutz, 1950, pp. 601 (in Portuguese), 619 (in English).

RANGE: Central America, Panama to (but not including) Mexico.

DISTINGUISHING CHARACTERISTICS: The most readily apparent differences between this form and the evidently closely related *P. helenae* are the markings on the sides and greater degree of webbing in *helenae*. It differs from *callidryas taylori* in its larger size, relatively larger disks, and less sloping, more truncate snout.

DESCRIPTION: Tongue elongate, openly emarginate behind. Vomerine teeth in two oblique series, convergent posteriorly, the anterior corder opposite anterior edge of the choanae. Head as long as broad. Eye strongly protuberant, directed somewhat forward; length of exposed part of eye equal to distance from its anterior edge to nostril. Snout more or less truncate in profile. Canthus rostralis straight, rounded. Loreal region plane, subvertical. Interorbital space broader than upper eyelid, approximately equal to exposed part of eye. Tympanum distinct, obliquely elliptic, its greatest length slightly more than one-half exposed part of eye (type description: tympanum nearly as large as the eye).

Outer fingers one-third to one-half webbed, inner fingers one-fourth or less. Toes three-fourths to one-half webbed; first toe shorter than second and not opposable to the others. Both fingers and toes with broad margins (fringes) extending to disks. Disks of outer fingers and toes larger than tympanum. Inner metatarsal tubercle prominent. Tibiotarsal articulation reaches to nostril or beyond tip of snout. Length of femur (vent-to-knee) contained slightly less than twice in snout-to-vent length. Heels overlap

slightly when legs are held at right angles to body.

Skin of dorsum relatively smooth (when viewed under microscope the pigmented portion is finely granular). No parotoids. Belly and lower surface of thighs coarsely granular, a more or less distinct row of larger tubercles along ventral side of thighs; remainder of lower surfaces smooth. Vent opening on a level with ventral surface of thigh.

LENGTH: Adult females average 64 mm.; adult males average 48 mm.

COLOR IN LIFE: "Very light yellow-green above, sides orange, amber with cream lines; chin and breast cream; concealed surfaces of thighs yellow-orange; inner digits orange; eye red." (E. H. Taylor's field notes.)

COLOR IN ALCOHOL: Dorsum bluish, including forearm, outer one or two fingers, tibia and tarsus to outer one or two toes; sides bluish, not as dark as dorsum, with numerous oblique light lines, not separated from the dorsal color as in *helenae*; white (glandular) lines on outer edge of forearm, hand, tarsus and foot; venter light; some specimens have distinct white warts on the back.

SPECIMENS EXAMINED: Five, as follows: SU 3986: one from Puerto Armuelles, Panama. UKMNH (field nos.) 7208: one; 7283: one; 7284: one; 7326: four from San Isidro el General, Costa Rica.

REMARKS: It must be noted that the type locality of calltdryas is Panama, while the description above is taken from specimens from Costa Rica.

The single Panama specimen available is small, poorly preserved and totally inadequate for comparison. It is most likely that there are more than these two geographic races of callidryas.

Phyllomedusa callidryas taylori, new subspecies Figures 7, 22; Map 1

Agalychnis callidryas (nec A. callidryas Cope, 1862) Taylor, 1952a, p. 32, fig. 3b (figure of snout profile; discussion of relations; San Andrés Tuxtla, Veracruz); 1952b, pp. 802, 807 (Tierra Colorado, Veracruz). ?Agalychnis callidryas (?) Cope, 1887, p. 15 (in part; specimens from Córdo-

ba, Veracruz).—Gaige, 1936. p. 292 (Mexican localities; probably c. taylori).—Taylor and Smith, 1945, p. 599 (Santo Tomás, Tabasco; probably c. taylori).—Smith and Taylor, 1948, pp. 71 (key), 72 (Mexican localities; probably c. taylori).

?Phyllomedusa helenae (nec Cope, 1862) Kellogg, 1932, pp. 142 (key), 145 (description of P. helenae (Cope); quotes life-color notes on specimen from Costa Rica, probably P. helenae; specimens from Veracruz and Puebla, probably c. taylori).

DIAGNOSIS: A Phyllomedusa belonging to the group in which the first toe is shorter than the second. Probably closely related to callidryas callidryas from which it differs in its slightly smaller size, larger eye and tympanum, lesser degree of webbing, slightly more sloping snout and shorter leg (heels barely or do not meet when legs are held at right angles to the body).

HOLOTYPE: Univ. of Kansas Museum of Natural History (field no.) 1279, adult male, 46 mm. snout-to-vent, from Tierra Colorado, Veracruz, Mexico, collected by E. H. Taylor and Hobart M. Smith, July 16, 1932.

PARATYPES: Thirty-four specimens: UKMNH (field nos.) 1240-41, 1243-44, 1246-50, 1252-53, 1255-56, 1258-59, 1261-62, 1264-65, 1267-68, 1270-71, 1273-74, 1276-77, 1282-83, 1289, 1294; and SU 15586-15588, 38 to 47 mm. snout-to-vent (average 42 mm. snout-to-vent), from the same locality, date, and by the same collectors.

ADDITIONAL SPECIMENS EXAMINED: Four, as follows from Mexico: USNM 116042: one from Sta. Tomás, Tabasco; 117447-48: two from La Venta, Tabasco;

42271: one from Berta, Veracruz.

DESCRIPTION OF HOLOTYPE: Tongue openly emarginate behind. Vomerine teeth in two distinct groups, convergent posteriorly, their anterior edges on a level with anterior edges of the choanae. Length of exposed part of eye equal to distance from its anterior edge to nostril. Snout sloping in profile, rounded when viewed from above. Upper lip very slightly notched on median line. Canthus rostralis straight, rounded, not sharply defined. Loreal region plane, sloping outward from canthus rostralis to lower lip. Interorbital space broader than upper eyelid, equal to exposed part of eye. Tympanum distinct, obliquely elliptic, its greatest diameter equal to one-half exposed part of eye.

Outer fingers one-third webbed, one-fourth webbed between thumb and second finger. Outer three toes one-half webbed, inner toes one-third webbed. First toe shorter than second, not opposable. Margins (fringes) of both toes and fingers extend to disks. Disks moderate, the largest do not cover three-fourths of tympanum. Inner and median metatarsal tubercles prominent. Tibiotarsal articulation reaches midway between eye and nostril. Heels

barely meet when legs are held at right angles to body.

Dorsum smooth, pigmented portion very finely granular under microscope. No parotoids. A prominent fold from above the eye, over tympanum and down behind it. Belly and lower surface of thighs granular. A distinct row of enlarged tubercles along ventral side of thigh. Remainder of venter smooth. Vent opening on a level with lower surface of thigh.

COLOR IN LIFE: "Leaf green above of varying shades; sides with lemon yellow bars on a lavender lateral stripe; concealed parts of limbs yellow; throat whitish; eye red." (E. H. Taylor's field notes. Not specifically

relevant to the type specimen.)

COLOR IN ALCOHOL: Gray-blue above, which color extends from the elbow to the outer finger, and along femur and tarsus to outer toe; sides slightly darker than dorsum with distinct white vertical bars; remainder of venter and concealed surfaces of limbs flesh white; a more or less distinct (glandular) white line from elbow to outer finger, over vent, and from heel to outer toe.

VARIATION IN PARATYPES: The vomerine teeth vary in size from a relatively long series to a very small group, but the anterior edge of the teeth is on a level with the choanae. In a few examples the canthus rostralis appears sharply angular and incurving; in such specimens the loreal region appears more vertical. The interorbital space is either equal to, or slightly longer than, the length of the exposed part of the eye. The tympanum may be slightly greater, or slightly less, than one-half the exposed part of the eye.

Webbing varies on the outer fingers from one-fourth to one-half, and on the toes from three-fourths to one-third, but the majority of specimens show the degree of webbing described for the holotype. The tibiotarsal articulation may reach anywhere between the eye and the nostril. In some examples the heels do not meet when legs are held at right angles to the

body.

The majority of specimens have a distinct row of enlarged tubercles along the lower surface of the thigh, but some do not.

The dorsal color (in alcohol) may extend from the elbow only to the wrist, or to the base of the outer fingers. The paratypes show from two to nine vertical bars on the sides, the majority falling between five and seven. Most of the specimens have no light spots on the back, but up to nine occur on some.

REMARKS: The author takes pleasure in naming this subspecies for Dr. Edward H. Taylor, of the University of Kansas. Dr. Taylor graciously sent the material to the author with the suggestion that the form was probably not the same as the Panama callidryas.

Phyllomedusa saltator (Taylor) Figures 7, 23; Map 1

Agalychnis saltator Taylor, 1955, p. 527, fig. 10 (type locality, 4 km. NNE Tilarán, Guanacaste, Costa Rica; holotype: Univ. of Kansas Museum of Natural History 35615, a male, length 44 mm.)

RANGE: Costa Rica.

DISTINGUISHING CHARACTERISTICS: Absence of any lateral markings, presence (in some specimens) of dark, wavy, transverse lines on the dorsum. Most similar to *P. callidryas* and *helenge*.

DESCRIPTION: Tongue heart-shaped, normally notched behind; vomerine teeth in two small oblique groups between the anterior borders of the choanae. Head approximately as broad as long; eye strongly protuberant, directed somewhat forward; length of exposed part of eye equal to or greater than the distance from its anterior corner to the nostril; snout bluntly rounded or slightly sloping in profile; rounded when viewed from above; canthus rostralis slightly incurved, rounded; loreal region plane or very slightly concave, sloping to lip. Interorbital distance greater than that of the upper eyelid, equal to or slightly greater than the exposed part of the eye; tympanum slightly elevated, circular, its diameter less than half that of the exposed part of the eye.

Outer fingers webbed one-third or less, inner fingers one-fourth or less; outer toes webbed one-half to one-third, inner toes only basally webbed; fringes extend to the disks on both fingers and toes; first toe shorter than second, not opposable. Disks of fingers considerably larger than the tympanum, of toes only slightly larger; tibiotarsal articulation reaches midway between anterior edge of eye and nostril, or beyond the nostril; heels overlap when legs are held at right angles to the body.

Skin of dorsum smooth; prominent skin fold behind tympanum continues over insertion of forearm; no parotoids; skin on chin, ventral surfaces of arms and lower legs smooth; remainder of venter granular; a more or less distinct row of enlarged granules on the posterior edge of the thigh; a light raised line on outer edge of arm from elbow to disk of outer finger, and from heel to disk of outer toe, on elbow and heel forming a small triangular dermal appendage.

LENGTH: 40 to 52 mm.

COLOR IN LIFE: "Above dark leaf-green with dim indications of transverse, darker, wavy lines or spots on dorsum; ventral and concealed surfaces of limbs yellow orange. The green color covers only outer finger and part of two outer toes; front and back of thigh and part of upper arm lavender, the green color forming a narrow line on top of thigh. Area about vent somewhat whitish; a cream white spot at back corner of eye; eye reddish." (Taylor, 1955)

COLOR IN ALCOHOL: The green and lavender life color has turned to bluish lavender; venter and concealed surfaces of limbs white. Darker, transverse, wavy lines are conspicuous on some specimens, less so on others. The male possesses a conspicuous dark nuptial spot on the thumb.

SPECIMENS EXAMINED: Four, all from: 4 km.? ENE of Tilarán, Prov. Guanacaste, Costa Rica, as follows: SU 17259-17260, two males, 41 and 44 mm. in length. UKMNH 35622; 35625, a male and a female, 40 and 52 mm. in length.

Phyllomedusa dacnicolor Cope Figures 7, 24; Map 1

Phyllomedusa dacnicolor Cope, 1864, p. 181 (type locality: near Colima, Mexico; holotype formerly in USNM, now lost, length 3 inches 6 lines).
—Boulenger, 1882a, p. 426 (description; San Blas, Mexico); 1882b, p. 328 (life color; Presidio, Mexico). —Brocchi, 1882, p. 68 (compiled description). —Nieden, 1923, p. 345 (compiled description).
—Kellogg, 1932, pp. 142 (key), 143 (notes on breeding; localities in Sinaloa, Nayarit, Colima and Guerrero, Mexico).

Agalychnis dacnicolor Cope, 1866, p. 86; 1887, p. 15 (check list).—Günther, 1901, p. 291 (description).—Taylor, 1942, p. 40, pl. 2, fig. 2, pl. 3, fig. 2; 1952a, p. 32, fig. 3a (Tepic, Nayarit; figure of snout profile; discussion of relations).—Taylor and Smith, 1945, p. 599, pl. 28, fig. 1 (Tierra Colorado, Guerrero; Tehuantepec, Oaxaca).

—Smith and Taylor, 1948, pp. 71 (key), 72 (Mexican localities; range). Phyllomedusa (Agalychnis) dacnicolor Bertha Lutz, 1950, pp. 601 (in Portuguese), 619 (in English).

RANGE: West of Mexican Plateau, from southern Sinaloa to Panama. DISTINGUISHING CHARACTERISTICS: Size large; long snout, sloping in profile; only basal webbing on fingers; range.

DESCRIPTION: Tongue large, openly emarginate behind. Vomerine teeth in two short or long, transverse or oblique, rows between anterior margins of the choanae. Snout rounded when viewed from above, very sloping in profile, longer than diameter of eye. Canthus rostralis not sharply defined. Loreal region oblique. Interorbital space broader than upper eyelid. Tympanum distinct, one-half to two-thirds diameter of eye.

Fingers slightly webbed at base. Toes one-third webbed; first toe a little shorter than the second, not opposable. Disks of fingers and toes smaller than tympanum. No fringes on fingers or toes. Subarticular tubercles very prominent; a prominent inner metatarsal tubercle. Tibiotarsal joint reaches tympanum.

Skin of upper parts usually smooth, may be rough in very large specimens; belly and underside of thighs strongly granulate, throat and ventral surface of lower leg smooth. Parotoids (or parotoid swellings) indistinct.

LENGTH: 55-95 mm.

COLOR IN LIFE: Bright grass-green above, capable of changing to olive or brown, occasionally with a few scattered yellow spots; yellowish white below; forearm, hand and foot margined with white; sides marbled with yellow and reddish brown; a few small yellow spots on anterior part of sides; iris black.

COLOR IN ALCOHOL: Gray-blue to brown above; usually immaculate, white or yellowish below; sides and lines on limbs as above.

SPECIMENS EXAMINED: Twenty-five, as follows: from Mexico: SU 2230: one, Colima. USNM 6837: three, Mazatlán; 14081: three, Presidio. SU 15571-74: four, 15 mi. S. Mazatlán; SU 15585: one, Presidio; 17032-33: two, 2 km. north of San Blas, Nayarit. USNM 46950: one, Rosario, Sinaloa; 46954-55: two, Acaponita, Nayarit; 47904: one, Omentepec, Guerrero; 116040: one, Tierra Colorado, Guerrero; 116041: one, Tehuantepec, Oaxaca; 58093: one, Colima. USNM 32237-39: three, ?Costa Rica; 74506: one from Toloa Jct., Honduras.

Phyllomedusa bicolor (Boddaert) Figures 7, 25; Map 3

Rana bicolor Boddaert, 1772, p. 19, pls. 1, 2 (original description; holotype (length 4 inches, 1/2 line) originally in collection of Johann Albert Schlosser, but now probably lost; footnotes on pp. 18 and 19 state that Schlosser's frog was from "Guinea" [=Guiana?] but that two in the possession of W. van der Meulen were from Surinam [=Dutch Guiana]; type locality hereby accepted as Surinam).—Shaw, 1802, p. 126 (name only).

Calamita bicolor Schneider, 1799, p. 156.—Merrem, 1820, p. 170 (reference). "La rainette bicolore" Latreille, 1802, p. 174, pl. (p. 169), fig. 2.

- Hyla bicolor Daudin 1803a, p. 22, pls. 5-6; 1803b, p. 40 (description).
 —Spix, 1824, p. 42, pl. 13, figs. 1-2 (Rio Tonantins, tributary of Rio Solimões, upper Amazon of Brazil).—Fitzinger, 1826, p. 63 (listed).—Gravenhorst, 1829, p. 26 (description).—Guérin-Méneville; 1829-1838, pl. 26, fig. 3.—Peters, 1872a, p. 220 (re-examination of Spix material).
- Phyllomedusa bicolor Wagler, 1830, p. 201.—Tschudi, 1838, p. 70 (in part).
 —Duméril and Bibron, 1841, p. 629 (in part).—Günther, 1858, p. 120 (in part).—Boulenger, 1882a, p. 427 (description).—Nieden, 1923, p. 337 (compiled description).—Miranda-Ribeiro, 1926, p. 103 (compiled description).
- Phyllomedusa scleroderma Cope, 1868, p. 112, footnote (type locality: Surinam; holotype in Acad. Nat. Sci. Philadelphia, length 4 inches, 1.5 lines).
- Phyllomedusa (Phyllomedusa) bicolor Bertha Lutz, 1950, pp. 601 (in Portuguese), 619 (in English).—Lutz and Kloss, 1952, p. 662 (description; Tacana).

RANGE: Northeastern Peru through the Amazon Basin to the Guianas; Magdalena Valley, Colombia (fide Dunn, in litt.).

DISTINGUISHING CHARACTERISTICS: Size large (up to 110 mm. or more); osteoderms in skin of dorsum; large disks; first and second toes equal, or second slightly shorter than first.

DESCRIPTION: Tongue entire or slightly nicked behind. Vomerine teeth in two oblique groups between the choanae. Snout longer than exposed part of eye, sloping in profile. Canthus rostralis angular. Loreal region almost vertical. Interorbital space much broader than upper eyelid. Tympanum a vertical oval, its greatest diameter one-half to two-thirds diameter of exposed part of eye.

Fingers free, first shorter than the second, fourth a little shorter than third. Toes free, first and second equal, or first slightly longer than the second; first toe is probably opposable to the others. Disks of fingers as large as tympanum, of toes a little smaller. No fringes on fingers or toes. Inner metatarsal tubercle not prominent. Tibiotarsal articulation reaches to shoulder or eye. Heels meet when legs are held at right angles to body.

Build robust. Skin of dorsum rough, presence of osteoderms making it appear granular; upper surfaces of thighs granulate. Parotoids very conspicuous, beginning above the eye and forming a pronounced angle—in effect the angle of the canthus rostralis is extended over the eye to the middle of the body by the parotoid glands (superbly shown in the Boddaert illustrations, see Figs., pp. 76-78). Venter with large flat granules.

LENGTH: 100-110 mm.

COLOR IN ALCOHOL: Blue-gray above, including forearm, two outer fingers, tibia, tarsus and two outer toes; remainder of digits and lower surfaces purplish white; small, white, purple-edged spots forming an irregular reticulation on sides of body and limbs; white, purple-edged spot on each

side of vent, in center of chest and along lower surface of forearm; a narrow white, purple-edged line along outer side of forearm, over vent, around heel and along tarsus to outer toe; tips of fingers and toes bluish.

SPECIMENS EXAMINED: Two, as follows: SU 6377: one, from Pebas, Peru;

11535: one from Loreto, Napo-Pastaza Prov., Ecuador.

REMARKS: According to Sr. Antenor Leitão de Carvalho, a skin of *P. bicolor* was brought to him for identification by Mr. Curt Nimuendajú, an ethnologist who spent most of his life among the Indians of South America. He told Carvalho that the people of the Ticuna Tribe [ca. Lat. 3° S., Long. 70° W. (Nimuendajú, 1948)] use the parotoid secretion of this frog to induce vomiting. The frogs are kept in little cages, and when the secretion is needed, the creatures are annoyed until they produce a sufficient quantity to be rubbed on the forehead and wrists. The effect was likened to symptoms of a mild poisoning—which it undoubtedly is.

Phyllomedusa spurrelli (Boulenger) figures 7, 8; Map 1, 2

Agalychnis spurrelli Boulenger, 1913, p. 1024, text-fig. 177, pl. 103, (type locality: Peña Lisa, Condoto, Chocó, Colombia; syntypes: in British Museum, length 95 mm. snout-to-vent).—Dunn, 1931, p. 415, (Barro Colorado Island, Panama; note).

RANGE: Colombia, west of the Andes, to Panama.

DISTINGUISHING CHARACTERISTICS: Fingers and toes fully webbed; white warts on back dark-bordered; range. Most similar to moreleti.

DESCRIPTION: Tongue oval, feebly emarginate behind. Vomerine teeth in two strong, transverse or slightly oblique series on a level with the front edge of the rather large choanae. Head moderately depressed, as long as broad, or slightly broader than long. Snout rounded when viewed from above, not projecting beyond lower jaw, sloping in profile. Canthus rostralis feeble. Loreal region concave and very oblique. Interorbital space broader than upper eyelid. Tympanum close to the eye and two-thirds to three-fourths its diameter.

Fingers much flattened and entirely webbed, the disks nearly as large as eye or about two-thirds its size. First toe shorter than second, not opposable to the others. Toes rather short, much flattened, entirely webbed (three-fourths webbed in the young), the disks a little smaller than those of the fingers. Subarticular tubercles very prominent. Tibiotarsal articulation reaches to between eye and tip of shout.

Skin smooth above; granular on belly and on basal half of lower surface of thigh; a regular series of enlarged granules extends along whole length of lower surface of thigh. A narrow dermal fold along outer edge of forearm, inner edge of tarsus, and across heel. A few scattered flat, white warts on the back; no parotoid glands.

LENGTH: 84-95 mm.

COLOR IN LIFE: Green above, the dorsal warts variable in number, and irregularly disposed, white, edged with purplish black; belly yellowish white; iris ruby red; lower eyelid with an open meshwork of golden lines.

COLOR IN ALCOHOL: Pale gray-blue above; the dorsal warts white, edged with black; yellowish white below.

SPECIMENS EXAMINED: One, USNM 48505, from Cabina, Panama.

REMARKS: It is very unlikely that spurrelli is a subspecies of moreleti, even though the ranges as now known might appear to resemble those of closely related allopatric species. In life these two are evidently much more different than would appear from the descriptions. Among other things, the eye color is red in spurrelli and yellow or black in moreleti, and there are differences in the degree of webbing.

Phyllomedusa moreleti (Duméril) Figures 7, 9; Map 1

Hyla moreletii Duméril, 1853, p. 169 (type locality: Cobán, Verapaz, Guatemala; ?syntypes: MHNP 428, parchment label 767, two, length 68.5 and 59 mm.—fide Kellogg, 1932, and Smith and Taylor, 1948).—Keferstein, 1867, p. 356 (Costa Rica); 1868, p. 297 (Costa Rica).—Brocchi, 1877, p. 122 (not seen); 1881, p. 31, pl. 13, fig. 1 (compiled description; Mexico).

Hyla holochlora Salvin, 1860, p. 460, pl. 32, fig. 2 (type locality: Cobán, Guatemala; holotype British Museum 64.1.26.142).—Cope, 1864, p. 181 (name only); 1865, p. 110 (name only).

Agalychnis moreletii Cope, 1864, p. 181 (name only); 1865, p. 110 (name only); 1876, p. 107 (San José, Costa Rica); 1887, p. 15 (in check list).—Boulenger, 1882a, p. 422 (description; Costa Rica, Guatemala).—Werner, 1896, p. 9 (Honduras); 1903, p. 351 (Cobán, Guatemala).—Günther, 1901, p. 289 (description).—Nieden, 1923, p. 333, fig. 267 (compiled description; Guatemala to Costa Rica).—Gaige, 1936, p. 293 (Campeche, Mexico).—Schmidt, 1941, p. 487 (check list; Valentin, British Honduras).—Taylor and Smith, 1945, p. 599, pl. 31 (Veracruz, Cuautlapan, Mexico; voice, egg-laying; Finca Juárez, Chiapas).—Smith and Taylor, 1948, p. 71 (key; range; Mexican localities).—Stuart, 1948, p. 36, figs. 7-8 (description of tadpoles).—Taylor, 1952a, p. 32, fig. 3d (snout profile; Cuautlapan); 1952b, p. 802, fig. 40 (description; Cartago, Costa Rica).

Phyllomedusa moreletii Kellogg, 1932, pp. 142, 143, 146, figs. 19a, 20a-b (description; figure of hand and foot; Mexico; Guatemala).

Phyllomedusa (Agalychnis) moreletii Bertha Lutz, 1950, pp. 601, 604, (in Portuguese), 619, 623 (in English).

RANGE: Atlantic slopes from central Veracruz and Pacific slopes from the Isthmus of Tehuantepec, Mexico, to Costa Rica.

DISTINGUISHING CHARACTERISTICS: Size large to medium; fingers and toes extensively webbed; snout very sloping in profile; if present, white warts on back not dark-bordered; range. Most similar to spurrelli.

DESCRIPTION: Tongue broad, notched behind. Vomerine teeth in two oblique series between anterior margins of choanae. Length of eye slightly less than distance from its anterior edge to nostril. Canthus rostralis distinct. Loreal region concave, oblique. Interorbital space slightly concave, wider than upper eyelid. Tympanum more than one-half, often three-fourths, width of eye.

Fingers one-half to two-thirds webbed, the membrane often extending to disks of second and fourth digits. First toe shorter than second, not opposable; toes two-thirds to fully webbed, the membrane often reaching disks of all digits. Disks of fingers slightly larger than those of toes, and often larger than tympanum. Tibiotarsal articulation reaches between eye and tip of snout. Heels barely touch when legs are held at right angles to body.

Skin of back smooth with a few scattered small warts; underparts, with exception of gular region, coarsely granulate. No parotoid glands.

LENGTH: 54-77 mm.

COLOR IN LIFE: Dorsum, including upper surface of forearm, fourth finger, tibia, tarsus and fifth toe grass-green; concealed surfaces of sides and limbs orange-yellow; venter pale tint of sides; throat and breast cream; eye bluish black, or yellow.

COLOR IN ALCOHOL: Blue-green or gray above, rarely with round yellow

spots; sides often with lateral yellow bands; concealed surfaces of limbs, hands and feet yellowish, with exception of outer finger and toe, which are same color as back; a white line along outer edge of forearm, lower hind limb and tarsus; underside white.

SPECIMENS EXAMINED: Seventy-nine, as follows: SU 3298: one from Costa Rica. USNM 29935: one from Costa Rica; 32242-43: two from Turrialba, Costa Rica; 12768: one; 24827-29: three from Guatemala; 35923: one from Sanchu, Guatemala; 63004: one from ?Guatemala; 25370: one from Mexico; 46916: one from Vulcán Tuxtla, Veracruz, Mexico; 116043-53: 11 from Cuautlapan, Veracruz, Mexico; 116054-116057; 116060-116069: 14 from Finca Juárez, Chiapas, Mexico. SU 15590-91: two from Finca Juárez, Chiapas, Mexico. SU 15590-91: two from Finca Juárez, Chiapas, Mexico. UKMNH 32729-51: 28 from Costa Rica; UKMNH (field nos.) 6866-68: three from Cartago, Costa Rica; 6505: one from Moravia de Chirripó, Costa Rica. EHT-HMS 17502; 17504-05; 17507-08; 17510: six from Escamilla, Veracruz, Mexico; 24895: one; and 6040: one from Cuautlapan, Veracruz, Mexico.

REMARKS: According to Edward H. Taylor (field notes) the specimens from Escamilla, Veracruz, had a bluish black eye. All other life-color observations on this species state that the eye is golden. It is probable that the specimens from Escamilla are examples of a distinct geographic race, and, considering the range of this species, it is likely that there are

several such races.

Phyllomedusa blombergi, new species Figures 7, 36; Map 3

DIAGNOSIS: A Phyllomedusa belonging to the group in which the first toe is longer than the second, but differing from all these species except P. hypochondrialis and rohdei in that the snout is truncate in profile. Unlike hypochondrialis and rohdei, it has distinct parotoid glands marked by a very distinct row of white tubercles. The structure of the parotoid glands (i.e., long and narrow, marked by a line of tubercles) is most similar to that of edentula and perlata, but the general body form and coloration appears close to feltoni.

HOLOTYPE: Stanford University 13241, very likely immature, 34.7 mm. snout-to-vent, from Santa Rosa de Sucumbio, Río Rumi-Yacu, Departamento Putumayo, upper Amazon, Colombia, collected by Rolf Blomberg, Jan. 20, 1954.

DESCRIPTION OF HOLOTYPE: Vomerine teeth in two oblique series between anterior edges of choanae. Snout bluntly rounded when viewed from above, sharply truncate in profile. Canthus rostralis slightly incurved, sharply angular. Loreal region plane, vertical. Head as broad as long, almost twice as broad as sacrum. Interorbital distance equal to width of upper eyelid, which is equal to distance from eye to nostril, which is equal to distance between nostrils. Length of snout from nostril to anterior corner of eye about two-thirds diameter of exposed part of eye. Tympanum distinct, its longest (vertical) diameter equal to about one-half exposed part of eye.

Fingers free; subarticular tubercles prominent; disks small, not wider than digit, the two largest covering an area not one-half that of tympanum. Toes free; first toe longer than second, opposable to the others; median metatarsal tubercle prominent, as is subarticular tubercle at base of fourth toe; disks slightly smaller than those of the fingers. No fringes on fingers or toes. Tibiotarsal articulation does not quite reach middle of eye. Heels barely meet when legs are held at right angles to body.

Skin smooth above. Parotoid glands form a narrow, sharply angular ridge from middle of eyelid to point of adpressed elbow, prominently defined on their outer edges by a row of small white tubercles. Throat and lower surface of legs smooth. Belly finely granular. Coarse granules on lower sur-

face of thighs.

COLOR IN LIFE: According to the collector, this specimen was bright grass-green above. A color photograph of the head and shoulders of the frog shows the chin and throat and under side of forearm dark grayish violet, with white spots on the throat and chest, a white line bordering the lips and outer edge of the forearm, and white parotoid tubercles. The iris is pale golden gray.

COLOR IN ALCOHOL: Blue-gray above, which extends (discontinuously over insertion of forearm) to base of fingers, and along top of leg to middle of fourth and fifth toes. Sides reddish violet with three very distinct white spots; back of thigh mottled reddish violet and front of foot from tibiotarsal articulation to disks of first four toes reddish violet with more or less distinct white spots. White line around margin of upper and lower jaws, extending from insertion of forearm to middle of body; other white lines from elbow to disk of outer finger, over vent, and from heel to disk of fifth toe. Tops of fingers and disks (except thumb) dark gray; chin dark gray with two white spots; single large white spot on chest; remainder of venter grayish white.

REMARKS: The author takes great pleasure in naming this species in honor of the collector, Rolf Blomberg, of Quito, Ecuador, who donated the specimen to the author for the Natural History Museum, Stanford University.

Phyllomedusa perlata Boulenger Figures 7, 34; Map 3

Phyllomedusa perlata Boulenger, 1883, p. 638, pl. 58, figs. 4-4a (type locality: Yurimaguas, Huallaga River, northern Peru; holotype in British Museum, immature, length 23 mm.).—Nieden, 1923, p. 342, fig. 271 (compiled description; figure from Boulenger).—Parker, 1935, p. 512 (Moraballi Creek, British Guiana).

Phyllomedusa (Pithecopus) perlata Bertha Lutz, 1950, pp. 604 (in Portuguese), 620 (in English).—Lutz and Kloss, 1952, p. 663 (description; Itacoai).

RANGE: Eastern Andean foothills of northern Peru, and British Guiana. DISTINGUISHING CHARACTERISTICS: Size small to medium; a single row of small, pearl-like tubercles along the length of the parotoid glands; distinct warts or tubercles on limbs. Most similar to edentula.

DESCRIPTION: Tongue entire. Vomerine teeth in two small oblique groups between the anterior edges of the choanae. Head very large, slightly longer than broad. Snout no longer than diameter of eye, vertically truncate in profile. Loreal region vertical, plane. Canthus rostralis sharply defined, curving. Interorbital space broader than upper eyelid. Tympanum about half diameter of eye.

Fingers free; first shorter than the second, fourth shorter than third. Toes free; first considerably longer than the second, probably opposable to the others. Disks of fingers and toes small; no fringes on fingers or toes. Metatarsal tubercles well developed. Tibiotarsal articulation reaches to eye.

Skin smooth above. Parotoid glands distinct, long and narrow, studded with a single series of small, white, pearl-like tubercles from eye to halfway down the body. Belly and lower surfaces of thighs granulate. A series of small light-colored tubercles on the lower outer edge of the forearm and tibia.

LENGTH: 23-51.5 mm. (see Specimens Examined).

COLOR IN ALCOHOL: Purple above; a white, dark-edged line along the outer border of the forearm, over vent and from heel to base of foot; lips white bordered, edged with purple; a white line from the corner of the mouth

running over the insertion of the forearm and becoming a series of white spots on the sides; lower surfaces purplish white.

SPECIMENS EXAMINED: Three, USNM 127165-66, two from Campo Santa Clara, Orelana(o), Peru; 41 and 51.5 mm. respectively, snout-to-vent; and SU 13220: one, from upper Río Arajuno, Napo-Pastaza Prov., Ecuador.

Phyllomedusa edentula Andersson Figures 7, 35; Map 3

Phyllomedusa edentula Andersson, 1945, p. 84 (type locality: Río Pastaza, eastern Ecuador; holotype in Natural History Museum, Stockholm, female, length 84 mm.).

RANGE: Known only from eastern Andean foothills of Ecuador.

DISTINGUISHING CHARACTERISTICS: Size large; parotoid glands studded with more than one row of tubercles or glandular ridges resembling tubercles; tubercles or small warts on sides of limbs. Most similar to P. perlata.

DESCRIPTION: Tongue entire, extensively free behind. Vomerine teeth in two straight oblique groups between the choanae. Head as long as, or slightly longer than, broad. Snout subacuminate, slightly longer than diameter of eye. Canthus rostralis distinct, curved. Loreal region vertical, slightly concave. Interorbital distance slightly broader than upper eyelid. Tympanum very distinct, somewhat larger than half diameter of eye.

Fingers free, first finger a little shorter than second, fourth shorter than third. Slight web between three outer toes, first toe longer than second, fourth very long; first toe opposable to the others. Disks of fingers about two-thirds tympanum; disks of toes somewhat smaller, no fringes on fingers or toes. Metatarsal tubercles well developed. Tibiotarsal articulation reaches to eye.

Upper parts smooth or minutely granular; belly and lower surface of thighs with larger flat granules; remainder of venter smooth. Parotoids distinct, forming a narrow glandular ridge from middle of upper eyelid to below point of adpressed knee. Parotoids are somewhat similar in structure to those of perlata in that they seem to be made up of small distinct tubercles, perlata having a single row of pearly white tubercles and edentula several rows of either tubercles or glandular ridges resembling tubercles which may be light in color, but are not white. Two more-or-less distinct rows of tubercles on upper surface of thighs; another row on outer margin of tibia; a row of distinct tubercles on under surface of forearm; and a ridge of small warts along its posterior edge; more distinct warts or tubercles scattered on lower surface of thigh and tibia.

LENGTH: 54-84 mm.

COLOR IN ALCOHOL: Visible surfaces dark bluish violet; concealed parts of sides and limbs, especially the hind ones, reddish lilac with small light spots; lower parts dirty white or lighter reddish lilac; white, rededged spots on chin and throat and sometimes beside vent; chin and throat may be marbled with reddish and brown in a pattern similar to that of burmeisteri.

SPECIMENS EXAMINED: Three, SU 10329, 13067-13068, all from the Río Copataza, upper Pastaza, eastern Ecuador.

REMARKS: The name *edentula* is an unfortunate misnomer. The holotype happened to lack vomerine teeth, but they are fully developed in the three specimens listed above.

Phyllomedusa hypochondrialis (Daudin) Figures 7, 33; Map 3

"La raine hypocondriale" Latreille, 1802, p. 177, pl. (p. 170), fig. 1 (nec fig. 3).

Hyla hypocondrialis Daudin, 1803a, p. 29, pl. 10, fig. 1 (type locality Surinam; holotype in coll. of Levaillant, length 1 pouce, 6 lignes); 1803b, p. 60.—Fitzinger, 1826, p. 63 (listed).—Gravenhorst, 1829, p. 29 (description).

Calamita hypochondrialis Merrem, 1820, p. 170 (reference).

Phyllomedusa bicolor Duméril and Bibron, 1841, p. 629 (in part). — Günther, 1858, p. 120 (in part).

Phyllomedusa azurea Cope, 1862, p. 355 (type locality: Paraguay; holotype Acad. Nat. Sci. Philadelphia 5832, length 1 inch 6 lines).

Phyllomedusa hypochondrialis Cope, 1862, p. 355 (differentiated from P. azurea, compared with P. bicolor).—Boulenger, 1882a, p. 430 (description); 1882c, p. 264, pls. 1-3 (behavior; life color).—Berg, 1896, p. 213 (Corrientes, Pilcomayo, Resistencia).—Budgett, 1899, p. 313, figs. 27-35 (breeding and larval development; Paraguayan Chaco).—Gadow, 1901, p. 204 (abstract of Budgett's account).—Mehelÿ, 1904, p. 230.—Bles, 1905, p. 605 (larval development).—Musshoff, 1906, pp. 255, 269 (photograph).—Nieden, 1923, p. 337, fig. 268 (compiled description).—A. and B. Lutz, 1939, p. 219 (reference).

Pithecopus azureus Cope, 1868, p. 113 (Brazil, Paraguay, Pernambuco).

Pithecopus hypochondrialis Cope, 1868, p. 112 (Dutch Guiana).

Phrynomedusa hypochondrialis Miranda-Ribeiro, 1923, pp. 3-4 (name only).

Bradymedusa megacephala Mirando-Ribeiro, 1926, p. 104, fig. 60 (type locality ?Rio de Janeiro; holotype in Museu National, Rio; length 40 mm.). Bradymedusa hypochondrialis Miranda-Ribeiro, 1926, p. 105 (compiled description).

Phyllomedusa (Pithecopus) hypochondrialis Bertha Lutz, 1950, pp. 601, 603 (in Portuguese), 619 (in English).

RANGE: Lowlands of eastern South America from Paraguay and Bolivia northward to the Guianas and to the eastern tip of Brazil.

DISTINGUISHING CHARACTERISTICS: Size small; lack of parotoid glands and vomerine teeth; distinct dark bands of color on concealed portions of sides and legs; dorsal color on head extends to (or almost to) margin of upper lip; dorsal color extends to outer digits; disks about one-half the tympanum. Most similar to rohdei.

DESCRIPTION: Tongue entire. Vomerine teeth absent. Length of snout equal to diameter of eye. Snout truncate in profile. Canthus rostralis distinct, curving. Loreal region nearly vertical, plane. Interorbital space broader than upper eyelid. Tympanum rather indistinct, its greatest diameter less than one-half exposed part of eye. Eye large, prominent.

Fingers free, first shorter than the second, third only slightly longer than fourth. Toes free, first considerably longer than second which is very much reduced; first toe opposable to the others. Disks small, only slightly wider than digits, about one-half the tympanum; no fringes on fingers or toes. Tibiotarsal articulation reaches to tympanum or middle of eye. Length of tibia contained almost three times in snout-to-vent length. Heels overlap slightly when legs are held at right angles to body.

Skin smooth above. Parotoid glands absent. Concealed surfaces of sides, arms and legs smooth. Venter, including lower surface of forearm and thigh, covered with round flat granules. The white line on outer edge of forearm, over vent, and from heel to fifth toe is possibly glandular in life.

LENGTH: 34 to 43 mm.

COLOR IN LIFE: Dorsum light green; concealed surfaces, including two inner fingers and three inner toes, bright orange with transverse purple-black bars; narrow white margin on the upper lip; black line from angle of jaw to middle of body, separated by a white streak from the green of the back; another blackish line around lower lip; white margin on outer edge of forearm to outer finger, and tarsus to outer toe; lower surfaces white, except for the tibia which is orange; iris silvery white.

COLOR IN ALCOHOL: Dorsum blue-gray, including upper surface of forearm to two outer fingers, upper surface of thigh, lower leg and foot to two outer toes; viewed from the side the dorsal color extends in a fairly straight line around lower edge of lip, over angle of the jaw to cover most of the side of the body; concealed surfaces of sides, arms and legs usually with very distinct dark-brown bands on a cream background; sometimes a fine dark line around the margin of lower lip, extending over the insertion of the forearms to the middle of the body; a white, dark-edged line on outer edge of forearm, tarsus, and metatarsus; venter cream or yellowish white.

SPECIMENS EXAMINED: Seventeen, as follows: USNM 48857: one from Bonita, Pernambuco, Brazil; 97090: one from Zona da Matta, Pernambuco. UMMZ 47215: one from Bonita, Pernambuco; 104001: six from Salobra, Matto Grosso, Brazil; 48294: one from Demerara R., Dunoon, British Guiana; 77516: two, and 80407: one, from Wismar, British Guiana; 66596: one from Sta. Cruz, Buenavista, Bolivia. SU 13056-13057: two from Mucuripé, Ceará, Brazil; 12729: one from São Luis de Cáceres, Estado do Matto Grosso, Brazil.

Phyllomedusa rohdei Mertens Figures 7, 32; Map 3

Phyllomedusa rohdei Mertens, 1926, p. 140 (type locality: Rio de Janeiro, Brazil; holotype probably in Senckenburg Museum, male, length 28.5 mm.).—Adolpho and Bertha Lutz, 1939, p. 240, pl. 2, fig. 3, pls. 4-6, pl. 7, figs. 7-8, 10-11, pl. 8, figs. 1, 6, 8 (description; tadpoles; life history).—Myers, 1946, pp. 14 (in Portuguese), 32 (in English) (Manguinhos; lowlands about Rio de Janeiro).—Cochran, 1955, pp. 196 (key), 204 (description), pl. 19, figs. E-G.

Bradymedusa moschata Miranda-Ribeiro, 1926, p. 104, fig. 61 (type locality: Teresópolis, Rio de Janeiro, Brazil; holotypes probably in the Museu Nacional, Rio de Janeiro, length 42 mm.).

Phyllomedusa (Pithecopus) rohde1 Bertha Lutz, 1950, pp. 604 (in Portuguese),
620 (in English).

RANGE: Region of Rio de Janeiro to Bolivia.

DISTINGUISHING CHARACTERISTICS: Size small; no parotoid glands, and (usually) no vomerine teeth; dark network of color on sides; dorsal color on head extends only a little beyond canthus rostralis and nostrils; hands and feet light; disks about equal to tympanum; range. Most similar to hypochondrialis.

DESCRIPTION: Form robust. Tongue entire. Vomerine teeth (usually) absent. Head depressed, somewhat broader than the sacrum. Shout truncate in profile, rounded when viewed from above. Canthus rostralis indistinct. Distance from anterior corner of eye to tip of shout longer than horizontal eye measurement. Loreal region sloping, concave. Interorbital distance one and a half times as broad as upper eyelid. Tympanum of adults indistinct, its greatest diameter half as wide as eye (tympanum of young often indistinguishable).

Fingers and toes without webs; first finger somewhat shorter than second; fourth finger shorter than third. First toe longer than second, opposable

to the others. Disks of fingers and toes very small, hardly wider than the last joint; no fringes on fingers or toes. Median metatarsal tubercle not prominent. Tibiotarsal articulation hardly reaches tympanum.

Upper side smooth; parotoids not present; belly and under side of thighs

granular.

LENGTH: 20-46 mm.

COLOR IN LIFE: Mineral green on dorsum, including forearm and lower leg, not covering side of head and upper lip, arm above the elbow, thigh or foot; hands and feet gray-white; a broad creamy band spotted with gray on side of head from nasal opening to and including tympanum; violet markings on flanks and sides of body; venter immaculate.

COLOR IN ALCOHOL: Dorsum blue-violet; viewed from the side the dorsal color on most specimens does not extend below the nostrils or canthus rostralis, and on all the specimens examined the dorsal color does not cover the tympanum, side of head or side of body. (In SU 12723-25 the dorsal color extends to the lip from in front of the eye.) Markings on side and thigh brown; venter whitish.

SPECIMENS EXAMINED: Fifty-three, as follows: UMMZ 64150: one from Manguinhos, Distrito Federal, Brazil; C8765: one, Tijuca, Distrito Federal; 67740: one from Huachi, Bolivia. USNM 96912-13: two from Passo Quatro, Minas Gerais, Brazil; 81146: one, Rio de Janeiro; 96154: one; 99110-14: five; 97243: one; 96121-25: four, all from Manguinhos, Distrito Federal; 97401-02: two; 97575: one, from Tijuca, Distrito Federal; 96399: one, Nicteroy, Estado do Rio de Janeiro; 101721: one, Teresópolis, Estado do Rio de Janeiro; 96155-61: seven, Bom Successo, Rio de Janeiro. SU 13058-13059: two, and 13060-13063: four, all from Jacarépaguá, Distrito Federal; 13242-45: four, Barro Branco, Estado do Rio de Janeiro; 12726-12728, 12730-12737: eleven, Caxias, Baixada Fluminense, Estado do Rio de Janeiro; 12723-12725: three, Santa Teresa, Estado Espirito Santo, Brazil.

Phyllomedusa coelestis (Cope) Figure 7; Map 4

Pithecopus coelestis Cope, 1874, p. 121 (type locality: Moyabamba, Peru; holotype probably in Acad. Nat. Sci. Philadelphia, length 57 mm.). Phyllomedusa coelestis Boulenger, 1882a, p. 429 (description).—Nieden,

1923, p. 342 (compiled description).

Phyllomedusa (Pithecopus) coelestis Bertha Lutz, 1950, pp. 602 (in Portuguese), 621 (in English), map.

RANGE: Known only from type locality.

DISTINGUISHING CHARACTERISTICS: Differs from other large species in which the first toe is longer than the second (except *P. niceforoi*) by the absence of parotoid glands; interorbital space equals upper eyelid. Most similar to *P. bolivtana*. (See Remarks, below.)

DESCRIPTION: Vomerine teeth present. Snout short, sloping in profile. Tympanum a vertical oval, one-fourth to one-third the diameter of eye. Interorbital space equals upper eyelid.

First finger opposable. First toe longer than second, third with a very small disk. Elbow reaches tip of snout. Tibiotarsal articulation reaches front of eye.

Skin smooth above, sides coarsely, belly finely granulate; no trace of parotoid gland; no dermal processes.

LENGTH: 57 mm.

COLOR IN ALCOHOL(?): Upper surfaces blue, the pigment of the upper surfaces extending on the humerus and outer two toes of both limbs; sides yellow with vertical purple bars; concealed surfaces light maroon with

yellow spots; two series of yellow spots on posterior face of femur. Belly and throat sea-green, unspotted; lower lip yellow bordered; upper lip without markings. Upper eyelids yellow bordered; a narrow yellow line on outer margin of forearm and outer toe, a similar one above vent.

SPECIMENS EXAMINED: The specimens laueled coelestis in the American Museum of Natural History were examined, but lack of time prevented taking

detailed notes.

REMARKS: In preserved material of this genus one of the most difficult characteristics to describe adequately is the parotoid glands. In series of most species which possess them there will be individuals in which they are strikingly prominent, while in others the glands are discernable only under microscopic examination. Most of the specimens in the American Museum possessed parotoid glands, and should probably be considered examples of boliviana. However, the author doubts the validity of coelestis as a distinct species; coelestis and boliviana are possibly geographic races of the same form. But the original description of coelestis is inadequate, and until the types are compared, and more collecting in this whole area of South America can be done, the author feels it best to retain both names as full species.

Phyllomedusa niceforoi Barbour Figures 7, 29; Map 3

Phyllomedusa nicefori Barbour, 1926, p. 191, pl. 12, figs. 1-2 (type locality: Villavicencio, eastern slope of Colombian Andes, altitude 452 meters; holotype: Museum of Comparative Zoology 11611, length 80 mm.).
Phyllomedusa (Pithecopus) nicefori Bertha Lutz, 1950, pp. 602 (in Portuguese), 621 (in English), map.

RANGE: Known only from the type locality.

DISTINGUISHING CHARACTERISTICS: No parotoid glands; interorbital space broader than the upper eyelid. Most similar to coelestis.

DESCRIPTION: Vomerine teeth in two small groups opposite middle of the choanae. Snout longer than diameter of eye, sloping in profile, acuminate when viewed from above. Interorbital space broader than upper eyelid. Tympanum about one-half diameter of eye.

Fingers free, first slightly shorter than the second, fourth nearly as long as third. Toes free, first toe longer than second. Disks of fingers and toes small. Tibiotarsal articulation reaches anterior border of eye; scarcely a trace of a metatarsal tubercle.

Skin smooth above; no parotoid glands; granular beneath, with several large prominent tubercles on each side of the vent.

COLOR IN ALCOHOL: Similar to that of coelestis. Blue above; lower lip white, the white line extending around forearm insertion and terminating as a cluster of white spots along side of chest; several white sternal spots; throat and chest lavender, fading posteriorly to dirty white, which is the color of the lower belly and inside of limbs. A white glandular line separating the dorsal and ventral colors on the forelimbs, while the hindlimbs show blue fading into the white with several light spots along the boundary. A few scattered white tubercles along the sides, more abundant ventrad than dorsad. Enlarged tubercles about the vent white.

SPECIMENS EXAMINED: None.

REMARKS: The specimens listed as ?niceforoi on page 16 consist of the following:

Collection	Catalogue No.	Sex	S-V Length	Local	ocality Collected		
UMMZ	54634	-	81	Colombia: Ar	ataka		
н	118171	M	73	" Sa	n Calixto,	Río '	Tarro
Ħ	117551	F	76	Venezuela: D	ist. Fed.,	El V	alle
**	128785	M	68	11	0 11	n	f1
11	128786	F	85	16	11 11	11	11
n	121163	M	74	n	0 11	Sta.	Lucia
B	128795	F	89	n W	iranda, Lo		

These frogs more closely resemble *niceforoi* than they do any other described species of *Phyllomedusa*, but do not agree sufficiently with the type description to justify placing them in that species. Furthermore, they all differ more or less from one another, and those specimens which have the most similar external morphology differ in sex, collection locality, and presence or absence of an omosternum.

Unfortunately, niceforoi is known only from the holotype, and no other species of Phyllomedusa are known from this particular area of South America, which is geographically somewhat isolated from the remainder of the continent. It is conceivable, however, that within the species niceforoi there is considerable intraspecific variation and that at least some, if not all, of the above specimens are referable to it.

Phyllomedusa orcesi, new species Figures 7, 27; Map 4

DIAGNOSIS: A *Phyllomedusa* belonging to the group in which the first toe is longer than the second. Apparently most similar to *feltont* and *boliviana*. The present form differs significantly from *feltoni* in the structure of the parotoid glands; from *boliviana* in the more acuminate snout; and from both in the very coarse, granular skin texture and coloration.

HOLOTYPE: Stanford University 10316, an adult female, 85 mm. snout-to-vent, from Chicherota (Chichirota), a settlement on the left bank of the Bobonaza River, Napo-Pastaza Province, eastern Ecuador (Lat. 2° 22' S., Long. 76° 38' W.); altitude approximately 280 meters.

DESCRIPTION: Tongue entire. Vomerine teeth in two distinct, slightly oblique groups between anterior edges of choanae. Length of exposed part of eye slightly longer than distance from its anterior corner to nostril. Snout sloping in profile, rounded over the nostrils, rather acuminate when viewed from above. Canthus rostralis rounded, curved. Loreal region slightly concave, obliquely sloping. Interorbital space as broad as upper eyelid. Tympanum distinct, its longest measurement about one-half exposed part of eye.

Fingers free, first shorter than the second and widely opposable to the others, fourth almost as long as third. Toes free, the first longer than second, fourth considerably longer than fifth. First toe opposable to the others. Disks of fingers and toes smaller than tympanum. No fringes on fingers or toes. Inner metatarsal tubercle not prominent. Tibiotarsal articulation reaches anterior corner of eye. Length of femur contained slightly more than twice in snout-to-vent length. Heels overlapping slightly when legs are held at right angle to body.

Skin of dorsum, including upper surface of arms and legs, very coarse, covered with small granules. Parotoid glands extending at least to point reached by adpressed elbow, rather indistinct due to the coarse texture of the whole dorsum. Skin of sides with rather large flat granules. Throat with small granules rather similar to those of dorsum; remainder of venter and lower surface of thighs with flat granules smaller than those on sides.

COLOR IN ALCOHOL: Dorsum gray-blue, including upper surface of arms and legs to two outer digits; sides of body same color as dorsum, with a single series of irregular white spots. A broad irregular white line from posterior edge of insertion of forearm to groin separates the color of the sides from the lighter venter. Concealed surfaces of arms and legs slightly lighter than dorsum with irregular white spots or patches, either distinct or merging with the ventral surfaces. Throat and chest dark gray-blue; venter and lower surface of thighs grayish, the tops of the granules darker. Lower lip white-edged, the white continuing as a distinct line from the angle of the jaw over the insertion of the forearm, to merge with the white spots on the sides. Prominent white spot in center of chest. patch on ventral surface of forearm at point of insertion, continuing along the lower surface of the arm and hand. A rather indistinct light, darkedged line from elbow to outer finger, marked by white granules from elbow to wrist. A very indistinct violet line over vent, and from heel to fifth toe.

REMARKS: The author takes pleasure in naming this species in honor of Dr. don Gustavo Orcés V., of the Escuela Politécnica Nacional, Quito, who donated the specimen to the author for the Natural History Museum, Stanford University.

Phyllomedusa theringi Boulenger Figures 7, 39; Map 4

Phyllomedusa iheringii Boulenger, 1885, p. 88 (type locality: São Lorenzo, southern border of Lagôa dos Patos, Rio Grande do Sul, Brazil; type(s) in British Museum, "numerous specimens", length 67 mm.); 1886, p. 464 (breeding key).—Ihering, 1886, p. 461, fig. (nest).—Nieden, 1923, p. 340, fig. 269 (compiled description; Rio Grande do Sul).—Miranda-Ribeiro, 1923, p. 3 (Rio Grande do Sul); 1926, p. 102 (compiled description).

Phyllomedusa (Pithecopus) burmeisteri iheringii Bertha Lutz, 1950, pp. 604, 605 (in Portuguese), 622 (in English), pl. 4, fig. 11, map.

Phyllomedusa (Pithecopus) burmeisteri distincta Bertha Lutz, 1950, pp. 604, 608 (in Portuguese), 622, 626 (in English), pls. 1-2, figs. 1-6, map (type locality; Rio Vermelho, Serra Alta, northern Santa Catarina, Brazil; holotype in Adolpho Lutz Collection, Instituto Oswaldo Cruz; female, length 70 mm.).

RANGE: Up to about 3000 feet, states of Rio Grande do Sul and Santa Catarina, Brazil.

DISTINGUISHING CHARACTERISTICS: Size medium to large (about 60 mm. adult); long, rather indistinct parotoids; sides and concealed surfaces of limbs unmarked or with delicate dark pencilings; disks small. Most similar to burmetsteri.

DESCRIPTION: Tongue slightly emarginate and extensively free behind. Vomerine teeth usually present in adults, in two distinct oblique groups between the choanae. Snout oval, truncate, barely sloping in profile. Loreal region nearly vertical. Canthus rostralis very distinct. Interorbital space broader than upper eyelid. Length of eye approximately equal to distance from its anterior corner to tip of snout. Tympanum distinct,

slightly more than half the length of the exposed part of eye.

Fingers free, first shorter than the second, fourth almost as long as third. Toes free, first considerably longer than second; opposable to the others. Disks of fingers and toes very small, hardly broader than width of digit; no fringes on fingers or toes. Subarticular and inner metatarsal tubercles not prominent. Tibiotarsal articulation reaches tympanum or eye.

Skin of dorsal surfaces smooth; parotoids not distinct, long and narrow, reaching to middle of body; throat, belly and lower surface of thighs granular.

LENGTH: 45-70 mm.

COLOR IN LIFE: Dorsum, including two outer digits, deep green; concealed surfaces vivid red on thighs and inside of forearm and tarsus, paler on hands, feet and inner digits; sides of body buff or orange-yellow; white line, underscored with dark, on forearm from elbow to outer finger, on tarsus from heel to outer toe, and around margin of lower jaw; white spot on posterior corner of eye; iris gray; disks of first and second fingers, first, second and third toes, white.

COLOR IN ALCOHOL: Dark gray-blue or purple above; concealed surfaces cream; from almost immaculate to heavily blotched with brown on throat, chest and lower surface of forearm and tarsus; sides with fine, non-symmettrical markings of purple.

SPECIMENS EXAMINED: Forty-two, from Estado da Santa Catarina, Brazil, as follows: UMMZ 58507: one, USNM 66582: one, Rio Humboldt; 98664-98666; 98691-98703: 36, Hansa; SU 15581-15584: four, Hansa.

Phyllomedusa trinitatis Mertens Figures 7, 37; Map 4

Phyllomedusa trinitatis Mertens, 1926, p. 145 (type locality: Port-of-Spain, Island of Trinidad; holotype: Senckenburg Museum 1428, 2a, female, length 88 mm.).

Phyllomedusa (Pithecopus) trinitatis Bertha Lutz, 1950, pp. 603 (in Portuguese), 621 (in English), map.

RANGE: Island of Trinidad.

DISTINGUISHING CHARACTERISTICS: Parotoid glands indistinct, disks longer than wide; color pattern; range.

DESCRIPTION: Tongue entire, extensively free behind. Vomerine teeth in two small, oblique, pointed groups which converge posteriorly from inner anterior edges of choanae. Palatine bone with a very sharp edge, producing a small tooth-like tubercle. Tip of snout sloping in profile. Loreal region concave. Canthus rostralis distinct. Nostril nearer tip of snout than front edge of eye. Interorbital space as broad as upper eyelid. Tympanum very distinct, two-thirds to one-half as broad as horizontal eye measurement.

Fingers free, first finger shorter than the second, fourth shorter than third. First toe longer than the second; opposable to the others. Remains of webs possibly distinguishable between toes; no fringes on fingers or toes. Disks of fingers two-thirds to three-fourths as large as the tympanum; disks of toes somewhat smaller. Median metatarsal tubercle not prominent. Tibiotarsal articulation reaches beyond anterior edge of eye.

Upper surfaces smooth. Parotoid glands rather large, extending from above middle of eye to middle of body, but indistinctly developed. Belly and underside of thighs granular.

LENGTH: 64-88 mm.

COLOR IN ALCOHOL: Dorsum dark blue-violet; sides of body and inner side of thighs with a finely flecked pattern; fingers and toes dark; white,

dark-bordered line on outer side of forearm and tarsus; throat and chest pale brownish violet, fading to white on belly; light spots on throat, chest, under side of thigh and tarsus; fine, white, dark-bordered line around margin of lower jaw.

SPECIMENS EXAMINED: Three as follows: UMMZ 83173: from Mayaro Beach, Trinidad. SU 10794: one from Trinidad. B.W.I.

The above specimens differ from the type description in that REMARKS: the canthus rostralis, described as indistinct, is very distinct, and its length is only about two-thirds that of the eye, the description stating one and two-thirds ("Vorderkopf mit undeutlichem Canthus rostralis, etwa 1 2/3 so lang wie der horizontale Augendurchmesser; ... "). The first point may have been a matter of preservation. Mertens noted that the tongue of the type was damaged, and it is quite possible that the type is not in as excellent condition as the specimens at the present author's disposal. second point is probably a typographical error in Merten's description. It is highly improbable that on an island the size of Trinidad two species of frogs could co-exist, identical in all respects except the length of the And considering the lack of variation in relative snout lengths snout. within other species of this genus, one would not expect to find such extreme variation here.

Phyllomedusa tarsius (Cope) Figures 7, 26; Map 3

Pithecopus tarsius Cope, 1868, p. 113 (type locality: Río Napo, below the mouth, upper Amazon, Peru; holotype: Smithsonian Mus. 6652 (probably now in U. S. Nat. Mus.), a male, length 3 inches, 9.25 lines).

Phyllomedusa tarsius Boulenger, 1882a, p. 428 (description; Pebas, Peru).

-Nieden, 1923, p. 343 (compiled description; upper Amazon).

Phyllomedusa (Pithecopus) tarsius Bertha Lutz, 1950, pp. 603 (in Portuguese), 621 (in English), map.

RANGE: Upper Amazon of Peru.

DISTINGUISHING CHARACTERISTICS: Size large; long, distinct parotoid glands; large disks. Most similar to bicolor and feltoni.

DESCRIPTION: Tongue slightly emarginate behind. Vomerine teeth in two more or less transverse groups on a level with the anterior edge of the choanae. Snout slightly longer than diameter of eye, sloping in profile, rounded when viewed from above. Upper lip somewhat projecting. Loreal region slightly oblique. Interorbital space broader than upper eyelid. Tympanum one-half diameter of eye.

Fingers and toes free; first toe longer than the second and probably opposable to the others. Disks of fingers larger than tympanum, of toes about equal; no fringes on fingers or toes. Heels just overlapping when legs are held at right angles to body. Tibiotarsal articulation reaches front of eye.

Skin minutely granular above, with a few flat warts or glands on the back. Parotoid glands distinct, extending from above the middle of the eye to the sacrum. Granular beneath, except arms, legs and feet.

LENGTH: 87-112 mm.

COLOR IN ALCOHOL: Blue-gray above, including forearm, femur, tibia, and tarsus; this color also on two outer digits; sides with small whitish spots; distinct light spots on chest, on either side of vent, and sometimes on the belly. Indistinct light line along outer margin of forearm, over vent, and around heel to outer toe; lower lip white-edged; lower eyelid white-edged.

SPECIMENS EXAMINED: Seven, all from Peru, as follows: USNM 35602: one from Pebas; 127165-66: two from Campo Sta. Clara, Orellana. UMMZ 1285-86: three from Pebas. SU 15592: one from Pebas.

Phyllomedusa vaillanti Boulenger Figures 7, 30; Map 4

Phyllomedusa vaillantii Boulenger, 1882a, p. 427, pl. 29, fig. 2 (type locality: Santarém, Pará, Brazil; holotype in British Museum, male, length 60 mm.).—Nieden, 1923, p. 339 (compiled description).—Miranda-Ribeiro, 1926, p. 103 (compiled description).

Phyllomedusa (Pithecopus) vaillantii Bertha Lutz, 1950, pp. 603 (in Portuguese), 621, 623 (in English), map.

RANGE: Santarém to the mouth of the Amazon (the latter based upon a distribution map (B. Lutz, 1950) upon which a locality is shown at, or close to, Belém do Pará).

DISTINGUISHING CHARACTERISTICS: Medium size; osteoderms in skin of dorsum; parotoid glands short, not extending beyond the angle of the jaws, probably no light spots on each side of vent.

DESCRIPTION: "Tongue entire. Vomerine teeth in two small oblique groups between the choanae. Snout a little longer than the diameter of the eye, obliquely truncated from behind forwards; loreal region oblique, very concave; interorbital space a little broader than the upper eyelid; tympanum half the diameter of the eye.

"Fingers free, first shorter than second, fourth a little shorter than third; toes free, first considerably longer than second; disks of fingers and toes much smaller than the tympanum; metatarsal tubercle indistinct. The hind limb carried forwards along the body, the tibiotarsal articulation

marks the posterior corner of the eye.

"Upper surfaces studded with bony deposits; parotoids distinct, short, not extending beyond the vertical of the angle of the jaws; chest, belly, and inferior surface of thighs granulate.

"Blue-green above; sides of limbs and body purple, minutely spotted with whitish; a narrow white, black-edged line along the outer side of forearm and tarsus; fingers light greenish; lower surfaces brownish white, with a few white spots on the throat and chest.

"Male with a subgular vocal sac. From snout to vent 60 millim." (Boulenger, 1882a.)

SPECIMENS EXAMINED: None.

REMARKS: Although the author has seen no examples of this species, it is a well established form and its presentation here as a distinct species seems fully justified.

Phyllomedusa feltoni Shreve Figures 7, 31; Map 4

Phyllomedusa feltoni Shreve, 1935, p. 214 (type locality: Sarayacu, eastern Ecuador; holotype: Museum of Comparative Zoology 19941, adult male, length 44 mm.).

RANGE: Eastern Andean foothills of Ecuador.

DISTINGUISHING CHARACTERISTICS: Size medium to large, skin gives appearance of possessing osteoderms; disks small; snout rather acuminate when viewed from above; glandular ridges on arms and legs prominent, but not always markedly different in color from the surrounding skin; finely reticulate markings on concealed surfaces of sides and thighs.

DESCRIPTION: Tongue entire. Vomerine teeth in two oblique groups between the choanae, the anterior edges of the former about on a level with the anterior edges of latter. Length of eye about equal to distance from its anterior edge to nostril. Snout sloping in profile, angular over the nostrils, acuminate when viewed from above. Loreal region nearly vertical, plane. Canthus rostralis straight, sharply angular. Interorbital space as broad as upper eyelid. Tympanum about one-half exposed part of eye.

Fingers free, first shorter than the second, fourth nearly as long as the third. Toes free; first toe much longer than the second and opposable to the others. Disks of fingers and toes smaller than tympanum; no fringes on fingers or toes. Inner metatarsal tubercle not prominent. Tibiotarsal articulation reaches eye. Length of femur contained slightly more than twice in snout-to-vent length.

Skin above smooth, but coarse, giving the appearance of possessing osteoderms (some large adult specimens may actually possess osteoderms, but the condition is not so readily apparent in young specimens). Parotoids distinct, frequently forming an angular ridge along side of body from posterior half of eyelid to, or beyond, point reached by adpressed elbow. Throat and chest smooth. Belly, lower half of sides, and lower surfaces of thighs covered with small round granules.

LENGTH: 44-88 mm.

COLOR IN ALCOHOL: Purplish blue above, including top of upper arm, forearm to outer one or two fingers, and leg to outer one or two toes; remainder of fingers and toes lighter brownish violet; concealed surfaces of arms and legs and posterior section of sides purplish brown with numerous small white spots; anterior section of side with a series of small to large light, sometimes dark-edged, spots; edge of lower lip often appearing white, continuing as an indistinct white line from angle of jaw to insertion of forearm; below this light line lower lip is often margined with a dark purplish blue line, which continues over insertion of forearm to merge with color of sides; one or more light, sometimes dark-edged, spots on throat and chest, and on lower surface of thigh on each side of vent; remainder of venter usually light; glandular ridges from elbow to outer finger, over vent, and from heel to outer toe conspicuously raised, lighter than surrounding skin, but not markedly white as in boliviana.

SPECIMENS EXAMINED: Five, all from eastern Ecuador, as follows: UMMZ 92100: two from Abitagua, Río Pastaza. SU 15589: one from Abitagua, Río Pastaza. EPN 54: one from Chicherota, Bobonaza River. OV 148: one from headwaters of Bobonaza R., alt. 800-900 meters.

REMARKS: The specimen from Chicherota exhibits the following differences from the above description: the canthus rostralis definitely curved; the throat and chest rather strongly tinged with black; no light spots on lower surface of thigh on each side of vent; more or less strongly developed series of tubercles on outer edges of forearm and leg. The other specimens, which show little variation, come from localities in the upper tropical, or lower subtropical, zone, while Chicherota is well down in the tropical zone out of the highlands. It is possible that these are different geographic races.

Phyllomedusa feltoni is probably most closely related to P. vaillanti or orcest, rather than burmeisteri, as is stated in the original description, and superficially it is most readily confused with orcest and boliviana. The most easily discernable differences between this form and boliviana are its more acuminate snout, more strongly developed canthus rostralis, probable presence of osteoderms, and different color pattern on the concealed surfaces. The most conspicuous differences between feltoni and orcesi are: structure of parotoids, skin texture and coloration.

Phyllomedusa sauvagei Boulenger Figures 7, 40; Map 4

Phyllomedusa sauvagit Boulenger, 1882a, p. 429, pl. 29, fig. 3 (type locality: Oran Salta, Buenos Aires, Argentina; type(s) in British Museum, described from a male and a female, type not designated, length 75 mm.).—Berg, 1896, p. 213 (Province of Salta, Argentina).—Agar, 1901, p. 893, pl. 84 (nesting habits; Paraguayan Chaco).—Nieden, 1923, p. 341, fig. 270 (figure from Boulenger, 1882a; compiled description; Salta, Argentina).

Phyllomedusa burmeisteri Berg, 1896, p. 212 (in part; Province of Salta).
Phyllomedusa rickettsii Günther, 1897, p. 365 (type locality: Santa Fé, northern Argentina; holotype in British Museum, length 68 mm.).—Nieden, 1923, p. 340 (compiled description; Santa Fé, Argentina).

Phyllomedusa (Pithecopus) sauvagit sauvagit Bertha Lutz, 1950, pp. 602, (in Portuguese), 620 (in English), pl. 3, fig. 7, map.

Phyllomedusa (Pithecopus) sauvagiti rickettsii Bertha Lutz, 1950, pp. 602, (in Portuguese), 620 (in English), map.

RANGE: Argentina, southern Brazil and southern Bolivia.

DISTINGUISHING CHARACTERISTICS: Flat tubercles may be present on dorsum; in alcohol dorsal color extends to all parts of body except belly; disks no wider than digits; parotoid glands very prominent and very short.

DESCRIPTION: Tongue heart-shaped, extensively free behind; vomerine teeth in two small groups on a level with the anterior edge of the choanae. Snout sloping in profile, rounded when viewed from above; canthus rostralis distinct, slightly incurved; loreal region sloping, plane or slightly concave. Interorbital distance much broader than upper eyelid. Tympanum distinct, its greatest diameter equal to about one-half the exposed part of the eye. Nostrils closer to tip of snout than to eye; distance between nostrils almost equal to the exposed part of the eye; distance between nostril and anterior corner of eye two-thirds to three-fourths length of exposed part of eye.

Fingers and toes free; fourth finger almost equal to third; first toe shorter than second, widely opposable to the others; second toe much reduced. Disks of fingers and toes small, no wider than the width of the digit; no fringes on fingers or toes.

Skin smooth above, or with smooth, flat warts on body and upper thighs. Parotoid glands large, but short, from above middle of eye they form a prominent mass of tissue on each side of head and neck. Belly and lower part of thighs coarsely granular.

LENGTH: 68-76 mm.

COLOR IN ALCOHOL: Blue-gray or violet above and beneath except on the belly; throat and chest with semi-symmetrical white or yellow markings, sometimes forming lines down throat and chest; white or yellow line around margin of lower jaw, extending to middle of body; yellow spots on each side of the groin, around vent and on lower side of thighs; usually a light line on outer edge of forearm and foot; usually a light line or a light spot on heel.

SPECIMENS EXAMINED: Eight, as follows: UMMZ 94081, from Oran Salta, Buenos Aires, Argentina. SU 11285-86, from Rayo Cortado, Santiago del Estero, Argentina; 11466-70, from Tucumán, Tucumán Prov., Argentina.

REMARKS: Previously P. sawvaget and rickettsi have been separated only on the basis of locality, the presence of dorsal warts in rickettsi, and a light heel spot and light line on the outer edge of the forearm and foot of sawvaget. Miss Lutz (1950) differentiated these forms subspecifically on

the basis of locality and the presence or absence of dorsal warts. However, UMMZ 94081, from the type locality of <code>sauvagei</code>, has prominent dorsal warts, a light spot on <code>one</code> heel, and very indistinct light lines on the outer edges of the forearm and foot, SU 11285 also has prominent dorsal warts, while SU 11286, collected at the same time and place, has no such warts. Both of the Stanford specimens are males—indicating that the warts are probably not a sexual character—and both have the characteristic <code>sauvagei</code> color pattern.

Phyllomedusa bahiana Adolpho Lutz Figure 7; Map 4

Phyllomedusa bahiana Adolpho Lutz, 1925b, p. 139 (diagnosis) (type locallity: São Salvador, Estado da Bahia, Brazil; holotype: Adolpho Lutz Collection 30, Instituto Oswaldo Cruz, length 75 mm.).—Adolpho and Bertha Lutz, 1939, p. 248 (description).

Phyllomedusa (Pithecopus) burmeisteri bahiana Bertha Lutz, 1950, pp. 605 (in Portuguese), 622 (in English), pl. 4, fig. 10, map.

RANGE: East coast of Brazil from north of Rio de Janeiro to northern Bahia.

DISTINGUISHING CHARACTERISTICS: Snout sloping in profile; rudimentary webs on toes; tibiotarsal articulation reaches only to axilla; conspicuous parotoid glands. Probably most similar to burme tstert.

DESCRIPTION: Tongue narrow in front, broadly cordiform behind. Vomerine teeth in two short, oblique, well-separated groups between the large choanae. Snout slightly longer than eye, rounded, sloping downward and forward in profile. Nostrils lateral, very small, at tip (or end) of snout. Canthus rostralis not very distinct. Loreal region sloping. Fye moderate, inserted obliquely. Interorbital space about one and a half times as wide as upper eyelid. Tympanum distinct, its diameter about one-half that of eye. Head massive; body elongate, tapering greatly posteriorly; width of head contained about three times in snout-to-vent length.

Fingers slender, long, free; first shorter than second, widely opposable to it; fourth almost as long as third. Webs just at base of fourth and fifth toes; first toe much longer than second, widely opposable to it. Disks on fingers and toes very small, covering only a very small area of tympanum. Subarticular, palmar and plantar tubercles and bolsters at base of first toe inconspicuous. Tibiotarsal articulation barely reaches to axilla. Heels just touch when laid at right angles to body.

Skin of dorsal surfaces thick and glandular, but not rough. Parotoids heavy, conspicuous, beginning behind eyes, overhanging and half encircling tympanum, reaching about to elbow when arm is adpressed. Throat and chest finely granular; belly and perianal region more coarsely granular; under thigh smooth; glandular ridges on forearm and foot reaching to tip of outer fingers and toes; a ridge over anus.

LENGTH: 75 mm.

COLOR IN LIFE: Dorsal surfaces dark green; glandular ridges citron; disks and distal parts of inner digits yellowish citron above; under parts off-white, immaculate, including hands and feet.

COLOR IN ALCOHOL: The specimens fade, first to dull gray-green, then to uniform drab, with vestiges of dull purple-brown pigment on concealed surfaces at shoulder, side, knee and tibiotarsal articulation. No vestiges of the spots or clear spaces such as are found on the concealed surfaces of sides, limbs, and throat in faded specimens of species with conspicuous markings such as *P. burmeisteri*.

SPECIMENS EXAMINED: None.

REMARKS: The foregoing description is taken from Adolpho and Bertha Lutz (1939). Miss Lutz (1950) designates this a subspecies of burmeisteri, but until more is known of this form and its relatives the author prefers to retain it as a full species on the basis of the following differences from burmeisteri: vestigial webbing on toes; very short leg, tibiotarsal articulation reaching only to axilla; structure of parotoids; quite different coloration.

Phyllomedusa burmeisteri Boulenger Figures 7, 38; Map 4

Phyllomedusa bicolor (nec Boddaert, 1772) Burmeister, 1856, p. 111, pl. 32, figs. 1-9 (southern Brazil).—Günther, 1858, p. 120 (in part).—Cope, 1868, p. 112 (key).

Phyllomedusa burmeisteri Boulenger, 1882a, p. 428 (syntypes, 13 specimens in British Museum, one from "Rio Janeiro", 11 from "Brazil", one from "Oran Salta, Buenos Ayres"; type locality hereby restricted to the city of Rio de Janeiro, specifically the Tijuca).—Berg, 1896, p. 212 (in part).—Nieden, 1923, p. 339 (compiled description; eastern Brazil, Argentina).—Miranda-Ribeiro, 1923, p. 3 (localities in Bahia, Rio de Janeiro, Espirito Santo, Minas Gerais); 1926, p. 102, pl. 5, figs. 6-6a (description).—Myers, 1946, pp. 14 (in Portuguese), 32 (in English) (Rio de Janeiro).—Cochran, 1955, pp. 196 (key), 198, pl. 19, figs. A-B (description; Bahia, Districto Federal, Rio de Janeiro, São Paulo).

Phyllomedusa (Pithecopus) burmeisteri burmeisteri Bertha Lutz, 1950, pp. 601 (in Portuguese), 619, 622 (in English), pl. 3, figs. 8-9, map.

RANGE: Southeastern coastal Brazil, southeastern Bahia, Minas Gerais, Espirito Santo, Rio de Janeiro, São Paulo.

DISTINGUISHING CHARACTERISTICS: Size medium to large (usually more than 60 mm. adult); large, very distinct parotoids; sides and concealed surfaces of limbs with distinct dark bands or light spots on a dark background; disks small. Most similar to *theringi* (?and/or bahtana).

DESCRIPTION: Tongue entire. Vomerine teeth in two oblique groups between the choanae. Snout longer than greatest diameter of exposed part of eye, distinctly sloping in profile. Loreal region oblique. Canthus rostralis distinct. Interorbital space broader than upper eyelid. Tympanum about half diameter of eye.

Fingers free, first shorter than the second, fourth nearly as long as third. Toes free, first longer than second and opposable to the others. Disks of fingers and toes much smaller than tympanum, not much wider than the digit; no fringes on fingers or toes. Inner metatarsal tubercle not prominent. Tibiotarsal articulation reaches to tympanum or eye.

Parotoids very distinct, extending from hind edge of eye to middle of body, forming a distinct ridge or edge on each side of body. Upper surfaces smooth or minutely roughened. Belly and lower surface of thighs granulate, remainder of venter smooth.

LENGTH: Males average 64 mm.; females average 73 mm.

COLOR IN ALCOHOL: Light to dark gray-blue above; sides with white, purple-edged spots or vertical purplish lines, becoming mottled or marbled on concealed surfaces of limbs; venter varying from a uniform purplish brown to almost pure white, variously spotted or blotched with brown; a white, purple-edged line along outer edge of forearm and tarsus, and over vent; a white spot at anterior corner of eye.

SPECIMENS EXAMINED: Twenty-one, from Brazil, as follows: USNM 96440:

one from Estrella, Rio de Janeiro; 96922-25: four from Campo Bello, Rio de Janeiro. UMMZ 65885: one from Brazil; 65895: one from Goyaz. SU 13050-13055: six from Barro Branco, Estado do Rio de Janeiro; 13048-13049: two from Estrada Velha da Tijuca, Distrito Federal; 13044-13045 and 13046-13047: four from Estrada da Cafunda, Jacarépaguá, Distrito Federal; 13043: one from Jacarépaguá, Distrito Federal.

REMARKS: Boulenger's (1882a) description of *P. burmeisteri* includes a specimen from Oran Salta, Buenos Aires, Argentina, but according to Lutz (1950) "the Argentinian specimen was later described as *P. sauvagii* by Boulenger." This can hardly be true since the description of *P. burmeisteri* in Boulenger's 1882a work is immediately followed by the original description of *P. sauvagei* based on different specimens from the one included under burmeisteri. The specimen was probably later placed under sauvagei.

Phyllomedusa boliviana Boulenger Figures 7, 28; Map 4

Phyllomedusa boliviana Boulenger, 1902b, p. 395 (type locality: Chulumani, Bolivia, 2000 m.; type(s) in British Museum, length 75 mm. (description based on two specimens, a male and a female; holotype not designated.)).—Nieden, 1923, p. 341 (compiled description).

Phyllomedusa (Pithecopus) boliviana Bertha Lutz, 1950, pp. 602 (in Portuguese), 621 (in English), map.

RANGE: Known from the eastern Andean foothills of Bolivia and Ecuador. DISTINGUISHING CHARACTERISTICS: Size large (75 mm.); skin smooth; snout rounded when viewed from above; parotoids very distinct; disks not large, about one-half size of tympanum; distinct white line on forearm, over vent, and along tarsus; marbling on sides clear-cut. Most similar to feltoni.

DESCRIPTION: Tongue scarcely emarginate behind. Vomerine teeth in two small, slightly oblique groups between the choanae. Snout as long as, or slightly longer than, diameter of exposed part of eye, not projecting beyond mouth, distinctly sloping in profile, rounded when viewed from above. Loreal region oblique, concave. Canthus rostralis curved, not strongly angular. Interorbital space as broad as upper eyelid. Vertical diameter of tympanum three-fifths to two-thirds diameter of exposed part of eye.

Fingers free, first shorter than the second, third and fourth approximately equal. Toes free, first longer than second and opposable to the others. Disks of fingers and toes about one-half tympanum. No fringes on fingers or toes. Subarticular tubercles prominent. Inner metatarsal tubercle not prominent. Tibiotarsal articulation reaches tympanum or eye.

Upper surfaces smooth or minutely granular (this latter condition may be the result of preservation). Parotoids very distinct, as long as or longer than, head. Throat, belly and lower surface of thighs granulate.

LENGTH OF SPECIMENS EXAMINED: Males average 64 mm.; females average 73 mm.

COLOR IN ALCOHOL: Gray-blue above, extending from upper arm to middle of first two fingers and first two toes; superciliary edge and lower lip pinkish or yellowish white, which color extends along sides forming a broad band marbled with the gray-blue color of dorsum; belly and lower surfaces of limbs grayish white; concealed portions of limbs speckled gray-blue and white; a distinct pinkish white streak, edged with dark, along outer side of forearm and outer finger, and another across heel and along outer edge of tarsus and outer toe; pinkish or yellowish white spots, often edged with purple, on throat, chest, and each side of vent.

SPECIMENS EXAMINED: Thirty-three, as follows: MCZ 365: one from Brazil. UMMZ 58955: two; 58956: one; 58597: two; all from Rurrenabaque, Bolivia.

UMMZ 60529: one; 60530: one; 60531: three; 60532: one; 63325: four; 66548: one; 66549: 11; 68162: one; SU 15593: one; USNM 118699: one; all from Buenavista, Dept. Sta. Cruz, Bolivia. UMMZ 92100-01: two from Abitagua, Río Pastaza, Ecuador.

REMARKS: The disks of one specimen of UMMZ 66549, an adult female, are exceptionally large, those of the fingers equalling the tympanum in size, and those of the toes covering about three-fourths the tympanic area.

SUMMARY

The genus Phyllomedusa is redefined to include the following genera: Agalychnis, Pithecopus, Hylomantis, Bradymedusa and Phrynomedusa. The range of this genus extends from Mexico, through Central and South America, to Argentina.

The author accepts Noble's (1931) statement that the evolution of the group has been from Hyla through the Agalychnis types to the forms which at present differ most from Hyla by a reduction in webs and relative size of disks, a shortening of the second toe and twisting of the first to produce the "grasping foot", and, usually, the development of parotoid glands. A phylogenetic arrangement of the species in the genus is proposed.

The least specialized "Agalychnis types" resemble the larger species of neotropical Hyla in the unspecialized foot with strong webbing and large disks, and in the absence of parotoid glands. A group of "intermediate" species shows varying degrees of reduction of webbing on an otherwise unspecialized foot. In the more specialized members of the genus the first toe is longer than the second, webs are absent, the disks are reduced, and parotoid glands are usually present. Some species show a tendency toward loss of the omosternum, but the presence or absence of the omosternum is of minor evolutionary significance compared with the unique progressive changes in the development of the hand and foot.

Any study such as the present one is to a certain extent necessarily incomplete. In no case can one say "This form gave rise to that form." The original "links" are long since gone—we have only the current examples to work with—and evolution continues.

In such a relatively poorly collected area as South America, one must be content with preserved material of most forms. Next to nothing is known of the habitat of most of these frogs, of their behavior, and of their appearance in life. Perhaps an ecological study would show significant differences. Then, too, the characters used to differentiate them are undoubtedly only a fraction of those available. There is room for much needed work on their osteology, musculature, and possibly on the chemistry of their pigments. It remains for future workers to find this multitude of so far unknown characters.

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Certain specific names (e.g., niceforoi, sauvagei) have been emended in accordance with recent provisions of the International Rules of Zoological Nomenclature. The authorship of the new names proposed in this paper is quoted as "A. Funkhouser" to distinguish such citations from those of her husband, Dr. John W. Funkhouser, who has also described new species of amphibians.]

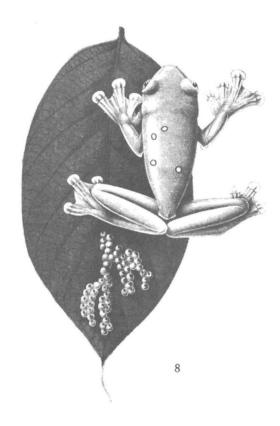


Fig. 8. Phyllomedusa spurrelli (Boulenger). After Boulenger, 1913, Proc. Zool. Soc. London.

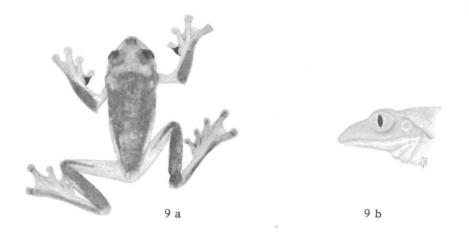


Fig. 9. Phyllomedusa moreleti (Duméril). a. Dorsal view (photo courtesy of Dr. E. H. Taylor). b. Profile of head.

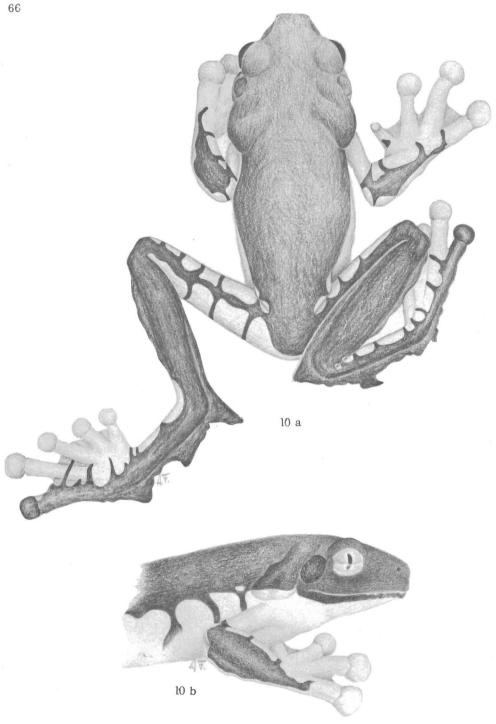


Fig. 10. Phyllomedusa craspedopus A. Funkhouser, new species. Holotype. SU 10310. a. Dorsal view. b. Profile, anterior part of body.

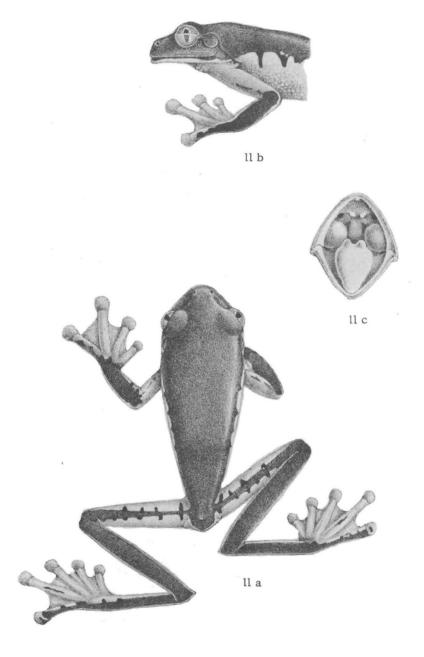


Fig. 11. Phyllomedusa calcarifer Boulenger. After Boulenger, 1913, Proc. Zool. Soc. London. a. Dorsal view. b. Profile, anterior part of body. c. Interior of mouth.



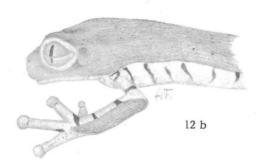


Fig. 12. $Phyllomedusa\ tomopterna\ (Cope)$. a. Dorsal view. b. Profile, anterior part of body (snout is foreshortened).

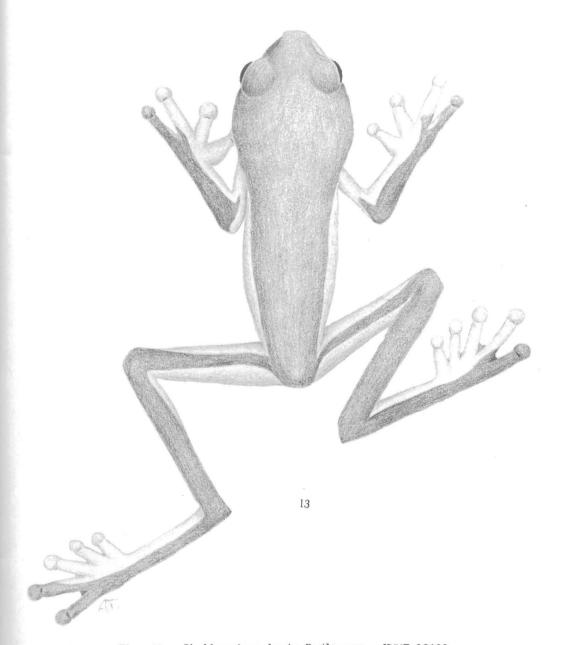


Fig. 13. Phyllomedusa loris Boulenger. UMMZ 92102.



Fig. 14. Phyllomedusa buckleyi Boulenger. After Boulenger, 1882, Cat. Batr. Sal. British Museum.



Fig. 15. $Phyllomedusa\ fimbriata\ (Miranda-Ribeiro)$. Redrawn after A. and B. Lutz, 1939.

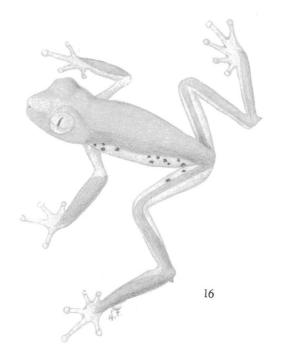


Fig. 16. Phyllomedusa guttata Adolpho Lutz. Redrawn after A. and B. Lutz, 1939.



Fig. 17. $Phyllomedusa\ aspera$ (Peters). After Peters, 1872, Monatsb. Akad. Wiss. Berlin.



Fig. 18. Phyllomedusa alcorni (Taylor). After Taylor, 1952, Copeia. Holotype. UKMNH 29763. a. Dorsal view. b. Profile of head.

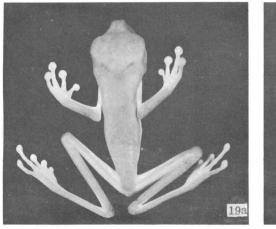




Fig. 19. Phyllomedusa lemur Boulenger. Photograph courtesy of Dr. E. H. Taylor. Females. Upper specimen UKMNH 31714; lower, UKMNH, 31711.

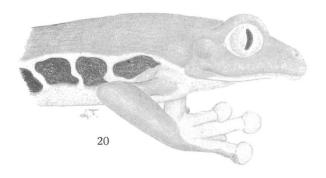


Fig. 20. Phyllomedusa helenae (Cope).

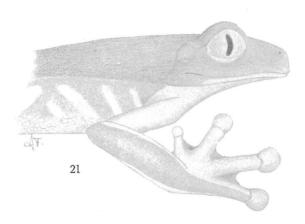


Fig. 21. Phyllomedusa callidryas callidryas (Cope)

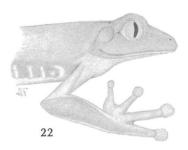


Fig. 22. Phyllomedusa callidryas taylori A. Funkhouser, new subspecies.





Fig. 23. Phyllomedusa saltator (Taylor). a. Dorsal view. b. Profile of head.

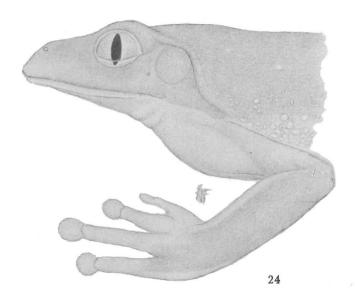


Fig. 24. Phyllomedusa dacnicolor Cope.



Fig. 25A. $Phyllomedusa\ bicolor$ (Boddaert). After Boddaert, 1772. a. View of dorsum.



Fig. 25B. $\it Phyllomedusa\ bicolor\ (Boddaert)$. After Boddaert, 1772. b. View of venter.

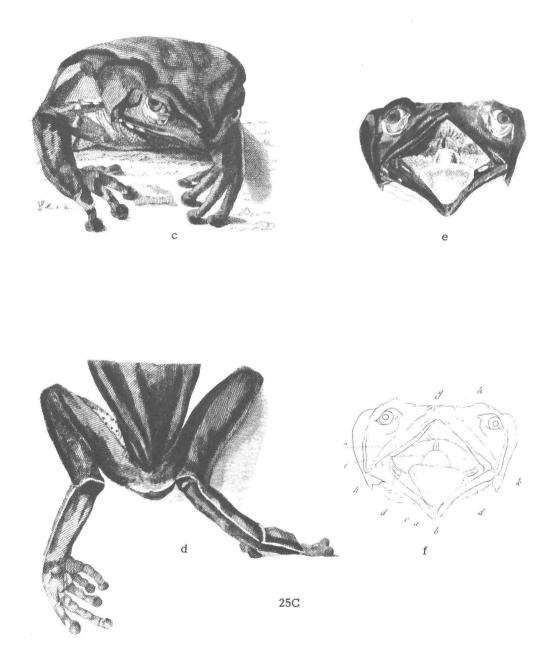


Fig. 25C. Phyllomedusa bicolor (Boddaert). After Boddaert, 1772. c. Anterior elevation. d. Dorsal view, rear half of body. e. Anterior view, front of head. f. Diagram of same.

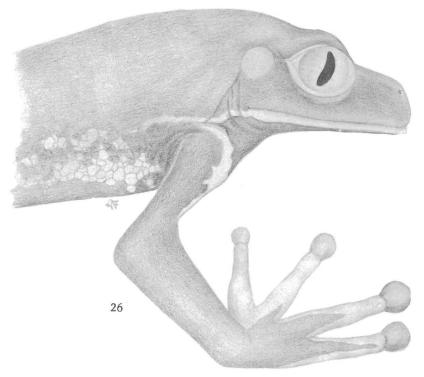


Fig. 26. Phyllomedusa tarsius (Cope).

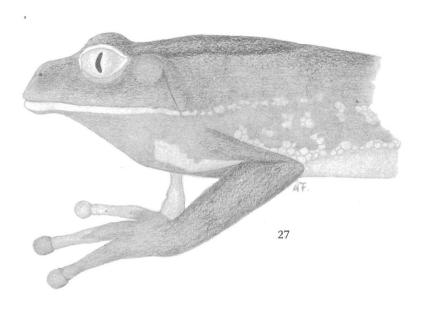


Fig. 27. Phyllomedusa orcest A. Funkhouser, new species. Holotype. SU 10316.

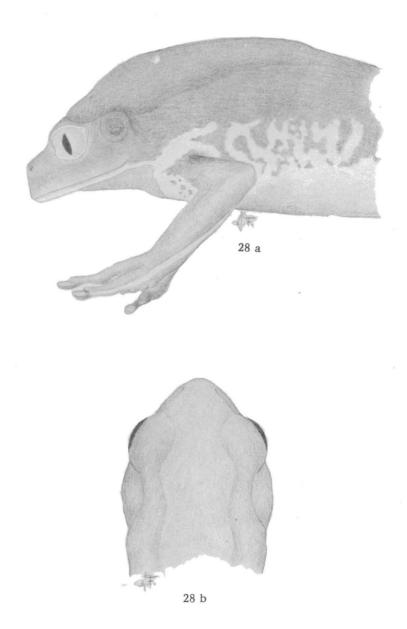


Fig. 28. $Phyllomedusa\ boliviana\ Boulenger.$ a. Profile, anterior part of body. b. head from above (male, UMMZ 58955).

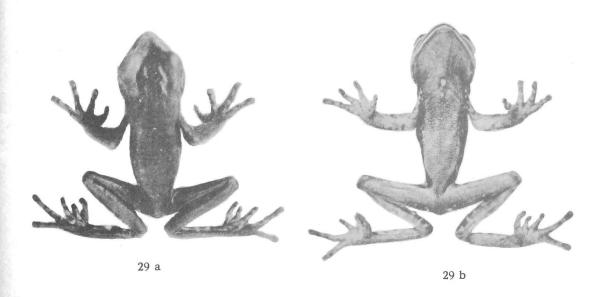


Fig. 29. Phyllomedusa niceforoi Barbour. Holotype. MCZ 11611. After Barbour, 1926, Occ. Pap. Boston Soc. Nat. Hist. a. Dorsal view. b. Ventral view.

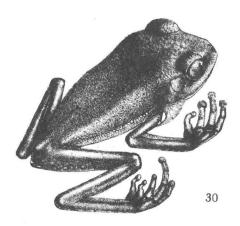


Fig. 30. $Phyllomedusa\ vaillanti\ Boulenger.$ After Boulenger, 1882, Cat. Batr. Sal. British Museum.



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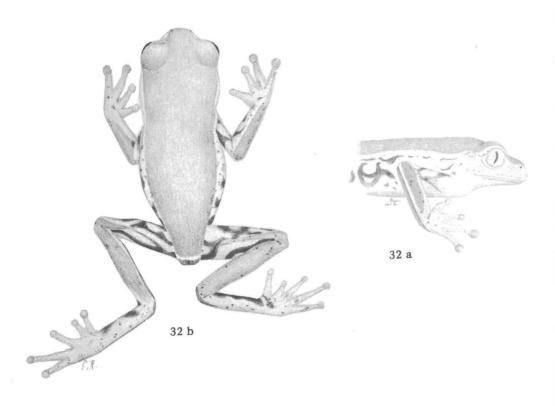


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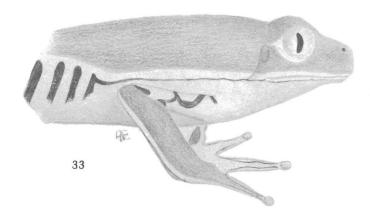


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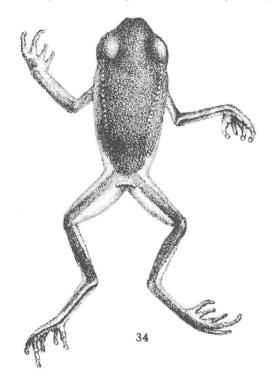


Fig. 34. *Phyllomedusa perlata* Boulenger. Holotype. After Boulenger, 1883, Proc. Zool. Soc. London.





Fig. 35 Phyllomedusa edentula Andersson. a. Dorsal view. b. Profile of head.

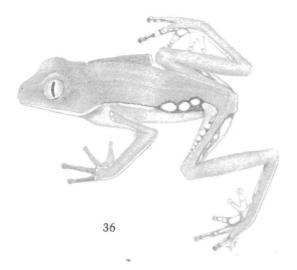


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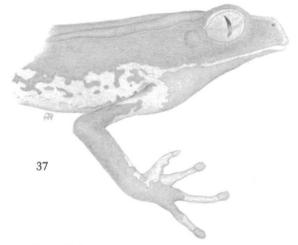


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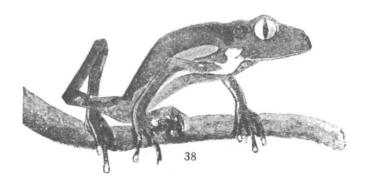


Fig. 38. $Phyllomedusa\ burmeisteri\ Boulenger.$ After Miranda-Ribeiro, 1926.

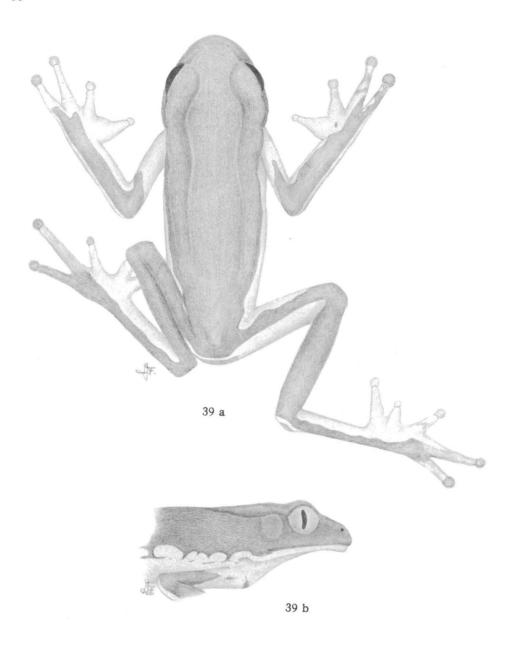


Fig. 39. $Phyllomedusa\ theringi\ Boulenger.$ a. Dorsal view. b. Profile, anterior part of body.



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