Variation and distribution in the tree-frog
genus *Phyllomedusa*
in Costa Rica, Central America

By

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With 6 figures

**Introduction**

Tree-frogs of the genus *Phyllomedusa* are among the most conspicuous anurans in the Costa Rican fauna. All of the species are bright green dorsally in life and many forms have bright yellow, orange or coral venters, are gaudily marked with purple or blue on the flanks and thighs or have bright red eyes. Although several authors (TAYLOR, 1952; FUNKHOUSER, 1957; DUellMAN, 1963) have treated the Costa Rican representatives of the genus, recently acquired material makes possible a detailed study of variation and geographic and ecologic distribution. Two of the species reported from Costa Rica for the first time in this paper have considerable ranges outside the country. Variation in two other nominal forms in Costa Rican material led to a complete analysis of geographic and character distribution. For these reasons this account includes discussion of the status and distribution of Costa Rican species throughout their known range based on all available material including extralimital samples.

At the present time seven nominal species, *Phyllomedusa annae* Duellman, 1963; *P. calcarifer* Bouleneger, 1902; *P. callidryas* Cope, 1862; *P. helenae* Cope, 1885; *P. lemur* Bouleneger, 1882; *P. saltator* Taylor, 1955; and *P. spurrelli* Bouleneger, 1913, are recognized in Costa Rica. Records for *P. dacnicolor* Cope, 1864, from the republic by FUNKHOUSER (1957) are based on misidentified *P. annae* (US 32237-39). Other records of *dacnicolor* from Central America appear to be misidentifications. DUNN (1931: 414) records juveniles from Barro Colorado Island, Canal Zone, Panama as this species. The principal reason for his identification is the slight finger and toe webbings. As pointed out by NOBLE (1931: 99-100) and others, the degree of webbing in hylid frogs increases through ontogeny, and recently transformed or late larval stages frequently have no webbing even in species in which the webs are extensive in adults. Since we have been unable to locate DUNN'S material positive identification is not possible. It seems certain that the examples are the young of *P. calcarifer,*
P. callidryas or P. spurrelli, all known from Barro Colorado Island. An Honduran example regarded as dacnicolor by Funkhouser (1957) is P. callidryas (US 74506). The population from Costa Rica referred to P. moreletii A. Duméril, 1831, by Taylor (1952: 802) and Funkhouser (1957: 40) was described as P. annae by Duellman (1963). As far as can be determined, dacnicolor is restricted to the west coast of Mexico, north of the Isthmus of Tehuantepec, and moreletii ranges from Veracruz, Mexico, to no farther south than Honduras.

**Variation**

In this section consideration will be given to interspecific and intraspecific variation in characteristics usually utilized in the systematics of Phyllomedusa. Discussion is restricted to variation in species found in Costa Rica.

**COLORATION.** In life, members of the genus Phyllomedusa include some of the most brilliantly colored and aesthetically beautiful frogs of the new world. Life colors also are of considerable use in distinguishing among species and form the principal basis for Duellman’s (1963) key to Middle American forms. Unfortunately many of the significant color differences are lost on preservation although certain pattern characteristics are retained. In the following account variation in nine features of coloration and pattern is described. These features include characters employed by previous workers or found to be significant in population definitions in this study.

**Flank Pattern:** A constant characteristic of living and preserved members of the genus is the basic flank pattern. In annae, lemur, saltator and spurrelli the flank area between axilla and groin is uniform in color and without contrasting markings. In callidryas and helena the flank is a solid purplish-blue color with a series of vertical white, yellow or cream-colored bars. Variations in the light interconnections between the upper portions of the light bars have served as the sole means of distinguishing these two forms (Taylor, 1912; Funkhouser, 1957; Duellman, 1963). A fuller analysis of variation in this character in callidryas and helena is presented in a subsequent section of this paper. P. calcarifer has a light flank, the same color as the venter, with a series of deep purple to black vertical bars.

**Flank Color:** In life the color of the flank region exhibits relatively little variation within a species and is a useful field character in some cases. The species with uniform flank patterns form two groups in terms of color, those with a bright yellow or orange flank, lemur and spurrelli; and those with a blue to purple flank, annae and saltator. In the callidryas-helena group the dark field of the flank is purple-brown to blue-purple and the light bars are white to cream-yellow. The light field in calcarifer is orange-yellow and the bars are black.

**Thigh Pattern:** Two basic patterns are exhibited by Costa Rican Phyllomedusa. In all species the dorsal surface of the thigh directly above the femur is green or purplish, in life or preservative, respectively. The anterior and posterior surfaces of the thigh are uniform in coloration in all species except calcarifer. In the latter species a series of regular purple-black transverse marks pass through the central green field on the dorsal surface of the thigh onto the upper portions of the light anterior and posterior surfaces.

**Thigh Color:** The anterior and posterior surfaces of the thighs are essentially light and of the same color as the ventral surface in many callidryas and helena and all calcarifer, lemur and spurrelli. In calcarifer and spurrelli these surfaces are orange in life. The light thigh surfaces of lemur range from yellow to yellow-orange in life.

The anterior and posterior surfaces of the thighs of annae, callidryas, most helena, and saltator are heavily suffused with purplish pigment and contrast with the light ventral surface. The color is blue-purple to lavender in live annae, helena and saltator. In calcarifer the variation is from lavender to purplish-brown.

**Upper Lip:** The upper lip has the same color as the side of head in all Costa Rican species except lemur. In the latter form the upper lip is marked by a white line. These differences are evident in both living and preserved specimens.

**Lower Eyelid Reticulation:** The surface of the lower eyelid is marked with a reticulum of gold lines on a black background in all species except calcarifer and lemur. In the latter two species the lower eyelid is pale yellowish-white and transparent. These differences are readily seen in living and preserved individuals.

**Iris Color:** The color of the iris of the eye in life is characteristic of each species. The iris is burgundy to ruby red in callidryas, helena, saltator and spurrelli. In annae the iris is yellow to yellow-orange, in calcarifer gray to purplish gray and in lemur silver, purplish gray or pale gold.

**Dorsum:** In life, the dorsal color of the head, body and limbs of annae, callidryas, helena, calcarifer, spurrelli is usually a pale, bright leaf green during the day, when the species is resting. At night some darkening takes place and these forms are a bright dark green. Taylor (1952: 811) noted the remarkable color changes in lemur and these are fully confirmed by our field observations. During the day P. lemur is yellow-chartreuse green and at night red-brown to magenta in dorsal color. P. saltator shows a similar change. At night individuals are red-brown to magenta but change to pale bright green during the day.

In most forms the greens change to blue-purple on preservation, but in lemur and saltator a whitish pigment suffusion masks the purple to a great degree, especially in individuals preserved during daylight hours.

Some indication of obscure transverse markings are present dorsally in annae, callidryas, helena, saltator and spurrelli. These markings appear as light wavy narrow bars in annae, callidryas, helena and spurrelli. They are only occasionally present in all forms, and are extremely rare in annae. P. saltator has a series of dark obscure wavy bars across the dorsum.

In certain forms, one to several large enamel-like white spots are present on the back. The spots may be outlined by black in some individuals. Funkhouser (1957) and Duellman (1963) both use black bordered white spots as a distinguishing characteristic of spurrelli. No white dorsal spots occur in our material of calcarifer or lemur. In all other species, including spurrelli, the white spots may be present or absent in individuals from the same locality. In annae, callidryas and helena the spots may be outlined by black or not. In saltator and spurrelli the white spots, when present, are always outlined with black.
Table 1

Variation in Webbing for Costa Rican *Phyllomedusa*

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Range</th>
<th>Modal Webbing Formula</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hand</td>
<td>I</td>
<td>II</td>
<td>III</td>
</tr>
<tr>
<td>anae</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>1+</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>2,5</td>
<td>3</td>
</tr>
<tr>
<td>spurrelli</td>
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<td>1</td>
<td>1,75</td>
</tr>
<tr>
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</table>

Foot

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Range</th>
<th>Modal Webbing Formula</th>
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<td>Hand</td>
<td>I</td>
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<td>1+</td>
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<td></td>
<td>1+</td>
<td>1</td>
</tr>
<tr>
<td>callidryas</td>
<td>123</td>
<td>2+</td>
<td>2</td>
</tr>
<tr>
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<td></td>
<td>2+</td>
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<tr>
<td></td>
<td></td>
<td>2+</td>
<td>3</td>
</tr>
<tr>
<td>solitator</td>
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<td>2+</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2+</td>
<td>3</td>
</tr>
<tr>
<td>spurrelli</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1,5</td>
<td>2</td>
</tr>
</tbody>
</table>
The variation in webbing is summarized in the accompanying table (Tab. 1). The following system of notation is used:

- A total of 266 specimens were examined as a basis for analysis of variation in webbing.
- Costa Rican Phyllomedusa may be placed into three groups on the basis of webbing characteristics. Phyllomedusa lemur stands alone in lacking finger and toe webs. A second group of forms with moderate amounts of webbing includes P. annae, P. calcarifer, P. callidryas, and P. helenae. P. calcarifer has the most webbing, P. callidryas, P. helenae somewhat less and P. saltator the least, as would be expected on the basis of differences in size. The ranges of variation in annae and saltator overlap the ranges for the other two forms, but the former two species usually may be distinguished by differences in webbing.
- The third group includes P. calcarifer and P. sparrelli, both with extensive webbing on hands and feet. The two species are distinguishable on the basis of webbing, with calcarifer having more webbing than sparrelli, again positively correlated with size differences.
- A series of figures (Figs. 1, 2) illustrate examples of the hands and feet of all species. On the basis of the analysis of variation and differences in relative lengths of phalanges shown in the illustrations, it is obvious that terms such as one-half or three-fourths webbed, as utilized by previous workers, have little objective meaning in descriptions of these frogs.
- MEASUREMENTS. – A summary of measurements for series of sexually mature individuals is presented (Tab. 2). The following system of notation is followed: s8-61,3-75, with the first number indicating the minimum, the second the mean and the last the maximum. Measurements of standard length are in millimeters, other measurements are recorded as percentages of standard length. The most obvious mensurational feature of these forms is the sexual difference in size, with females noticeably larger than males in all species except minimum webbing. Also indicated is the modal webbing formula for each species. Phyllomedusa lemur is omitted from the table since it lacks webbing entirely.
Fig. 2: Characteristics of hand and feet in Costa Rican Phyllomedusa lemur. Head lengths are proportionately longer and tibia lengths shorter in males as compared to females, except in lemur. The features of sexual dimorphism appear to be correlated with the differences in standard length as expressions of allometric growth.

The Systematic Status of Phyllomedusa callidryas and helenae

In the course of the analysis of variation summarized above, it became obvious that the species known from Costa Rica were amply distinguished from one another with the exception of Phyllomedusa callidryas and P. helenae. These forms are essentially similar in characters of webbing, measurements and most features of coloration. In addition, samples intermediate in the diagnostic characteristics presumed to distinguish the nominal species according to Funkhouser (1957) and Duellman (1963) were noted. As a result we have extended our study of these forms to include most of the Middle American material in United States collections.

Phyllomedusa callidryas Cope, 1862, was originally described from Panama. Subsequently it has been reported from Panama, Costa Rica, Nicaragua, British Honduras and the Atlantic lowlands of Mexico and Guatemala (Funkhouser, 1957: 33-34). Funkhouser (1957: 34) proposed a new taxon, Phyllomedusa callidryas taylori, for Mexican, Guatemalan, and British Honduran populations and called the Costa Rican and Panamanian samples Phyllomedusa callidryas callidryas.

Phyllomedusa helenae Cope, 1885, was originally described from Nicaragua and was recorded by later workers from Panama, Costa Rica, Nicaragua and Mexico (Funkhouser, 1957: 32). The principal differences between callidryas and helenae as emphasized by the latest students of the problem (Taylor, 1952; Funkhouser, 1957; Duellman, 1963) are in the details of flank pattern.

Fig. 3: Basic patterns of flank coloration in Phyllomedusa callidryas
In *P. c. callidryas* and *P. c. taylori*, the dark flanks are supposed to be interrupted by a series of vertical light bars, that are not connected to one another at their dorsal tips. According to these authors *P. belenae* has the dorsal tips of the vertical light flank bars connected by a light stripe that separates the dorsal color from the dark field on the flanks. These authors further agreed that the *callidryas* flank pattern is found in two allopatric geographic segments: Atlantic lowlands of Mexico to Honduras (*P. c. taylori*) and lowlands from Nicaragua to Panama (*P. c. callidryas*). *P. belenae* is stated to be found from Mexico to Panama (Funkhouser, 1957) or Caribbean lowlands of Nicaragua and Costa Rica (Duellman, 1963).

Examination of our material indicated that considerably more variation occurred in the nature of the lateral flank pattern than previous authors had realized. Five different basic patterns are recognized in this paper (Fig. 3):

A. All vertical light bars connected at dorsal tips by a light stripe that separates the dark flank field from the dorsal coloration; typical belenae pattern.

B. One to several vertical light bars not connected to others by light stripe.

C. All vertical light bars without dorsal expansion; typical *callidryas* pattern.

D. All vertical light bars connected at dorsal tips by a light stripe that separates the dorsal color from the dark field on the flanks.

E. All vertical light bars with dorsal tips expanded or T-shaped, none connected dorsally to adjacent bars.

F. One to several vertical light bars with dorsal tips expanded or T-shaped, others expanded or T-shaped.

G. All vertical light bars without dorsal expansion nor T-shaped; typical *callidryas* pattern.

All available material of the *callidryas-belenae* group was examined and the character of the flank pattern for both flanks of the 837 individuals tabulated. In all samples studied some individual variation in flank pattern was apparent except in the series of 11 frogs from the outer portion of the Yucatan Peninsula, Mexico. Many individuals conformed to one pattern on one flank and had another pattern on the other. The geographic distribution and percentage frequencies of each of the five pattern categories for 12 pooled populational segments are mapped (Fig. 4). These data indicate that not only is there considerable individual variation within a population, but the geographic pattern exhibits a complex but clinal change in the frequency of flank patterns, as well.

The population samples and number of individuals are as follows:

<table>
<thead>
<tr>
<th>Population</th>
<th>Region</th>
<th>Number of Specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Eastern Mexico</td>
<td>198</td>
</tr>
<tr>
<td>2</td>
<td>Yucatan</td>
<td>11</td>
</tr>
<tr>
<td>3</td>
<td>Guatemala - British Honduras</td>
<td>101</td>
</tr>
<tr>
<td>4</td>
<td>Honduras</td>
<td>8</td>
</tr>
<tr>
<td>5</td>
<td>Eastern Nicaragua</td>
<td>36</td>
</tr>
<tr>
<td>6</td>
<td>Western Nicaragua</td>
<td>124</td>
</tr>
<tr>
<td>7</td>
<td>Northeastern Costa Rica</td>
<td>87</td>
</tr>
<tr>
<td>8</td>
<td>Northwestern Costa Rica</td>
<td>86</td>
</tr>
<tr>
<td>9</td>
<td>Northwestern Panama - Southeastern Costa Rica</td>
<td>20</td>
</tr>
<tr>
<td>10</td>
<td>Golfo Dulce</td>
<td>48</td>
</tr>
<tr>
<td>11</td>
<td>Central Panama</td>
<td>77</td>
</tr>
<tr>
<td>12</td>
<td>Darien, Panama</td>
<td>36</td>
</tr>
</tbody>
</table>

The flank pattern of samples from eastern Mexico, the Yucatan Peninsula, Guatemala and British Honduras (populations 1-3) are essentially similar, with relatively low frequencies of BC and AB individuals. All of these populations have a very high frequency (86-100%) of the typical *callidryas* flank coloration (C). The race described as *P. c. callidryas* by Funkhouser (1957: 34) from Mexico: Veracruz: Tierra Colorado (Holotype CM 100166) is from this region. In the small sample from Honduras the C pattern predominates with slightly higher values for BC and AB patterns than to the north. All Honduran examples are from the northwestern area of the country and are separated by an approximate 325 kilometer gap in records between Lancetilla, Departamento de Yoro, and the northernmost Nicaraguan locality at Mamas, Departamento de Zelaya. Material from southern part of this gap, over the eastern Nicaraguan lowlands (population 1) has a high frequency (76%) of typical belenae patterns (A). Nevertheless, many individuals exhibit other variants (24%). The highest proportion (86%) of flank pattern A is found in the northeastern Costa Rica sample (population 7). Most of the individuals from eastern Nicaragua and adjacent Costa Rica would be considered belenae on the basis of flank pattern. The holotype of *P. belenae* (US 13737) is from Nicaragua, probably from somewhere along the Rio San Juan, and has an A pattern on both flanks.

From southeastern Costa Rica and adjacent Panama to the Darien region of eastern Panama a gradual decrease in the belenae pattern (A) occurs. Population 9 has 21% A and 55% AB; population 11, 37% A and 35% B; population 12, 29% A and 17% AB. As the belenae-like individuals decrease in number the frequencies for callidryas patterns increase. Population 9, has 34% of pattern C; population 11, 19%; population 12, 53%. It seems evident that a substantial gene flow exists between populations of these frogs along the Caribbean coast of Costa Rica and Panama. The gradual change from typical belenae (population 7) to populations intermediate between *belenae* and *callidryas* (populations 11-12) suggests that only a single species is involved.

Fig. 4: Distributional records and variation in frequencies of basic flank patterns in *Phyllomedusa callidryas*

It should be noted that the holotype of *P. callidryas* (AP 2091, Panama) is from an intermediate population and has a B pattern on the left side and a BC pattern on the right.
Only one population (6) of frogs of this group occurs on the Pacific lowlands of Middle America, where it is known to range in Tropical Moist and Tropical Wet Forests (FOREST, 1964) from San Pablo, Provincia de Chiriqui, Panama, northwest to between San Ramon, Provincia de Alajuela, and Esparza, Provincia de Puntarenas, Costa Rica. This population was regarded as typical P. callidryas by previous workers. Pacific lowland callidryas are ecologically isolated from the Caribbean populations by the towering Cordillera of the Talamanca—Chiriqui axis. To the east the lowland Dry Forest habitats of western Panama may also serve as a barrier to gene exchange with the Central Panamanian population. Members of the Pacific lowland and Golfo Dulce sample agree in every particular with the populations referred to P. c. taylori by FUNKHOUSER (1957) and DUELLMAN (1963). The several characteristics of flank color, dorsal color, finger webbing and length of hind limb utilized by these authors to separate the two nominal races of callidryas exhibit variable distributions in Golfo Dulce area material and will not serve to distinguish it from P. c. taylori. The flank pattern in the Golfo Dulce population is typical (97.9%) of callidryas (C) in almost all specimens. If any gene exchange takes place directly between the Pacific lowland population and the Caribbean lowland form (belenae) it is probably across the low divide in the Cordillera of Tilaran of northwest Costa Rica. Tropical Moist Forest habitats are found along the Pacific slope of the Cordillera and it is possible that callidryas—like populations may be taken further north than the present known limit between Esparza and San Ramon. In any event samples are available from the continental divide near Tilaran, from both Atlantic and Pacific versants (population 8). Frogs from this area were referred to P. callidryas by TAYLOR (1955: 527) but the available material is predominately belenae-like in flank pattern (A). The relatively high frequency of AB (16%) patterns suggests some gene influence by the lowland Pacific form and may indicate that Caribbean and Pacific populations exhibit a variable distribution of flank pattern among the species. The western Nicaraguan sample (6) is extremely variable with relatively low frequencies for flank pattern A (22.9%) and C (6.9%). Most examples are intermediate in pattern between eastern Nicaragua—Costa Rica and the Golfo Dulce populations. Although Phyllomedusa apparently does not occur in the Tropical Dry Forest of Pacific Nicaragua, the western Nicaraguan populations substantiate the picture of the essential variability of flank pattern in the callidryas-belenae group.

In summary: The flank patterns utilized by previous workers to distinguish between callidryas and belenae are subject to considerable individual and populational variation. Populations with a high frequency of belenae pattern (A) are found in eastern Nicaragua and Costa Rica. As populations are sampled in any direction away from this area the frequencies of pattern A decrease and other patterns increase. To the north of the region of greatest frequency of pattern A a considerable range gap, the result of lack of collecting, exists in eastern Honduras. Western Honduranan, Guatemalan, British Honduranan and Mexican samples have very high frequencies of pattern C (82—100%). Populations with intermediate combinations in flank pattern are to be expected when eastern Honduras is adequately sampled. Southward along the Atlantic lowlands there is a definite clinal decrease in the frequency of flank pattern A and an increase in pattern C from southeastern Costa Rica to the Panama-Colombia border. A majority of examples from this area are intermediate in flank pattern between typical belenae (A) and typical callidryas (C). To the west of the Nicaraguan-Costa Rican lowland populations the frequency of intermediate and callidryas patterns increases in western Nicaragua where a population similar to those of central Panama is found. The Pacific lowland samples of Costa Rica and western Panama are predominately flank pattern C and are essentially similar to the Mexico-Honduras Caribbean lowland populations.

The other characteristic of coloration presumed to distinguish between callidryas and belenae also shows individual variation. DUELLMAN (1965) indicates that belenae has the posterior surfaces of the thighs deep blue while callidryas has clear orange thighs. In Caribbean lowland samples of this group most individuals have a blue to purple thigh suffusion. In the Golfo Dulce populations the suffusion is slight or absent and the posterior surface of the thighs yellow-orange. In other areas, particularly eastern Nicaragua and southeast Costa Rica, the thigh colors are variable and do not necessarily correlate with the flank pattern. Generally speaking the greatest amount of purple or blue suffusion of the posterior surface of the thighs is found where flank pattern A is common. Peripheral to this area the thighs have less and less purple pigment and it is usually absent completely in regions where flank pattern C is predominant.

The Caribbean lowland populations with high frequencies of flank pattern A, tend to have the ventral region brightly colored. In the Golfo Dulce area the belly is white in life. In other populations the amount of red or orange of the undersurfaces is reduced peripheral to the eastern Nicaragua—Costa Rica populations (5, 7). Some individuals corresponding to belenae in flank pattern and thigh color may have white venters and individuals with flank patterns B or BC are rather variable, with some red or red-orange and others white in ventral color.

Populations 5 and 7 tend to average larger than callidryas from the Golfo Dulce area. Measurements of individuals from the eastern and western lowlands of Costa Rica are indicated as belenae and callidryas, respectively, in the accompanying table (Table 2). Adult size decreases away from the Nicaragua—Costa Rica lowland area, so that Panamanian (populations 11—13) and northern (populations 1—4) also have smaller sizes and resemble the Golfo Dulce samples in this regard.

On the basis of the available data and the geographic distribution of the principal distinguishing features discussed above, it is apparent that P. callidryas, P. c. taylori and P. belenae represent a single interbreeding species population. The species must be called by its earliest name Phyllomedusa callidryas COPE, 1862.

Phyllomedusa callidryas and the Subspecies Problem

The geographic relationship of the eastern Nicaragua-Costa Rica populations to other populations of P. callidryas conforms to the classical concept of the subspecies (Mayr, 1963). Subspecies, frequently called varieties in the older literature, were originally established during the late 19th century for large geographic segments of a species that differed in some obvious feature from other such segments. In addition since most geographic races were originally described as species, the use of the trinomial saved a familiar species name from synonymy.

Three principal arguments have been advanced to justify the continued use of the subspecies in vertebrate biology:

1) it is a convenient device for recognizing and discussing large geographic segments of the species populations that differ markedly from one another in obvious characteristics;

2) it is a useful device for describing geographic variation;

3) it is an evolutionary significant segment of the species, an incipient species.
It is apparent to most workers, that with the possible exception of 1), the subspecies does not in fact provide these advantages. In terms of evolution a subspecies stands, not as a genetically integrated unit, but as a purely subjective grouping of a cluster of demes, any one of which may be an incipient species. Wilson and Brown (1955) have demolished effectively the concept of the value of the subspecies in studying variation. They cite numerous examples where emphasis on one or two geographically consistent characters (subspecies characters) have completely obfuscated the actual variation pattern (also demonstrated by Gillham, 1956, and Hagegier, 1958). In addition as we hope to have shown above (Fig. 4) there are better ways to analyze and describe populational variation than through arbitrarily grouping all populations into two to several units, or subspecies.

Several workers (Auffenberg, 1955; Mount, 1965) demonstrate the inapplicability of the subspecies concept for adequate variation studies, but apparently feel constrained to arbitrarily group the divergent variation patterns into subspecific categories.

Perhaps a case may be made for continued use of the subspecies as a convenient device for discussing large geographic segments of species as advocated by Inger (1961) and Mayr (1963). However, the continuing tendency of systematists working on well-known groups to recognize smaller and smaller units (demes in many cases) as subspecies, based on smaller and smaller differences, as discussed by Wilson and Brown (1955) and Burt (1954) and advocated by Durkant (1955), leads to the ridiculous situation where a category of convenience has become one of inconvenience. When it is necessary to study samples of fifty specimens and subject their characteristics to detailed statistical analysis before a decision can be made as to which subspecies they belong (see Clark Hubbs, 1952, on Gibbonsia; Schwartz, 1959, on Leocepalus; and Mertens and Wermuth, 1960, on Lucerta as examples) whatever taxonomic utility the subspecies may have had has long since been lost.

Because of these factors and the questionable value of the subspecies concept, we agree with the conclusions of Wilson and Brown (1955) and have refrained from utilizing trinomials in this report. In our opinion the use of the subspecies as a taxonomic category hides more information than it elucidates and should not be used in lieu of an analysis of variation and its evolutionary significance.

Interpretation of geographic variation in Phyllomedusa callidryas suggests that the original population had a wide range in moist lowland situations in Middle America. This population probably had flank pattern C. Subsequently, possibly following isolation of the Golfo Dulcean population from adjacent populations by the final uplift of the Talamanca-Chiriqui range in Pleistocene and the development of dry forest conditions at about the same time in western Central America and Panama, the gene combination responsible for flank pattern A became established in eastern Nicaragua or Costa Rica.

Since that time flank pattern A has come to dominate the populations in eastern Nicaragua and Costa Rica to produce a series of peripheral populations along the northeast lowlands of Middle America, in central and southern Panama and in the Golfo Dulce area where pattern C persists. In Panama, exclusive of the southwest, the populations are intermediate in character between flank patterns A and C. Additional intermediate populations are to be expected from western Honduras.

Species Diagnoses

The seven species of Phyllomedusa found in lower Central America may be distinguished by the following combinations of characteristics.

Phyllomedusa annae: 1) No contrasting pattern of dark and light areas on flanks; 2) No transverse dark bars on dorsal surface of femur; 3) Lower eyelid reticulate; 4) Flank blue to blue-lavender in life; 5) Posterior surface of femur blue to blue-lavender in life; 6) Iris yellow to yellow orange in life; 7) Mean webbing formulae: hand I 2-3 II 1-3-3 III 2-2 IV 2-1-5; 8) Snout rounded to obtuse in profile; 9) Vomerine teeth usually present.

Phyllomedusa calcarifer: 1) A series of dark vertical bars on flanks, contrasting with light ground color; 2) A series of dark transverse bars on dorsal surface of thigh; 3) Lower eyelid not reticulate; 4) Flanks bright orange in life; 5) Posterior surface of thigh orange in life; 6) Iris dark gray; 7) Mean webbing formulae: hand I 2-2+ II 1-2 III 1-2-3 IV 1-2+ V; 8) Snout rounded to obtuse in profile; 9) Vomerine teeth present.

Phyllomedusa callidryas: 1) Flanks with a series of narrow light bars on a dark field; 2) No dark transverse bars on dorsal surface of thigh; 3) Lower eyelid reticulate; 4) Dark field of flanks purple-blue to lavender brown in life; 5) Posterior surface of thigh yellow-orange or suffused with blue in life; 6) Iris dark red; 7) Mean webbing formulae: hand I 2-2+ II 2-3 III 2-2-2 IV 2-1-5; 8) Snout rounded to obtuse in profile; 9) Vomerine teeth present.

Phyllomedusa lemur: 1) No contrasting pattern of light and dark areas on flanks; 2) No transverse dark bars on upper surface of thigh; 3) Lower eyelid not reticulate; 4) Flanks yellow in life; 5) Posterior surface of femur yellow in life; 6) Iris gold to silver in life; 7) No webs on hands or feet; 8) Snout vertical to acute in profile; 9) No vomerine teeth.

Phyllomedusa saltator: 1) No contrasting pattern of light and dark areas on flanks; 2) No transverse dark bars on dorsal surface of thigh; 3) Lower eyelid reticulate; 4) Flank purple in life; 5) Posterior surface of thigh yellow or somewhat suffused with purple; 6) Iris red in life; 7) Mean webbing formulae: hand I 2-3-3 II 2-3 III 2-2-2 IV 3-2 V; 8) Snout obtuse in profile; 9) Vomerine teeth present.

Phyllomedusa spurrelli: 1) No contrasting pattern of light and dark areas on flanks; 2) No transverse dark bars on upper surface of thighs; 3) Lower eyelid reticulate; 4) Flanks orange in life; 5) Posterior surface of thigh orange in life; 6) Iris dark red in life; 7) Mean webbing formulae: hand I 2-2 II 1-2 III 1-2-3 IV 1-5-5 V 1-5-0; 8) Snout vertical to obtuse; 9) Vomerine teeth usually present.

Geographic Distribution

Phyllomedusa annae – Range: Pacific and Atlantic slopes of the Cordilleras de Talamanca, Central and Tilaran of Costa Rica at intermediate elevations;
certain to be found in extreme western Panama. Specimens examined and literature records of unquestionable identity are from the following localities (Fig. 5):

**COSTA RICA:** CARTAGO: Cartago; 2 km. S. of Cartago; Chirripó; Moravia de Chirripó; Tapanti; Tapanti bridge over Rio Grande on S. bank of river; GUANACASTE: Finca Silencio de Tilarán; HEREDIA: Cindona; SAN JOSE: S. margin of Río Maria Aguilar; Ciudad Universitaria; Guadalupe; La Palma; San José; San Pedro de Montes de Oca.

**San Isidro del General:** PANAMA: CANAL ZONE: Barro Colorado Island. 4.5 mi. S. of Rincón de Osa; tapa; Rio Ferruviosa, 4.5 mi. S. of Rincón de Osa; SAN JOSE: 10 mi. S. W. of Santa Rosa; 1.2 km. W. of Siquirres; PUNTARENAS: 3 km. N. W. Buenos Aires; Golfo; 4 km. E. S. E. Palmare Sur; Parrita; Potero Grande; Rio Ferruviosa, 4.5 mi. S. of Rincón de Osa; 13.6 mi. W. of San Ramón; Villa Neily; SAN JOSE: San Isidro del General; 5 and 1.5 km. N. of Rincón de Osa; RIOMARIA: ALTA VERAPAZ: Finch Chama; Finch Samanana; El PETEN: 1 km. S. E. La Libertad; Tikal; Tooocog, 15 km. S. E. La Libertad;IZABEL: 3 km. S. Puerto Barrios; HONDURAS: COLON: Belfate; CORTEZ: Agua Azul, Rio Lino; ATILANTIDA: Tolos Jct; YORO: Lancetilla; MEXICO: CAMPECHE: 7.5 km. W. Escarcega; Mazamoros; Pocaimus, Rio Canalela; Tuxpena Camp; OAXACA: 2 and 2.3 mi. N. of Donají; 2.3 mi. N. of Sarabia; 2 mi. S. Tollocos; 0.5 km. S. Tuxtepec; 0.6 mi. S. of Ubero; 1.6 and 2.0 km. S. Valle Nacional; TABASCO: 6 mi. S. Cárdenas; Teapa; 6, 8, and 15 mi. N. of Teapa; VERA CRUZ: 1.0 and 1.5 mi. E. S. E. of Alvarado; 2.8 mi. S. of Amuleta; 8.4 mi. S. of Caremoco; 10.0 mi. S. of Costazule; Coatalapan; 0.5 km. S. of Encinal; 6.4 mi. S. E. of Huyapan; 1.2 mi. S. of Naranja; 2.0 km. S. of Santiago Tuxela, rd. to Isla; 5.0 mi. S. of Veracruz, rd. to Antón Lizardo; 3.5 km. (by road) W. of Villa Lerdo de Tejada; YUCATAN: Chichén Itzá; 1.5 mi. E. Chichén Itzá; 6.5 mi. S. Chichén Itzá; Culuba, 28 km. E. of Succop; NICARAGUA: JINOTEPE: Jinogena; MANAGUA: Casa Colorada; MASAYA: 22 km. S. Masagua; MATAGALPA: Hacienda La Cumplida; Matagalpa; 19 km. N. Matagalpa; Finca Tepayac, 9 km. E. Matagalpa; ZE LAYA: Cukra; Little Corn Island; Rio Escondido; Rio Grande; Warupac River, Maswas; PANAMA: BOCAS DE TORO: Big Zapastillo Key; CANAL ZONE: Barro Colorado; Camp Chagres; Garío; Madden Preserve; CHIRIQUI: Progreso; San Pablo; COLON: Ashio; DARIEN: Camp Townsend, Camp Creek; nr. mouth of Rio Canalon; Laguna; Subcut: Tucarcuna; PANAMA: South slope Cerro La Campana; Tapia.

**Phylomedusa annae** - Range: Lowlands of northwestern Ecuador through the Colombian Choco, to the Caribbean versant of Panama and Costa Rica. Specimens examined and literature records of unquestionable identity are from the following localities (Fig. 6):

**COLOMBIA:** CHOCO: Rio Arato, Rio Quevedo; Peña Lisa, Condoto; CARTAGO: Rio Claro, Rio La Honda; Finca Tepayac, 9 km. E. Matagalpa; ZELAYA: Cukra; Little Corn Island; Rio Escondido; Rio Grande; Waspuc River, Maswas; PANAMA: BOCAS DE TORO: Big Zapastillo Key; CANAL ZONE: Barro Colorado; Camp Chagres; Garío; Madden Preserve; COLOMBIA: CHOCO: Rio Atrato, Rio Quesado; Peña Lisa, Condoto; COSTA RICA: GUANACASTE: Finca Jenkins-Finca San Bosco de Tilarán; SAN JOSE: S. margin of Río Maria Aguilar; Ciudad Universitaria; Guadalupe; La Palma; San José; San Pedro de Montes de Oca.

**Panama:** MOUNTAIN LOCALITIES: Barro Colorado Island; DARIEN: Camp Townsend, Camp Creek; nr. mouth of Rio Canalon; Laguna; Subcut: Tucarcuna; PANAMA: South slope Cerro La Campana; Tapia.

**Phylomedusa lemur** - Range: Atlantic versant of northern Costa Rica. The type locality (Finca Jenkins—Finca San Bosco de Tilarán) is Atlantic drainage contrary to DUELLMAN (1963: 11). Specimens examined are from the following localities (Fig. 1):

**COSTA RICA:** GUANACASTE: Finca Jenkins—Finca San Bosco de Tilarán; HEREDIA: Finca La Selva.

**Phylomedusa saltator** - Range: Caribbean lowlands from Panama to central Veracruz, Mexico; Pacific lowlands of the Golfo Dulce region of Costa Rica and western Panama. Specimens examined are from the following localities (Fig. 4):

**BRITISH HONDURAS:** CAYO: 3 and 5 mi. N. of Millionario; Cobune Ridge; COSTA RICA: ALAJUELA: Laguna Montes Alegre; 2 mi. N. E. Muelle de Arenal; San Carlos; CARTAGO: Tunnel Camp nr. Peralta; Turrialba; 2 mi. S. W. Turrialba; GUANACASTE: Finca San Bosco; 2 km. E. Tilarán; 4 km. E. N. E. of Tilarán; Finca Silencio de Tilarán; 2.4 mi. from Tilarán toward Arenal; HEREDIA: Puerto Viejo; COSTA RICA: CARTAGO: Cartago; 2 km. S. of Cartago; Chirripó; Moravia de Chirripó; Tapanti; Tapanti bridge over Rio Grande on S. bank of river; GUANACASTE: Finca Silencio de Tilarán; HEREDIA: Cindona; SAN JOSE: S. margin of Río Maria Aguilar; Ciudad Universitaria; Guadalupe; La Palma; San José; San Pedro de Montes de Oca.

The variation and distribution in the tree-frog genus Phylomedusa...
The illustration provides an overview of the geographic distribution and habitat of a species. It includes a map highlighting areas where the species is known to occur. The map is labeled with various regions and states, indicating the species' range. The map is accompanied by a key describing the different symbols used to represent various aspects of the species' distribution.
Variation and distribution in the tree-frog genus Phyllomedusa

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Resume

The frog genus Phyllomedusa is represented in Costa Rica by six species. Analysis of variation in coloration, webbing, and measurements delineates features that distinguish the various forms. The characters of the flank pattern in the nominal species P. callidryas and P. belenae, utilized by previous authors to separate them, are shown to be subject to individual and geographic variation. The two forms represent two of many populations within a single species, P. callidryas. Reasons for not using the term subspecies for geographic segments of callidryas are presented. The diagnostic features and the geographic and ecologic distribution of the Costa Rican species, P. annae, P. calcarifer, P. callidryas, P. lemur, P. saliator and P. spurrelli, based on the entire species ranges, are discussed.

Resumen

El génera de ranas Phyllomedusa está representado en Costa Rica por seis especies. El análisis de variación en coloración, membranas interdigitales y medidas, da los caracteres especiales que distinguen las diferentes formas. Se demuestra que el tipo de coloración de los costados en las especies nominales P. callidryas y P. belenae, empleado por autores anteriores para diferenciarlas, es un carácter propenso y variación individual y geográfica. Las dos formas mencionadas representan dos de las varias poblaciones que constituyen una sola especie: P. callidryas. Se dan las razones para no usar el término «subespecies» en las poblaciones geográficas (geographic segments) de callidryas. Se discuten las características para la diagnosis y la distribución geográfica y ecológica de las formas costarricenses, P. annae, P. calcarifer, P. callidryas, P. lemur, P. saliator y P. spurrelli, basadas en las áreas completas de distribución de las especies.