Nicht einzeln im Buchhandel erhältlich!

Sonderdruck aus

Beiträge zur Neotropischen Fauna
Band V, Heft 2, 1967
Gustav Fischer Verlag · Stuttgart

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

By

Jay M. Savage and W. Ronald Heyer

Department of Biological Sciences, University of Southern California,
Los Angeles, California, U. S. A.

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* Boulenger, 1902; *P. callidryas* Cope, 1862; *P. helenae* Cope, 1885; *P. lemur* Boulenger, 1882; *P. saltator* Taylor, 1955; and *P. spurrelli* Boulenger, 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 Honduranean example regarded as *dacnicolor* by Funkhouser (1957) is *P. callidryas* (US 74506). The population from Costa Rica referred to *P. moreletii* A. Duméril, 1853, 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 *helenae* 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, 1952; Funkhouser, 1957; Duellman, 1963). A fuller analysis of variation in this character in *callidryas* and *helenae* 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-helenae* 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 *helenae* 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,* many *callidryas,* most *helenae,* 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, helenae* and *saltator.* In *callidryas* 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, helenae, 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, helenae, 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, helenae, saltator* and *spurrelli.* These markings appear as light wavy narrow bars in *annae, callidryas, helenae* 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 *helenae* the spots may be outlined by black or not. In *saltator* and *spurrelli* the white spots, when present, are always outlined with black.

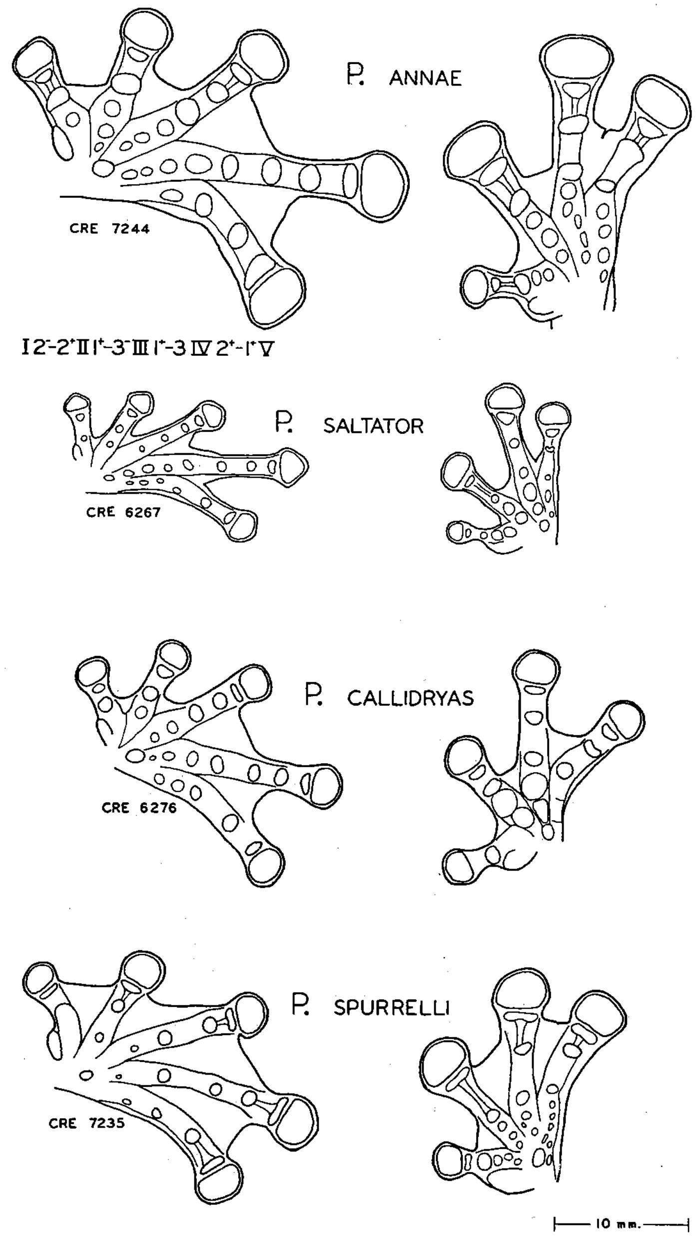

Fig. 1: Characteristics of hands and feet in Costa Rican *Phyllomedusa.* Ventral views, feet at left, hands at right. Webbing formula for illustrated foot of *P. annae* at upper left. CRE numbers indicate specimens at the University of Southern California

Table 1

Variation in Webbing for Costa Rican *Phyllomedusa*

Species	No.	Range								Modal Webbing Formula							
Hand		I	II		III		IV			I	II		III		IV		
annae	41	1,75	2	1^{+}	2^{+}	1,5	1,5			2	2,5	1,5	3^{-}	2	2		
		2^{+}	3	2^{-}	3	2^{+}	2^{+}										
calcarifer	2	2^{-}	2^{+}	1	2	1,5	1,25										
		2		1^{+}	2^{+}	1,7	1,5										
callidryas	123	2^{-}	2	1^{+}	2	2^{-}	1,5			2	2,5	2^{-}	3^{-}	2^{+}	2^{+}		
		3	3	2	3	2,5	2,5										
saltator	3	2^{-}	2,5	1,75	3	2,25	2^{+}			2^{+}	3	2^{-}	3	2,5	2^{+}		
		2,5	3	2		2,5	2,25										
spurrelli	15	1	1,75	0	1,5	0	0			2^{-}	2	1	1,75	1	1		
		2^{-}	2	1^{+}	2^{-}	1,5	1^{+}										
Foot		I	II		III		IV		V	I	II		III		IV		V
annae	41	1^{+}	2^{-}	1	2	1^{+}	2^{+}	1	1^{+}	2	2^{+}	1,5	3	1,5	2,5	2^{+}	1,5
		2	2,5	2	3	2^{-}	3	2,5	2								
calcarifer	2	0	1,5	0	2^{-}	0	2^{-}	2^{-}	1^{+}								
		1^{+}				1		2	1,3								
callidryas	123	2^{-}	2^{-}	1^{+}	2,5	1	2	2^{-}	1	2	2^{+}	2^{-}	3	1,5	2,5	2	1,5
		2^{+}	3^{-}	2	3^{+}	2	3^{+}	3^{-}	2								
saltator	3	2	2^{+}	2^{-}	3	2^{-}	3	3^{-}	1,75	2	2^{+}	2^{-}	3	2	3	3^{-}	2^{-}
		2^{+}	2,25	2	3^{+}	2			2								
spurrelli	15	0	0	0	0	0	1	0	0	1	2^{-}	0	2^{-}	0	1,5	1,5	0
		1,5	2^{-}	1	2	1^{+}	2	1,75	1^{+}								

Table 2 Variation in Measurements for Costa Rican *Phyllomedusa*

Species	N	Standard Length	Head Length	Head Width	Eye to Nostril	Diameter of Eye	Interorbital	Tympanum	Arm	Tibia	Foot
Males											
annae	10	58,0–60,4–67,4	31–33,4–35	30–31,4–33	9– 9,6–10	9– 9,8–10	10–11,2–12	4–5,2–6	56–64,8–72	43–46 –49	36–37,7–40
calcarifer	1	45,8	36	36	11	9	12	8	64	53	36
callidryas	10	41,2–45,0–47,8	34–35,4–37	33–33,9–35	10–10,5–11	10–11,4–12	11–11,8–12	5–6,1–8	64–71 –73	49–50,6–54	33–36 –39
helenae	10	44,8–48,8–51,9	34–35,4–38	33–34,1–37	10–10,7–12	10–11,3–13	10–10,8–12	5–5,5–6	61–66,2–70	50–54,1–56	33–36,2–38
lemur	10	31,6–32,8–34,5	33–34,9–37	31–32,3–34	10–10,8–12	10–11,6–13	10–11,3–12	3–4,1–5	61–64,9–68	51–52,9–56	34–36,6–39
saltator	3	38,6–40,9–42,6	33–34,3–36	29–30,3–31	11–11,3–12	10–11 –12	10–10,7–11	4–4,7–5	63–66,3–68	51–52,3–54	37–37,6–39
spurrelli	10	49,4–52,5–55,5	32–33,9–36	30–31,3–32	10–10,8–12	9–10,5–11	10–11,1–12	5–5,7–6	60–64,2–70	46–48,9–53	36–38,4–40
Females											
annae	4	67,4–72,8–75,4	32–32,5–33	33–33,2–34	9– 9,2–10	9– 9 – 9	11–11,2–12	4–4,8–5	66–69,2–74	45–48 –51	37–39,5–41
calcarifer	1	77,6	34	38	10	8	12	8	74	55	40
callidryas	5	52,9–54,7–58,6	34–34,6–35	32–34 –35	10–10,4–11	10–10,2–11	11–11,6–12	5–5,2–6	69–72,6–76	50–51,8–55	34–35,8–37
helenae	8	61,8–65,5–73,6	33–34 –35	32–33,8–35	10–10,5–11	9– 9,8–10	10–11,4–13	5–5,4–6	67–70,3–75	51–52,8–55	35–37,2–40
lemur	10	32,6–37,4–41,7	33–34 –35	31–31,9–34	10–10,8–12	10–10,7–12	10–11,2–12	3–4 –5	60–68,9–75	49–53,6–56	33–36,8–40
spurrelli	3	60,8–64,0–68,7	32–33,6–35	32–32,7–33	10–10,7–12	9–10 –11	11–11,7–12	5–5,7–6	66–70 –73	51–52 –53	39–40,3–41

Venter: The throat region is white to cream in live *callidryas, helenae, lemur, saltator* and *spurrelli. Phyllomedusa annae* and *calcarifer* have yellow throats in life.

The undersides of the body are white in most *callidryas,* all *lemur* and *saltator.* The belly is white with a distinct yellow to orange cast in *spurrelli.* In all other species, *annae, calcarifer,* and most *helenae,* the venter is a bright orange, apricot or red-orange, in life.

WEBBING. – The degree of webbing on fingers and toes has been emphasized by many authors as a feature for recognition of different species (DUELLMAN 1963; TAYLOR 1952; FUNKHOUSER 1957). While certain forms are readily distinguishable on the basis of these characters, others exhibit considerable intraspecific variability and reduce the reliability for identification. A total of 266 specimens were examined as a basis for analysis of variation in webbing.

Information on webbing was recorded by the use of the following system of notation: I 2–2,5 II 2^{-}–3^{-} III 2^{+}–2^{-} IV 3–3^{-} V. Roman numerals represent fingers or toes; arabic numerals represent the number of phalanges completely or partially free of webbing. A notation of 0 indicates that the web reaches to the base of the finger or toe disk, 1 indicates that the web reaches the base of the terminal phalanx. A superscript of + indicates that the web reaches the proximal margin of the subarticular tubercle, and a – stands for a web that reaches the distal margin of the subarticular tubercle. The position of the web was determined as the point of union with the digit, excluding narrow fleshy fringes on the digits (Fig. 1). In general females have slightly more webbing than males. Larger specimens of a particular sex have slightly more webbing than smaller examples.

The variation in webbing is summarized in the accompanying table (Tab. 1) where the upper arabic figure represents the maximum of webbing, the lower, minimum webbing. Also indicated is the modal webbing formula for each species. *Phyllomedusa lemur* is omitted from the table since it lacks webbing entirely.

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. callidryas, P. helenae* and *P. saltator. P. annae* 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. spurrelli,* both with extensive webbing on hands and feet. The two species are distinguishable on the basis of webbing, with *calcarifer* having more webbing than *spurrelli,* 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: 58–61,5–75, 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 perccentages 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

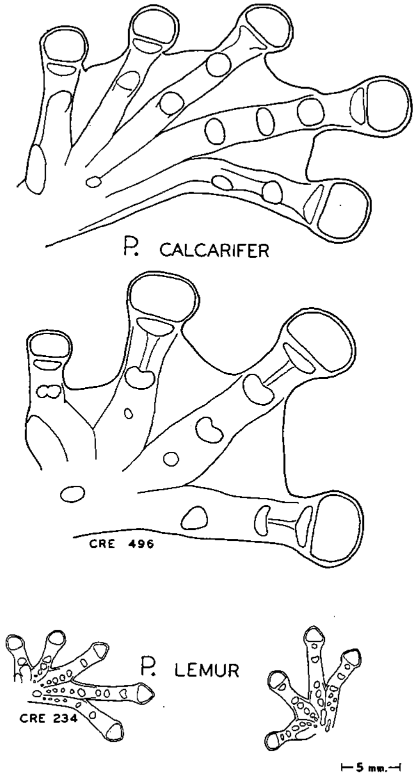

Fig. 2: Characteristics of hand and feet in Costa Rican *Phyllomedusa*

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 Honduranean 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.

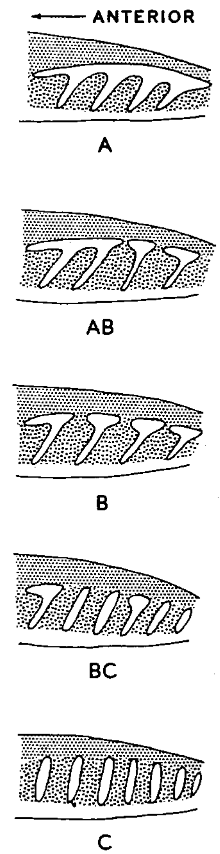

Fig. 3: Basic patterns of flank coloration in *Phyllomedusa callidryas*

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. helenae* 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. helenae* 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 *helenae* pattern.

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

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

BC. One to several vertical light bars without dorsal tips expanded or T-shaped, others expanded or T-shaped.

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

All available material of the *callidryas-helenae* 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:

Population	*Region*	*Number of Specimens*
1	Eastern Mexico	198
2	Yucatan	11
3	Guatemala – British Honduras	101
4	Honduras	8
5	Eastern Nicaragua	38
6	Western Nicaragua	124
7	Northeastern Costa Rica	87
8	Northwestern Costa Rica	86
9	Northwestern Panama – Southeastern Costa Rica	20
10	Golfo Dulce	48
11	Central Panama	77
12	Darien, Panama	36
		837

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. taylori* 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 Honduranean 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 Nicaragua locality at Masawas, Departamento de Zelaya. Material from south of this gap, over the eastern Nicaraguan lowlands (population 5) has a high frequency (76 %) of typical *helenae* patterns (A). Nevertheless many individuals exhibit other variants (24 %). The highest proportion (80 %) 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 *helenae* on the basis of flank pattern. The holotype of *P. helenae* (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 *helenae* pattern (A) occurs. Population 9 has 25 % A and 45 % AB; population 11, 2 % A and 34 % B; population 12, 1 % A and 17 % AB. As the *helenae*-like individuals decrease in number the frequencies for *callidryas* patterns increase. Population 9, has 0 % of pattern C; population 11, 19 %; population 12, 52 %. 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 *helenae* (population 7) to populations intermediate between *helenae* and *callidryas* (populations 11–12) suggests that only a single species is involved.

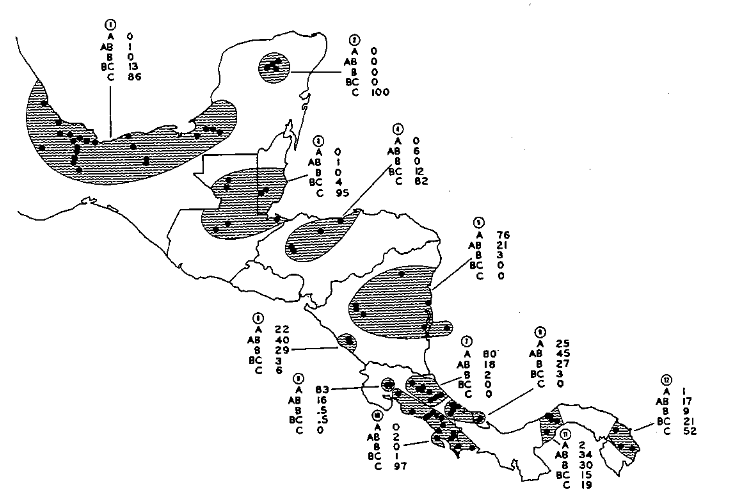

Fig. 4: Distributional records and variation in frequencies of basic flank patterns in *Phyllomedusa callidryas*

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 (10) 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 (Holdridge, 1964) from San Pablo, Provincia de Chiriqui, Panama, northwest to between San Ramon, Provincia de Alajuela, and Esparta, 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 Cordilleras 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 or 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 individual variation 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 %) of *callidryas* (C) in almost all specimens.

If any gene exchange takes place directly between the Pacific lowland population and the Caribbean lowland form *(helenae)* it is probably across the low divide in the Cordillera de 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 Esparta 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 *helenae*-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 are in contact.

The western Nicaraguan sample (6) is extremely variable with relatively low frequencies for flank pattern A (22 %) and C (6 %). 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-helenae* group.

In summary: The flank patterns utilized by previous workers to distinguish between *callidryas* and *helenae* are subject to considerable individual and populational variation. Populations with a high frequency of *helenae* 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 Honduranean, Guatemalan, British Honduranean 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 *helenae* (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 *helenae* also shows individual variation. Duellman (1963) indicates that *helenae* 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 Dulcean populations the suffusion is slight or absent and the posterior surface of the thighs yellow-orange. In other areas, particularly western 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 *helenae* 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 *helenae* and *callidryas*, respectively, in the accompanying table (Table 2). Adult size decreases away from the Nicaragua – Costa Rica lowland area, so that Panamanian (populations 11–12) 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. helenae* 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 (1953) 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 HAGMEIER, 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 (1953) and BURT (1954) and advocated by DURRANT (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 *Leiocephalus;* and MERTENS and WERMUTH, 1960, on *Lacerta* 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 (1953) 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 2–2,5 II 1,5–3^- III 2–2 IV; foot I 2–2^+ II 1,5–3 III 1,5–2,5 IV 2^+–1,5 V; 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 1,5–1,5 IV; foot I 1–1,5 II 0–2 III 0,5–2^- IV 2^-–1^+ 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 2–2,5 II 2^-–3^- III 2^+–2^+ IV; foot I 2–2^+ II 2^-–3 III 1,5–2,5 IV 2–1,5 V; 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 flank; 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 II 2^-–3 III 2,5–2^+ IV; foot I 2–2^+ II 2^-–3 III 2–3 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 1–1,75 III 1–1 IV; foot I 1–2^- II 0–2^- III 0–1,5 IV 1,5–0 V; 8) Snout vertical to obtuse; 9) Vomerine teeth 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; Tapantí; Tapantí bridge over Río Grande on S. bank of river; GUANACASTE: Finca Silencio de Tilaràn; HEREDIA: Cinchona; SAN JOSE: S. margin of Río Maria Aguilar; Ciudad Universitaria; Guadalupe; La Palma; San José; San Pedro de Montes de Oca.

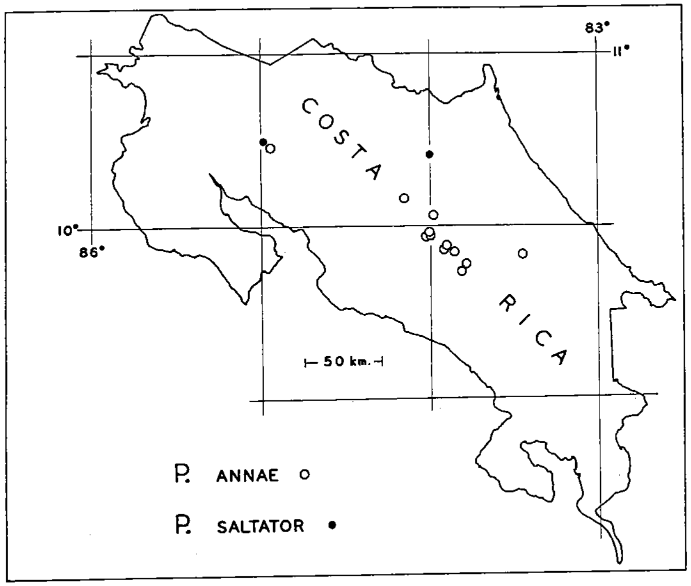

Fig. 5: Distribution of *Phyllomedusa annae* and *P. saltador*

Phyllomedusa calcarifer – 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: Río Atrato, Río Quesado; Peña Lisa, Condoto; *COSTA RICA:* HEREDIA: Finca La Selva; *ECUADOR:* ESMERALDAS: Río Durango; *PANAMA:* CANAL ZONE: Barro Colorado Island; DARIEN: Laguna.

Phyllomedusa callidryas – 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; Cohune 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; 4.2 km. W. Puerto Viejo; LIMON: Batán; confluence of Rios Lari and Dipari about 13 mi. S. W. of Amubre; La Lola; Pandora; Puerto Viejo; Suretka; El Tigre, 9 km. S. W. of Siquirres; PUNTARENAS: 3 km. N. W. Buenos Aires; Golfito; 4 km. E. S. E. Palmar Sur; Parrita; Potrero Grande; Río Ferruviosa, 4.5 mi. S. of Rincón de Osa; 13.6 mi. W. of San Ramón; Villa Neilly; SAN JOSE: San Isidro del General; .5 and 1.5 km. N. E. Alfombra; *GUATEMALA:* ALTA VERAPAZ: Finca Chama; Finca Samanzana; EL PETEN: 3 km. S. E. La Libertad; Tikal; Toocog, 15 km. S. E. La Libertad; IZABEL: 8 km. S. Puerto Barrios; *HONDURAS:* COLON: Belfate; CORTEZ: Agua Azul, Río Lindo; ATILANTIDA: Toloa Jct; YORO: Lancetilla; *MEXICO:* CAMPECHE: 7.5 km. W. Escarcega; Matamoros; Pocaitun, Río Candelaria; Tuxpena Camp; OAXACA: 2 and 2.3 mi. N. of Donaji; 2.3 mi. N. of Sarabia; 2 mi. S. Tollocito; 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 13 mi. N. of Teapa; VERACRUZ: 1.0 and 1.5 mi. E. S. E. of Alvarado; 2.8 mi. S. of Aquilera; 6.4 mi. S. of Catemaco; 5.0 mi. S. W. of Coatzocoalcos; Cuatotalapan; 0.5 km. S. of Encinal; 6.4 mi. S. E. of Hueyapan; 1.2 mi. S. of Naranja; 2.0 km. S. of Santiago Tuxtla, 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 Sucopo; *NICARAGUA:* JINOTEGA: Jinotega; MANAGUA: Casa Colorada; MASAYA: 22 km. S. Managua; MATAGALPA: Hacienda La Cumplida; Matagalpa; 19 km. N. Matagalpa; Finca Tepayac, 9 km. E. Matagalpa; ZELAYA: Cukra; Little Corn Island; Río Escondido; Río Grande; Waspuc River, Masawas; *PANAMA:* BOCAS DE TORO: Big Zapatillo Key; CANAL ZONE: Barro Colorado; Camp Chagres; Gatún; Madden Preserve; CHIRIQUI: Progreso; San Pablo; COLON: Aschiote; DARIEN: Camp Townsend, Camp Creek; nr. mouth of Río Canclon; Laguna; Subcutí; Tacarcuna; PANAMA: South slope Cerro La Campana; Tapia.

Phyllomedusa lemur – Range: Intermediate elevations on both slopes of the Cordilleras de Talamanca, Central and Tilarán of Costa Rica; extending into Panama. Specimens examined and literature records of unquestionable identity are from the following localities (Fig. 6):

COSTA RICA: ALAJUELA: Cinchona; 3 mi. S. Ciudad Quesada; CARTAGO: Moravia de Chirripó; bridge over Río Grande at Tapantí; road from Turrialba to Peralta at Río Chitaria; El Silencio de Sitio Mata, La Suiza; Tapantí; HEREDIA: Cariblanco; LIMON: El Tigre, 9 km. S. W. of Siquirres; confluence of Rios Lari and Dipari, 13 mi. S. W. of Amubre; PUNTARENAS: 2½ mi. E. Monteverde; SAN JOSE: confluence of Río Claro and Río La Hondura; 0.7 mi. W. La Hondura; La Palma; 0.5 and 0.9 mi. S. La Palma; *PANAMA:* PANAMA: South slope Cerro La Campana.

Phyllomedusa saltator – 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. 5):

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

Phyllomedusa spurrelli – Range: Lowlands of the Colombian Choco; Barro Colorado Island, Panama; and the Golfo Dulce region of Costa Rica. Specimens examined and literature records of unquestionable identity are from the following localities (Fig. 6):

COLOMBIA: CHOCO: Peña Lisa, Condoto; *COSTA RICA:* PUNTARENAS: Rincón de Osa; Río Ferruviosa, 4.5 mi. S. of Rincón de Osa; SAN JOSE: 10 mi. S. W. San Isidro del General; *PANAMA:* CANAL ZONE: Barro Colorado Island.

Localities where species have been collected sympatrically are as follows: COSTA RICA: GUANACASTE; Finca Silencio de Tilarán, 780 m, *annae – callidryas;* COSTA RICA: SAN JOSE; La Palma, 1500 m, *annae – lemur;* COSTA RICA: HEREDIA; Finca La Selva, nr. Puerto Viejo, 100 m, *calcarifer – callidryas – saltator;* COLOMBIA: CHOCO; Peña Lisa, Condoto, 90 m, *calcarifer – spurrelli;* COSTA RICA: LIMON; confluence of Ríos Lari and Dipari about 13 mi. S. W. of Amubre, 800 m, El Tigre, 9 km S. W. of Siquirres, 680 m, *callidryas – lemur;* COSTA RICA: GUANACASTE; Finca Jenkins (above Finca San Bosco) de Tilarán, 700 m, *callidryas – saltator;* COSTA RICA: PUNTARENAS; Rio Ferruviosa, 4.5 mi. S. of Rincon de Osa, 20 m, *callidryas – spurrelli.*

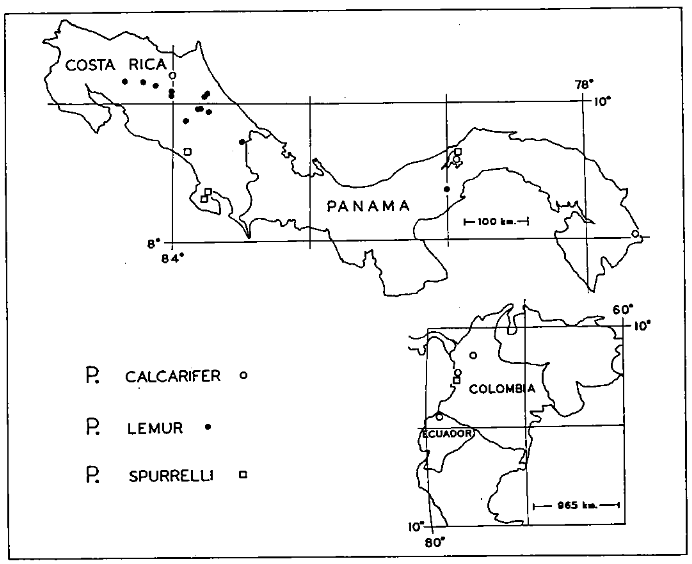

Fig. 6: Distribution of *Phyllomedusa calcarifer, P. lemur* and *P. spurrelli*

Ecologic distribution

In the following discussion, principal bioclimates and vegetational associations are denoted after the model of Holdridge (1964). The species of the genus in Costa Rica are found in areas with mean annual biotemperatures greater than 18° C and having precipitation in excess of 1000 mm. The species are restricted to Tropical and Subtropical life zones and humid and perhumid bioclimates.

Of the seven species, one, *P. calcarifer,* is known only from the Tropical belt, two, *P. annae* and *P. lemur,* are restricted to the Subtropical zone, and the remaider occur in both life zones. None occur above the frost line. *P. annae* is distributed from 780–1500 m in Subtropical Moist, Wet and Rainforest bioclimates. An old specimen (MCZ 8031) from the Museo Nacional de Costa Rica, is listed from Costa Rica: Provincia de Puntarenas: Esparta (208 m). We believe the data to be in error and the specimen probably is from a higher elevation to the east away from this lowland dry forest locale. *P. lemur* occurs from 650–1500 m in Subtropical Wet and Rainforest environments. *P. calcarifer* is known from Tropical Moist and Wet Forest environments, below 150 m in elevation. *P. callidryas* ranges from near sea-level to 970 m. The species is known from Tropical Moist and Wet Forest, Subtropical Wet and Rain Forest. Records from Campeche and the Yucatán Peninsula in Mexico are from Dry Forest habitats. In these situations there is a marked long dry season of at least five months. *P. saltator* is known from two localities, one at 100 m in Tropical Moist Forest and the other at 700 m in Subtropical Rainforest. *P. spurrelli* is found from near sea-level to 900 m in Tropical Moist and Wet Forest communities.

A Key to the Lower Central American Species of Phyllomedusa

1a. Considerable webbing on fingers and toes.
2a. Flanks uniform, no series of contrasting dark and light areas.
3a. Web between second and third fingers originates proximal to penultimate subarticular tubercle of third finger (Fig. 1); web between third and fourth toe originates proximal to penultimate subarticular tubercle (Fig. 1); flank blue to purple blue in life, dark in preservative.
4a. Web between fourth and fifth toes originates distal to proximal subarticular tubercle of fourth toe (Fig. 1); iris yellow to yellow-orange in life; standard length of adult males 58–68 mm.; females 67–84 mm. *annae*
4b. Web between fourth and fifth toes originates at or proximal to proximal subarticular tubercle of fourth toe (Fig. 1); iris red in life; standard length of adult males 38.6–44 mm.; female 52 mm. *saltator*
3b. Web between second and third fingers originates distal to penultimate subarticular tubercle of third finger (Fig. 1); web between third and fourth toes originates distal to penultimate subarticular tubercle of fourth toe (Fig. 1); flanks orange in life, light in preservative. *spurrelli*
2b. Flanks with a contrasting pattern of light and dark areas.
5a. Flanks with a series of light vertical bars on a dark field; no transverse dark bars on upper surface of thigh; lower eyelid reticulate; no toes webbed to base of disks; iris red in life. *callidryas*
5b. Flanks with a series of dark vertical bars on light ground color; a series of transverse dark bars on upper surface of thighs; lower eyelid not reticulate; at least one toe webbed to base of disks; iris gray in life. *calcarifer*
1b. No webbing on fingers or toes (Fig. 2). *lemur*

Acknowledgements

We wish to acknowledge the assistance of the following institutions and individuals for allowing us to examine specimens, and for aid in locating geographic data. Abbreviations in parentheses are as used in the text to indicate the catalogued specimens. Academy of Natural Sciences, Philadelphia (AP), James E. Böhlke and Edward V. Malnate; American Museum of Natural History, Charles M. Bogert and Richard G. Zweifel; British Museum (Natural History), Alice G. C. Grandison; Chicago Natural History Museum (CM), Robert F. Inger and Hymen Marx; Museum of Comparative Zoology (MCZ), Harvard University, Ernest E. Williams; United States National Museum (US), James A. Peters; Universidad de Costa Rica, Jaime Villa R.; University of Kansas Museum of Natural History, William E. Duellman; University of Michigan Museum of Zoology, Donald W. Tinkle and Charles F. Walker.

Fieldwork on this problem was carried out during the senior author's tenure as a John Simon Guggenheim Memorial Fellow during 1963–1964 and while the junior author was supported by a National Science Foundation Summer Fellowship for Teaching Assistants, 1964.

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 characteristics of the flank pattern in the nominal species *P. callidryas* and *P. helenae*, 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. saltator* and *P. spurrelli*, based on the entire species ranges, are discussed.

Resumen

El género 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. helenae*, 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 «subespecie» en las poblaciones geográficas (geographic segments) de *callidryas*. Se discuten las caracteristicas para la diagnosis y la distribución geográfica y ecológica de las formas costaricenses, *P. annae, P. calcarifer, P. callidryas, P. lemur, P. saltator* y *P. spurelli*, basadas en las áreas completas de distribución de las especies.

References

Auffenberg, W. (1955). A reconsideration of the racer, *Coluber constrictor*, in eastern United States. – Tulane Studies in Zoology. **2**, 89–155.

Burt, W. H. (1954). The subspecies category in mammals. – Systematic Zoology. **3**, 99–104.

Duellman, W. E. (1963). A new species of tree frog, genus *Phyllomedusa*, from Costa Rica. – Costa Rica: Revista de Biologia Tropical. **11**, 1–24.

Dunn, E. R. (1931). The amphibians of Barro Colorado Island. – Occasional Papers of the Boston Society of Natural History. **5**, 403–421.

Durrant, S. D. (1955). In defense of the subspecies. – Systematic Zoology. **4**, 186–190.

Funkhouser, A. (1957). A review of the neotropical tree-frogs of the genus *Phyllomedusa*. – Occasional Papers of the Natural History Museum of Stanford University. **5**, 1–90.

Gillham, N. W. (1956). Geographic variation and the subspecies concept in butterflies. – Systematic Zoology. **5**, 110–120.

Hagmeier, E. M. (1958). Inapplicability of the subspecies concept to North American marten. – Systematic Zoology. **7**, 1–7.

Holdridge, L. R. (1964). Life zone ecology, pp. 1–190. – San José, Costa Rica: Tropical Science Center.

Hubbs, Clark (1952). A contribution to the classification of the blennoid fishes of the family Clinidae, with a partial revision of the Eastern Pacific forms. – Stanford Ichthyological Bulletin. **4**, 41–165.

Inger, R. F. (1961). Problems in the application of the subspecies concept in vertebrate taxonomy. In: Vertebrate speciation. Ed. by W. Frank Blair, pp. 262–285. – Austin: University of Texas Press.

Mayr, E. (1963). Animal species and evolution, pp. 1–797. – Cambridge: The Belknap Press of Harvard University Press.

Mertens, R. & Wermuth, H. (1960). Die Amphibien und Reptilien Europas, pp. 1–264. – Frankfurt am Main: W. Kramer & Co.

Mount, R. H. (1965). Variation and systematics of the scincoid lizard, *Eumeces egregius* (Baird). – Bulletin of the Florida State Museum. **9**, 184–213.

Noble, G. K. (1931). The biology of the Amphibia, pp. 1–577. – New York: McGraw-Hill Book Co.

Schwartz, A. (1959). Variation in lizards of the *Leiocephalus cubensis* complex in Cuba and the Isla de Pinos. – Bulletin of the Florida State Muesum. **4**, 97–143.

Taylor, E. H. (1952). The frogs and toads of Costa Rica. – University of Kansas Science Bulletin. **35**, 577–942.

Taylor, E. H. (1955). Additions to the known herpetological fauna of Costa Rica with comments on other species. No. II. – University of Kansas Science Bulletin. **37**, 499–575.

Wilson, E. O. & Brown, W. L., Jr. (1953). The subspecies concept and its taxonomic application. – Systematic Zoology. **2**, 97–111.

Anschrift der Verfasser: W. Ronald Heyer und Jay M. Savage, Dept. Biolog. Sciences Univ. of Southern California, Los Angeles, California 90007 (USA).