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The tree-frogs (Family Hylidae) of Costa Rica: diagnosis and distribution

by

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Since 1959 field parties from the University of Southern California have been engaged in accumulating materials toward a distributional and ecological analysis of the herpetofauna of Costa Rica. A prominent component of this fauna is the family Hylidae, a group of essentially arboreal frogs. These anurans are conspicuous animals freguently encountered in the course of field studies and are represented by 39 species in the republic. Because of these factors and a desire to make this material available to other workers interested in the family on a broader geographic scale, this report is presented in advance of a more detailed study of the ecology and distribution of the frogs of Costa Rica.

The present paper is based primarily on the approximately 2,400 Costa Rican frogs of the family obtained for the University of Southern California. Pertinent data from an additional 800 Central American hylids from other collections examined by us are also included.

Particular emphasis is given in this account to characteristics that aid the biologist in recognition of the species in the field. The most obvious field character for the family, the presence of well-developed adhesive climbing disks on the fingers and toes, is shared with two other groups in Costa Rica, the family Centrolenidæ and the genus *Eleutherodactylus* (family Leptodactylidæ). Frogs of the families Centrolenidæ and Hylidæ are basically arboreal forms, rarely found on the ground. Hylids usually do not descend into the waters of streams, ponds or marshes except during the breeding season. The eggs of all centrolenids are deposited in gelatinous masses on vegetation overhanging streams and only occasionally are adults found in the water. In some hylids, *Phyllomedusa* and some *Hyla,* the eggs are also deposited in masses on vegetation overhang-

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ing ponds or backwaters. Many *Eleutherodactylus* are arboreal but some are terrestrial or riparian in habits at all seasons of the year. All members of this genus lay their eggs out of water in concealed places and undergo direct development, so that they lack a larval stage. A tadpole stage occurs in all Costa Rican species of both hylids and centrolenids.

Technically, the Hylidæ differ from the Centrolenidæ in having the astragalus and calcaneum separate, while these bones are fused into a single element in the Centrolenidæ. Both of these families are distinguished from the Leptodactylidae by possessing an intercalary cartilage between the penultimate and ultimate phalanges of each finger and toe. Costa Rican centrolenids may be separated from hylids, in life, by having forward directed eyes, always a green dorsal ground color, the outer finger and toes with truncate disks and the wall of the abdomen transparent so that blood vessels and viscera are clearly visible. Some hylids have a green dorsum but their eyes are usually directed laterally, the digital disks are always round and the venter is never transparent, although in a few small species some of the viscera may be obscurely visible through an opaque abdominal wall.

Costa Rican *Eleutherodactylus* differ from both hylids and centrolenids in having a well-developed ventral disk demarcated by a fold of skin that encircles the abdomen. Unfortunately this feature is most conspicuous in living material. Most of the Costa Rican species of this genus have truncate disks on the outer fingers and toes as compared to the rounded disks in all of the hylids. A few species of *Eleutherodactylus* have a green dorsal ground color; the eyes are always laterally directed and the venter is never transparent. These last two features will aid in distinguishing members of this genus from centrolenids.

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Abbreviations in parentheses denote catalogued specimens in the text. Other institutions cited include:

Ber. M. - Zoologische Museum, Berlin;
CRE - University of Southern California - Costa Rica Series;
FS - Frederick A. Shannon Collection, now at University of Illinois;
KM - Jagellonian University, Cracow;

LA - Los Angeles County Museum of Natural History;
PM - Muséum d'Histoire Naturelle, Paris;
RCT - Private collection of Richard C. Taylor.

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SPECIES GROUPS

Within the three genera of Hylidae in Costa Rica containing more than single forms, groups of related species may be recognized. In some cases the species clearly belong to groups found elsewhere in the American tropics. Others form groups apparently restricted to Central America. The groups are based upon obvious characteristics and represent ideas of probable relationships based upon our studies of Costa Rican forms. Whether the groups will prove to be of evolutionary significance and justified by a more profound analysis of characteristics on a broader geographic scale must await the completion of revisional studies now under way by William E. Duellman.

Hyla

1. *Miliaria* group - a fleshy fringe along posteroventral border of lower arm and leg; prepollex with a protuberant free tip in both sexes, bearing a sharp spine in mature males; no nuptial asperities; vomerine teeth in curved series; disk on toe I smaller than disk on toe II; considerable finger and toe webbing; ground color lavender-brown; bones colorless: *H. fimbrimembra, H. immensa, H. richardtaylori.*

2. *Faber* group - no fleshy fringes on arms and legs; prepollex with a protuberant free tip in both sexes and a spine in adult males; no nuptial asperities; vomerine teeth in curved series; a frontoparietal foramen; disk on toe I smaller than disk on toe II; considerable webbing between all fingers and toes; ground color brown; bones colorless: *H. rosenbergi.*

3. *Albomarginata* group - no fleshy fringe on arms or legs; prepollex with a protuberant free tip with a spine in males; no nuptial asperities; vomerine teeth in curved to linear series closely bordering posterior margin of choanae; a frontoparietal foramen; disk on toe I smaller than disk on toe II; considerable finger and toe webbing; ground color green in life, yellowish in preservative; bones green: *H. rufitela.*

4. *Leucophyllata* group - no limb fringes; no free prepollical tip; nuptial asperities white or absent in males; vomerine teeth in linear series between choanae, rarely extending posteriorly; a frontoparietal foramen; disk of toe I smaller than disk on toe II; moderate to considerable webbing on fingers and toes II-V; dorsal ground color light brown or yellow; posterior thigh surfaces immaculate yellow-orange or red in life; bones colorless: *H. ebraccata, H. loquax, H. microcephala, H. phlebodes.*

5. *Rubra* group - no limb fringes; no free prepollical tip; white nuptial asperities in males; vomerine teeth in linear patches entirely between choanae; no frontoparietal foramen; disks of toes I-II subequal; no finger webbing, toes II to V with considerable webbing, web reduced and running obliquely between toes I-II; ground color gray or brown; bones green or colorless: *H. boulengeri, H. elaeochroa, H. staufferi.*

6. *Uranochroa* group - no limb fringes; no free protruding prepollical tip; nuptial asperities black or brown in males; vomerine teeth in linear series; a frontoparietal foramen; disk of toe I smaller than disk of toe II; webbing reduced on fingers and toes; ground color variable; bones colorless: *H. debilis, H. pictipes, H. rivularis, H. tica, H. legleri, H. lythrodes, H. rufioculis, H. uranochroa.*

7. *Zeteki* group - no fleshy limb fringes; no protuberant free prepollical tip; white nuptial asperities in males; vomerine teeth in linear patches entirely posterior to choanae; disk on toe I smaller than disk on toe II; reduced webbing on fingers and toes; ground color brown; bones colorless: *H. picadoi, H. zeteki.*

8. Unassigned to group: *H. angustilineata, H. colymba, H. lancasteri, H. pseudopuma.*

Phyllomedusa

1. *Callidryas* group - webs on fingers and toes; vomerine teeth present; quadratojugal meets maxilla: *P. annae, P. calcarifer, P. callidryas, P. saltator, P. spurrelli.*

2. *Lemur* group - no webs on fingers and toes; no vomerine teeth; quadratojugal not meeting maxilla: *P. lemur.*

Smilisca

1. *Baudinii* group - large frontoparietal process; squamosal-maxillary contact: *S. baudinii, S. phaeota.*

2. *Sordida* group - small frontoparietal process; squamosal not meeting maxillary: *S. sila, S. sordida, S. puma.*

SPECIES ACCOUNTS

CHARACTERISTICS: A total of 36 characters were analyzed for a series of each Costa Rican species. Several features that may have significance in other groups were found to exhibit broader intraspecific than interspecific variation and were discarded. For this reason loreal cross-sectional shape, tongue shape, finger disk size, supernumerary tubercle development and subarticular tubercle form on toes are not included in the character summaries.

Most of the features enumerated in the species accounts are standard characters utilized in anuran systematics and their description is self explanatory. The following are features which may cause difficulty in interpretation without comparative material or are defined in a special sense for this report.

Vocal sac - *external:* when inflated definitely expanded externally, when deflated marked by modification in throat integument or pigmentation; *internal:* not markedly protruding when calling, throat not differentiated. Only *Anotheca* among Costa Rican hylids lacks a vocal sac. Individual males of *Smilisca sordida* have external, internal, or intermediate sacs, perhaps indicative of a seasonal development of external sacs.

Vocal slits - Position may be lateral or posterior to tongue or hidden under it; may be parallel or oblique to lower jaw. All adult male treefrogs of Costa Rica have paired symmetrical slits, except *Anotheca coronata,* which lacks them entirely.

Vomerine teeth - *form:* paired and separate patches following curvature of inner posterior margin of choanae (Fig. 3) or in paired linear, usually transverse series (Figs. 1-2); *position:* the patches may lie entirely between the choanae (Fig. 1) or situated at or extending posterior to posterior margin of choanae (Fig. 2). *Phyllomedusa lemur* always lacks vomerine teeth and they may be absent in juvenile or occasional aberrant individuals of other hylids.

Webbing - data for finger (Fig. 6-7) and toe webbing are given after the system of notation described by us (SAVAGE and HEYER, 48), as follows: I 2-2 1/2 II 2^{-}-3^{-} III 2^{+}-2^{-}-IV 3-3^{-}-V. Roman numerals represent fingers and toes; arabic figures indicate the number of phalanges partially or completely free of webbing. The figure 0 indicates that the web reaches the base of a digital disk and 1 that the web reaches the base of the terminal phalanx. A superscript of + indicates that the free margin of 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 location of the web is determined as the point where the outer margin of the web meets the digits. In forms

having a fleshy fringe along the digits the web position is determined as the point of intersection of fringe and web. Deeply emarginated webs are treated in the same manner without reference to the amount of web indentation between digits. The webbing formulae given for each species represent the mode for our sample. The range of variation within a species is approximately 1/2 phalanx on either side of the mode.

Prepollex - in several forms *(H. fimbrimembra, H. immensa, H. richardtaylori, H. rosenbergi* and *H. rufitela)* the prepollex projects from the base of the thumb to form a definite protuberance with the free apex. The prepollex is tipped by a spine that protrudes through the skin in males of these forms. In these frogs the free prepollex is usually clearly discernible in females. The prepollex in other Costa Rican species is closely bound to the base of the thumb and its tip is never protuberant and free of the hand tissue, although its inner lateral margin may be enlarged to produce a broad swelling at the base of the thumb in several forms.

Dorsal texture - differences in the degree of development of warts and tubercles on the back are best observed in living specimens. A number of forms are esentially smooth, others appear weakly granular (at least under magnification) but several *(H. boulengeri, fimbrimembra, immensa, lancasteri, richardtaylori, staufferi, tica, P. venulosa* and *S. sila)* are very rugose, warty or tuberculate as viewed with the unaided eye. In preserved material the condition may need to be verified in the smaller forms with magnification.

Standard length - all references to size refer to adult standard length (distance from snout to cloaca) in millimeters unless otherwise indicated. For purposes of comparison the following adult size categories are recognized: small- 20-30 mm; medium - 31-50 mm; large - 51-80 mm; and very large - 81 mm or larger.

Tibia length - expressed as a percentage of standard length.

Eye color - color of the iris of eyes in life.

Summaries of characteristics for all hylid species, except members of the genus *Phyllomedusa,* are presented below. The variation and distinguishing features for Costa Rican *Phyllomedusa* have been published elsewhere (SAVAGE and HEYER, 48), but diagnoses for these forms are provided and they are included in the key for the sake of completeness. Also included are skeleton synonymies, distributional data and a reference to published illustration of each form. Since *H. pictipes* has not been figured previously a plate (Figs. 17-18) illustrates this species. One of us (S) has seen preserved material of all Costa Rican forms but examples of the following were not available for detailed study and the data for them as presented in the character summaries are based on the literature: *colymba, fimbrimembra, immensa* and *richardtaylori.* One or both of us have collected all Costa Rican species except the latter four forms and *A. coronata, H. rufitela* and *P. calcarifer,* and have seen them in life.

The geographic (Figs. 19-48) and altitudinal (Fig. 49) distribution is plotted for each species. On the distribution maps the dotted line indicates the 1500 m contour.

Anotheca coronata (Stejneger)

1858 *Opisthodelphys ovifera,* Gunther: 117 (misidentification of specimen from Mexico: Veracruz: Córdova).

1882 *Nototrema oviferum,* Boulenger: 418 (description of Gunther's 1858 specimen); 1901, Gunther: 288, pl. 74, Fig. A (misidentification of specimen from Costa Rica: Provincia de San José: Carrillo, and Gunther's 1858 record).

1911 *Gastrotheca coronata,* Stejneger: 287 (Holotype: US 48279, Costa Rica: Provincia de Cartago: Cantón de Paraíso: Palomo, 1064 m).

1939 *Anotheca coronata,* H. M. Smith: 190, pl. 1, Figs. 1-3; pl. 2, Fig. 6 (new genus, material from Mexico: Veracruz: Cuautlapan); 1952, Taylor: 797, Fig. 39; 1954, Taylor: 589, Figs. 1-3 (specimens from Costa Rica; Provincia de Cartago: Moravia de Chirripó; description of egg-eating tadpole); 1960a, Starrett: 32 (misidentification of tadpole); 1961, Robinson (tadpoles from México: Veracruz: Volcán San Martín, 1050 m, agree with Taylor's 1954 account).

DIAGNOSIS: Unique among Costa Rican members of the family in having a series of large light-outlined dark bars, rings or spots on the lower limb surfaces. In addition all adult *Anotheca* have the posterior surface of the head covered by a series of large knob-like cephalic projections, underlain by bone and the males lack vocal slits. No other hylid in Costa Rica has cranial projections, and vocal slits are present in adult males of all other forms.

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout pointed, upper lip semicircular; snout rounded in profile; canthus rostralis sharp; tympanum large, distinct, horizontal diameter equal to 2/3 diameter of eyes; much of skin on top of head fused to underlying bone in adults; edge of skull with bordering row of prominent, bony projections that form obvious external knob-like structures; no vocal sac nor vocal slits in males; vomerine teeth between choanae, transverse; outer finger disks (III, IV) large, 3/4 to equal the diameter of the tympanum; no finger webbing; subarticular tubercles under outer finger (IV) single or double, always single under thumb; nuptial asperities present in male, on inner dorsal portion of thumb, brown in preservative; no ulnar ridge; no projecting prepollex or spine; dorsal texture smooth; belly, area below anus, and on ventral thigh granular, rest of ventral surfaces smooth; toe disk size from inner to outer I<II<III<IV=V; outer toe disks large, about 3/4 size of finger disks; toe webbing formula I 2⁻-2 1/4 II 1 1/3-3 III 1 1/3-3 IV 3⁻-1 1/2 V; large inner metatarsal tubercle, no outer; low but distinct inner tarsal fold, no outer; entire heel surface slightly warty; males to 71 mm; tibia 51; dorsum dark with darker large and small oblong spots, outlined by a narrow light border, slate gray to dark gray in preservative; light hourglass pattern on chest complete or nearly complete, rest of belly uniform, maybe trace of brown in preservative; arms and legs purple-gray barred, or ringed with solid black, light outlined markings, pattern continuing onto ventral surfaces; sole of foot heavily suffused

with melanophores.

DISTRIBUTION: From the Atlantic lowlands of Costa Rica to Veracruz, México, presumably occurring elsewhere along the Caribbean border in Central America.

LOCALITIES: PROV. DE ALAJUELA: 3 km W La Fortuna, 400 m; PROV. DE CARTAGO: Moravia de Chirripó, 1220 m; Valle de Orosi, Palomo, 1200 m; PROV. DE SAN JOSE: Carrillo, 450 m (Fig. 19).

Hyla fimbrimembra Taylor

1948 Taylor: 235, Fig. 2 (Holotype: RCT 764, Costa Rica: Provincia de Heredia: Cantón de Heredia: Isla Bonita, 1600 m); 1952, Taylor: 821, Fig. 45 (redescription).

DIAGNOSIS: Among Costa Rican tree-frogs (family Hylidae) *H. fimbrimembra* differs from all other forms, except *H. immensa* and *H. richardtaylori*, by having well-developed fleshy fringes along the posteroventral margins of the lower arm and leg. From *H. immensa* this species is most readily separated by having reduced webbing so that the ultimate and penultimate phalanges are free of the hand web and at least 1/2 phalanges are free of the toe webs, while in *H. immensa* the web reaches to or almost to the base of the disk on fingers II-III-IV and on at least one side of all toes. The differences between *H. fimbrimembra* and *H. richardtaylori* are minute. In the latter the lips and upper surfaces of the digital disks are black and in the former they are not.

H. fimbrimembra might be confused with *H. rosenbergi* or *H. rufitela*, species that agree with the fringe-limbed form in possessing a protuberant prepollex. *H. rosenbergi* always has a narrow middorsal dark stripe on the head (no mid-dorsal dark line in *H. fimbrimembra*). *H. rufitela* has a green dorsal ground color (yellowish-white in preservative) and bright red digital webs in life (*H. fimbrimembra* is brownish-gray above with no red on webs in life).

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout strongly truncate; vertical snout profile; canthus rostralis rounded; tympanum distinct, diameter a little greater than 1/2 eye; vomerine tooth fasciculi between choanae; outer finger disks (III, IV) moderate, equal to or slightly greater than tympanum; strong serrate fringe along lower arm; free tip of prepollex protruding externally, female lacking spine; scattered warts and tubercles on dorsum; ventral surface granular; inner toe disk (I) smaller than outer disks; diameter of outer toe disks (IV, V) little less than diameter of tympanum; large distally free inner metatarsal tubercle, outer metatarsal tubercle indistinct; outer tarsal segment with serrate fringe; strong, pointed heel tubercles; only known specimen a juvenile female 31 mm; tibia 55; dorsum uniform, brownish gray in life, lavender brown in preservative with dark eyelids and slight median darker mark behind occiput; grayish white spot below eye in preservative; small brown

flecks forming a short diagonal line on side in life; groin with flecks of brown in life, yellow wash in preservative; chin and venter white with strong lavender reticulation on chin in life; upper limb surfaces faintly barred, ashen gray in life; lavender stripe on lower ventral margin of arm and tarsal segment of hind limb; yellow wash on part of anterior surface of thigh in preservative; an indefinite darker line running laterally for a short distance on posterior thigh; tip of heel white in preservative; dorsal surface of disks cream in preservative; white mark around anus with two small black spots above in preservative.

DISTRIBUTION: Known only from the type locality.

LOCALITY: PROV. DE HEREDIA: Volcán Poás, Isla Bonita, 1500 m (Fig. 20).

REMARKS: Four allied nominal species of fringe-limbed hylas are currently recognized from Costa Rica and Nicaragua, each based upon single specimens: *miliaria* Cope (US 14193, Nicaragua) and the three forms discussed in this paper. All four individuals have fringed limbs and a protuberant prepollex. Differences among the animals, when allowance is made for age and sex, are principally in head shape, degree of attachment of the cephalic integument to the cranium and amount of webbing. The characteristics are summarized below for each form:

I. Fingers II-III-IV and toes webbed to, or almost to base of disks			II. Fingers II-III IV and toes with 1 or 2 phalanges free of webs	
A. Snout rounded in dorsal outline		B. Snout blunt in dorsal outline		C. Snout rounded in dorsal outline
1. Skin of upper head co-ossified to cranium	*immensa* 100 mm male			*richardtaylori* 71 mm female
2. Skin of upper head not co-ossified to cranium		*miliaria* 62 mm female (?)	*fimbrimembra* 31 mm juv. female	

The available information suggests several possibilities:

1) Four species are involved;
2) The two individuals, *immensa* and *miliaria,* with extensive webbing represent one species population (differences between them in head shape due to sexual dimorphism and those in degree of cranial and

cephalic coalescence due to age); the two *fimbrimembra* and *richardtaylori* individuals with reduced webbing are a second species (difference between them due to age);

3) Three species, *fimbrimembra-richardtaylori, immensa* and *miliaria* are represented;
4) only a single variable species is involved.

Alternates 1 and 4 are the least plausible; alternate 3 has a higher probability but assumes that head shape and degree of skin-cranial coalescence change ontogenetically; alternate 2 also seems highly probable but requires ontogenetic change in cranial-skin coalescence and assumes that the blunt snout is characteristic of juvenile females in one form *(fimbrimembra-richardtaylori)* and adult males *(immensa-miliaria)* in the other. Until additional material is available and direct comparison of the types of all four forms has been made, it seems best not to upset the current taxonomic arrangement. Whichever of the several possibilities discussed above proves correct, it seems very likely that *fimbrimembra* will prove to be the juvenile of *richardtaylori.*

Hyla immensa Taylor

1952 Taylor: 815, Fig. 42-43 (Holotype: KU 30404, Costa Rica; Provincia de Cartago: Cantón de Turrialba: Instituto Interamericano de Ciencias Agrícolas, 602 m).

DIAGNOSIS: Readily distinguished from all other hylids in the area, except *H. fimbrimembra* and *H. richardtaylori,* by having well-developed fleshy fringes along the posteroventral margin of lower arm and leg. *H. immensa* differs from the latter two species in having extensive hand and foot webs, with the web extending to the base of at least one finger disk, and almost to the base of the disk on other fingers, except I, and to the disk on at least one side of each toe. In *H. fimbrimembra* and *H. richardtaylori* the webbing is less extensive, does not extend to the base of the disk on any finger and the penultimate phalanges on all fingers are free of the web, and the web does not extend to the distal subarticular tubercle on any toe.

The only other species which might be confused with the very large *H. immensa* are *H. rosenbergi* and *H. rufitela* because they share the character of a large protuberant prepollex, with a free spine in males. Coloration provides an obvious basis for discrimination. *H. immensa* has a purplish-brown dorsum obscurely mottled with lighter coloration; *H. rosenbergi* is brown dorsally and always has a narrow mid-dorsal dark stripe on the head; *H. rufitela* has a bright green ground color in life, that changes to yellow-white in preservative.

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout truncate; canthus rostralis moderately sharp; tympanum large, horizontal diameter more then 1/2 diameter of eye; males with vocal slits, behind tongue; vomerine teeth on level with posterior margins of choanae, slightly curved posteriorly; outer

finger disks (III, IV) larger than tympanum; finger webbing formula I 1 1/2-2 II 1-1 III 1-1 IV; subarticular tubercles single; scalloped ridge on outer margin of forearm; free tip of prepollex with projecting spine in male; dorsal and ventral surfaces tuberculate; toe disk size from inner to outer I<II=III=IV=V; outer toe disks (IV, V) slightly smaller than outer finger disks; toe webbing formula I 0-0 II 0-1 III 0-1 IV 1-0 V; inner metatarsal tubercle moderately large, outer small and rounded; inner tarsal fold well defined, irregular fringe on outer tarsus; numerous heel tubercles; males to 100 mm; tibia 52, dorsum slightly mottled, lavender-brown in preservative; sides brown in preservative with some dark markings more or less light edged; legs indefinitely barred on upper surfaces; disks of finger blackish above, webs darker than digits; posterior thigh suffused with melanophores.

DISTRIBUTION: Known only from the type locality.

LOCALITY: PROV. DE CARTAGO: Turrialba, IICA, 602 m (Fig. 20).

Hyla richardtaylori Taylor

1948 *Hyla richardi* Taylor: 233, Fig. 1 (Holotype: RCT 761, Costa Rica: Provincia de Alajuela: Cantón de Grecia: Caribbean slope Volcán Poás, 2 mi. W. Isla Bonita); 1952, Taylor: 819, Fig. 44 (redescription).

1954 *Hyla richardtaylori* Taylor: 624, Fig. 9 (substitute name for *H. richardi* Taylor, preoccupied by *Hyla richardi* Baird, 1854:60).

DIAGNOSIS: Another of the three nominal species of fringe-limbed hylids in Costa Rica. The three forms are distinct from other species in the area in having well-developed fleshy fringes along the posteroventral margin of the lower arm and leg. *H. richardtaylori* has less hand and toe webbing than the fringe-limbed *H. immensa.* In the former the ultimate and penultimate phalanges of all fingers and at least 1 1/2 phalanges of the toes are free of the web, while in the latter the web reaches to or almost to the disk on fingers II-III-IV and all toes. The differences separating *H. richardtaylori* from *H. fimbrimembra,* another fringe-limbed form with reduced webbing, are slight. In the former the lips and upper surfaces of the toe disks are black; in the latter they are not black in color.

H. rosenbergi and *H. rufitela* agree with *H. richardtaylori* in having a protuberant prepollex. *H. richardtaylori* differs from these nonfringe-limbed forms in being essentially uniform brownish dorsally without a mid-dorsal dark stripe or red in coloration (in life).

In *H. rosenbergi* a mid-dorsal dark stripe is present at least on the head and *H. rufitela* has a green dorsal ground color (pale yellowish-white in preservative) and bright red digital webs in life.

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout nearly semicircular; snout obtuse in profile; canthus rostralis distinct, slightly rounded; tym-

panum distinct, about 2/3 eye; vomerine teeth between the choanae; finger disk of outer fingers (III, IV) larger than tympanum; serrate fringe along lower arm; tip of prepollex free projecting externally, female without spine; shagreened dorsal texture; ventral surfaces granular; disk on inner toe (I) smaller than outer disks; disks on outer toes (IV, V) slightly smaller than finger disks; large inner metatarsal tubercle, outer metatarsal tubercle small, rounded, indistinct; serrate fringe along outer lower leg and foot; two or three conical tubercles on heel; standard length in female 71 mm; tibia 52; dorsal pattern uniform with very indistinct darker markings, lavender-brown in preservative; narrow black line on edge of upper lip; upper surface of limbs uniform with faint trace of darker bars; all disks blue-black.

DISTRIBUTION: Known only from the type locality.

LOCALITY: PROV. DE HEREDIA: Volcán Poás, 2 mi W Isla Bonita, 1500 m (Fig. 20).

Hyla rosenbergi

1898 *Hyla rosenbergi* Boulenger: 123, pl. 16 (Syntypes: BM 98. 4. 28. 147-151, Ecuador: Provincia de Esmeraldas; Cachabe); 1925, Breder: 324 (photographs, breeding in Darién, Panamá); 1946, Breder: 409 (additions to 1925 report); 1954, Taylor: 626 (Costa Rica record).

DIAGNOSIS: *H. rosenbergi* is distinctive within the Costa Rica fauna by having the following combination of characteristics: a mid-dorsal dark stripe on head, obscure dark bars along the flanks, a protuberant prepollex, with a spine in males and large size. The species may be readily distinguished from other forms having a protuberant prepollex since it lacks arm and leg fringes (present in *H. fimbrimembra, H. immensa* and *H. richardtaylori)* and by coloration (dorsal ground color green in life, yellowish-white in preservative, webs red in life, and no mid-dorsal or lateral stripe or bars in *H. rufitela).* The dorsum and webs are light brown in *H. rosenbergi.*

The only other species in Costa Rica with barred flanks are two members of the genus *Phyllomedusa, P. calcarifer* and *P. callidryas.* These forms differ from *H. rosenbergi* in having a vertically elliptical pupil and a nearly uniform green dorsum (deep bluish-purple in preservative, versus a horizontally elliptical pupil and brown dorsum in *H. rosenbergi).* The brown flank bars are narrow, obscure and wavy in *H. rosenbergi;* dark purple on a light field in *P. calcarifer;* and cream on a purplish field in *P. callidryas.*

SUMMARY OF CHARACTERISTICS: Snout subovoid to almost pointed in dorsal outline; snout rounded in profile; canthus rostralis rounded; tympanum distinct, horizontal diameter 2/3-3/4 diameter of eye; male vocal sac internal, single; male vocal slits elongate, not hidden by tongue, almost parallel to jaw; vomerine teeth in arched series, extending from between the choanae medially to posterior to the choanae laterally; outer finger disks (III, IV) large, smaller

than tympanum, 3/4 to almost equal to tympanum; finger webbing formula I 2-2+ II 0-2⁻- III 1 1/2-1 IV; subarticular tubercles single to double under outer finger (IV), always single under thumb; male without nuptial asperities; ulnar fold moderately to distinctly developed; free tip of prepollex protuberant, spine present in males, absent in females; dorsal surface smooth-granular to very granular; chin smooth-granular; belly and ventral surface of thigh granular; toe disk size from inner to outer, I<II<III=IV=V or I<II=III=IV=V; toe disks large, equal to or just smaller than pad of finger disk; toe webbing formula I 0-1 1/3 II 0-1 1/2 III 0-1 1/2 IV 1 2/3-0 V; inner metatarsal tubercle large, outer metatarsal tubercle present or absent; distinct inner tarsal fold; series of low warts on outer tarsal area; heel with non-distinct raised wart to clearly distinct flap; males and females to 75 mm; tibia 59; dorsal pattern almost uniform to reticulated, buff in life, tan to brown in preservative; black mid-dorsal pin stripe from tip of snout to crown and usually to shoulder region; dorsal surface of arm uniform or with light bars, upper thigh with cross reticulations at times approaching stripes; rest of leg with broad cross bands; posterior surface of thigh suffused with melanophores, tinged with salmon in life; sole of foot suffused with melanophores; iris dull white.

DISTRIBUTION: From southwestern Costa Rica to northwestern Ecuador.

LOCALITIES: PROV. DE PUNTARENAS: Golfito, 10 m; Palmar, 20 m; Rincón de Osa, 10 m; Rincón, by Río Rincón, 20 m; Rincón, Camp Seattle, 50 m; 7.2 km S. of Rincón at Río Ferruviosa, 30 m; 1.1, 7.1, and 21.8 km by road NW of Villa Neily, 60-70 m. (Fig. 21).

REMARKS: A close ally of *rosenbergi, H. crepitans* occurs in western Panamá and may range into Costa Rica. The latter form is immediately distinguished from *rosenbergi* by its reduced finger webbing (no web between thumb and finger II and at least two phalanges on each finger free of web in *H. crepitans* versus considerable webbing between thumb and finger II and less than two phalanges free of web on fingers II-III-IV in *rosenbergi*).

Hyla rufitela Fouquette

1886 *Hypsiboas albomarginata,* Cope: 273 (Nicaragua).
1901 *Hyla albomarginata,* Gunther: 284 (records, description); 1952, Taylor: 893 (redescription).
1961 *Hyla rufitela* Fouquette: 595 (Holotype: FM 13453, Panamá: Canal Zone: Barro Colorado Island).

DIAGNOSIS: This species is unlikely to be confused with any other Central American form in life since it is the only form with a green dorsal ground color, green bones and the webs of fingers and toes bright red in color.

In preservative *H. rufitela* is pale yellow dorsally with dark punctations and has a protuberant prepollex with a spine in males and the vomerine tooth

patches curved or bordering posterior margin of choanae (Fig. 3). The only species with which preserved specimens are likely to be confused are *H. colymba* or *H. rosenbergi.* The former has dorsolateral light stripes, a circular mental gland and the disks on fingers and toes barely wider than digits (no stripes or mental glands and disks much wider than digits in *H. rufitela);* the latter has narrow lateral dark bars and a mid-dorsal dark stripe from snout onto back (no lateral bars or dorsal stripe in *H. rufitela*).

SUMMARY OF CHARACTERISTICS: Snout rounded to nearly semicircular in dorsal outline; snout rounded in profile; canthus rostralis rounded to sharp; tympanum moderately distinct, horizontal diameter 2/5-1/2 diameter of eye; male vocal sac internal, single; male vocal slits almost entirely hidden by tongue, elongate, parallel to jaw; vomerine tooth patches border inner margin of choanae, in straight or curved series; outer finger disks (III, IV) large, equal to or 1 1/4 times tympanum; finger webbing formula I 3^{+}-3 II 1 1/2-2^{+} III 2^{-}-1 1/4 IV; subarticular tubercles single under all fingers; no nuptial asperities on male thumb; ulnar ridge distinct to not apparent; projecting free tip of prepollex in male with spine, rudimentary in female, spine lacking; dorsal texture smooth; chin, chest, belly, ventral surface of thigh granular; ventral surface of arm smooth-granular; ventral surface of tibia smooth; toe disk size from inner to outer I<II<III=IV=V; or I<II=III=IV=V; large oblong inner metatarsal tubercle, outer metatarsal tubercle not apparent; no inner or outer tarsal folds; distinct heel flap; males to 51 mm, females 53 mm; tibia 51; dorsum with randomly scattered melanophores, green in life, cream with brown flecks in preservative; heavily flecked with large spots of white and black above in life; occasionally an ivory line from tip of snout over eye onto flank in life; no distinct pattern on dorsal limb surfaces, only scattered melanophores; abdomen and chest white in life and preservative; webs of hands and feet red, disks yellow in life; posterior surface of thigh without melanophores, red-orange to red in life; sole of foot without melanophores; iris yellow-gray.

DISTRIBUTION: From the Atlantic lowlands of Nicaragua and Costa Rica to the Chocó of Colombia.

LOCALITIES: PROV. DE ALAJUELA: Cantón San Carlos; PROV. DE HEREDIA: 4 km E Puerto Viejo, 100 m; PROV. DE LIMON: La Castilla, 10-20 m; 3.2 km S. mouth Río Tortuguero, 5-10 m (Fig. 22)

Hyla ebraccata Cope

1874 *Hyla ebraccata* Cope: 69 (Holotype: apparently lost, Nicaragua) 1952, Taylor: 885, Fig. 886 (redescription); 1966, Duellman: 267 (synonymizes *weyerae).*

1931b *Hyla leucophyllata,* Dunn: 406. (apparently regards *ebraccata* as synonym).

1954 *Hyla weyerae* Taylor: 633 (Holotype: KU 34850, Costa Rica: Provincia de Puntarenas: Cantón de Osa: Las Esquinas).

DIAGNOSIS: Typical examples of these small (males to 27 mm) to medium sized frogs (females to 35 mm) cannot be confused with any other Central American species. In most individuals the posterior surface of the thigh is uniform yellow-orange (yellow in preservative) a large suborbital light spot is present, a dark lateral band extends from the tympanum usually to mid-body and the upper surfaces are marked by bold dark brown blotches, usually outlined by white or yellow on a lighter brown ground color (Fig. 12). In the latter cases the dorsum is marked by a large dark hour-glass shaped blotch that extends from between the eyes to the sacrum. Some specimens are nearly uniform dorsally, have a dorsolateral light stripe and may be mistaken for *H. microcephala* or *H. phlebodes*. *H. ebraccata* differs from these forms in the other features mentioned above except thigh coloration.

SUMMARY OF CHARACTERISTICS: Snout rounded to rounded truncate in dorsal outline; snout rounded in profile; canthus rostralis sharp; tympanum indistinct, horizontal diameter 1/4-2/5 eye diameter; male vocal sac external, single; male vocal slits not entirely hidden by tongue, oblique to jaw; vomerine teeth between choanae, transverse; outer finger disks (III, IV) large, 1 1/4-2 times tympanum; finger webbing formula I 2-3 II 1^{+}-2^{+} III 2^{+}-2^{-} IV; subarticular tubercles double under outer finger (IV), single under thumb (I); males lacking nuptial asperities on thumb; low series of warts along ulnus present or absent; tip of prepollex not protruding; dorsum smooth; belly and lower surface of thigh granular, rest of undersides smooth; toe disk size from inner to outer I<II=III=IV−V or I<II<III=IV=V; outer toe disks (IV, V) equal to or slightly smaller than outer finger disks; toe webbing formula I 1-2^{-} II 1/2-1 1/2 III 1-2 IV 2^{+}-1 V; large oblong inner metatarsal tubercle; outer metatarsal tubercle small, round; distinct inner tarsal fold; no outer tarsal fold; heel smooth to warty; males to 27 mm, females to 35 mm; tibia 55; dorsum uniform or with contrasting pattern of spots and blotches, yellow with brown spots (if present) in life, cream, brown, and/or chocolate in preservative; face and dark lateral band brown in life; light suborbital spot yellow in life; throat yellow in life; remainder of venter yellow-flesh or bright clear yellow in life; dorsal arm pattern as back; upper femur with narrow line of back color along length or absent, rest of upper leg patterned as back; no melanophores on posterior thigh, orange yellow in life; usually no melanophores on sole of foot, occasional specimens with a few scattered melanophores, orange in life; iris dull copper or golden brown.

DISTRIBUTION: Caribbean lowlands from southern Mexico to Colombia; also Pacific lowlands of Costa Rica and western Panamá.

LOCALITIES: PROV. DE ALAJUELA: Las Playuelas, 75 m; PROV. DE CARTAGO: Moravia de Chirripó, 1116 m; 2 km S Paraíso, 1320 m; Turrialba, IICA, 604 m; Turrialba, 3 km from IICA on Pavones road, PROV. DE GUANACASTE: Arenal, laguna, 509 m; Finca San Bosco de Tilarán, laguna de

Finca Jenkins, 700 m; Finca Silencio de Tilarán, laguna, 780 m; 3.8 km ENE Tilarán, 620 m; PROV. DE HEREDIA: Finca La Selva, 100 m; PROV. DE LIMON: Bambú, 60 m; Guácimo, 60 m; PROV. DE PUNTARENAS: 1.6 km S Agua Buena, 1150 m; 3.2 km NE Boca del Barranca, 100 m; Rincón de Osa, Camp Seattle; Río Ferruviosa, 7.2 km S. Rincón de Osa; 7.1 NW Villa Neily, 60 m (Fig. 23).

Hyla loquax Gaige and Stuart

1934 *Hyla loquax* Gaige and Stuart: 1 (Holotype: UM 75446, Guatemala: Departamento de El Petén: N La Libertad: Ixpuc Aguada); 1952, Taylor: 868, Fig. 58 (redescription, Costa Rica records, places *stadelmani* in synonymy); 1966, Duellman: 271 (synonymizes *stadelmani* and *axillamembrana).*

1936 *Hyla stadelmani* K. P. Schmidt (Holotype: MCZ 21310, Honduras: Departamento de Yoro: Valle de Subirana).

1955 *Hyla axillamembrana* Shannon and Werler: 383, Fig. 6 (Holotype: FS 4083, México: Veracruz: on San Andreas Tuxtla - Minatitlán road, 5 mi. S Lake Catemaco).

DIAGNOSIS: Unmistakable in life, by being the only tree-frog in lower Central America having a bright yellow venter and bright red posterior thigh surfaces. The only other species in which some individuals have red *(H. rufitela* or coral-orange *P. callidryas)* posterior thigh surfaces have a green dorsal ground color in life.

In preservative *H. loquax* may retain the bright ventral and thigh color for some time but otherwise lacks the obvious color characteristics typical of other species: dark thigh bars, lateral or dorsal light stripes, dark mid-dorsal stripe, light suborbital spot, lateral dark band, spotted or reticulated groin, dark spotting or heavy suffusion on venter, spotted posterior thigh surface and bold dorsal pattern. The species also lacks arm and limb fringes, and protuberant prepollex and the vomerine tooth patches are not curved and lie between the choanae.

H. loquax is a medium-sized species (males to 46 mm, females to 48 mm) as compared to its close allies the small, less than 30 mm, *H. microcephala* and *H. phlebodes.* Juvenile *H. loquax* occasionally may be confused with individuals of the latter two species that lack distinct narrow dark dorsal markings. *H. microcephala* always has a dark dorsolateral stripe (never present in *H. loquax)* and *H. phlebodes* usually has a similar dorsolateral stripe, a dark interorbital stripe, and a dark canthal stripe (no dark dorsolateral stripe, interorbital stripe, or canthal stripe in *H. loquax).*

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout rounded to almost semicircular; snout rounded in profile; canthus rostralis rounded, approaching angulate; tympanum distinct, horizontal diameter 1/2 to 4/5 eye diameter; male vocal sac external, single; male vocal slits not entirely hidden by tongue, oblique to jaw; vomerine teeth between choanae, transverse; outer finger

disks (III, IV) 1 to 1 1/4 times as large as tympanum; finger webbing formula I 2-3 II 1+-2 III 2⁻-1+ IV; subarticular tubercles single to double under outer finger (IV), always single under thumb (I); male lacking nuptial asperities on thumb; low series of warts along ulnus; tip of prepollex not protruding; dorsum smooth; belly and under surface of thigh granular, rest of underside smooth; toe disk size from inner to outer I<II<III=IV=V; outer toe disks (IV, V) equal to or slightly smaller than outer finger disks; toe webbing formula I 0-1 II 0-1+ III 0-1+ IV 1+-0 V; large oblong inner metatarsal tubercle; outer metatarsal tubercle small, round, or lacking; inner tarsal fold moderately distinct; outer tarsus with a series of low warts or not; entire heel surface warty-tuberculate; males to 46 mm, females to 48 mm; tibia 50; dorsum uniform, spotted, or blotched, yellow, gray, or fawn-brown in life, tan to brown in preservative; bright lemon-yellow on throat and belly in life; axillary web, axilla, and groin bright tomato-red in life; dorsal arm pattern uniform; dorsal leg pattern with a thin stripe of dorsal color along mid-thigh; upper tibia uniform or banded; under surfaces of foot and tibia bright tomato-red in life; dorsal toe webs bright tomato-red in life; hands and palms duller tomato-red in life; posterior surface of thigh with or without a suffusion of melanophores; anterior and posterior surfaces of thigh tomato-red in life, ventral surface bright lemon-yellow in life; sole of foot suffused with melanophores; iris golden, brown, or copper.

DISTRIBUTION: Caribbean lowlands from Veracruz, Mexico to Costa Rica.

LOCALITIES: PROV. DE CARTAGO: Moravia de Chirripó, 1116 m; Turrialba, IICA, 600 m; PROV. DE GUANACASTE: Finca San Bosco de Tilarán, laguna de Finca Jenkins, 700 m; Finca Silencio de Tilarán, laguna, 780 m; 3.8 km ENE Tilarán, 620 m; PROV. DE HEREDIA: Finca La Selva, 100 m (Fig. 24).

Hyla microcephala Cope

1886 *Hyla microcephala* Cope: 281 (Holotype: apparently lost, Panama: Provincia de Chiriquí); 1958, Taylor: 23, Fig. 9 (redescription).

1894 *Hyla cherrei* Cope: 195 (Holotype: apparently lost, Costa Rica: Provincia de Alajuela).

1898 *Hyla microcephala* Boulenger (nec. Cope, 1886): 481, pl. 39, Fig. 3 (Syntypes: BM 1947. 2.23.28-29, Costa Rica: Provincia de Guanacaste: Cantón de Cañas: Bebedero, 7 m).

1899 *Hyla underwoodi* Boulenger: 277 (substitute name for *microcephala* Boulenger, 1898); 1952, Taylor: 891, Fig. 65 (comments).

DIAGNOSIS: One of four species in Costa Rica that has a well-developed

dorsolateral light stripe from the eye above the tympanum onto the back (the other three are *H. angustilineata, H. colymba,* and some *H. ebraccata).* The narrow stripe is white in life (some times faded in preservative) and is bordered below by a narrow dark brown stripe (Fig. 14). *H. microcephala* may be distinguished from the other forms with which it may be confused by: having the dark dorsolateral stripe extending posteriorly past mid-body (stripe, if present, reaching only to point level with elbow in *H. phlebodes,* no dorsolateral light stripe), finger webbing (no hand webs in *H. angustilineata),* outer finger disks much broader than digits (equal to disks in *H. colymba)* and lacking webbing between fingers I-II, and no suborbital light spot (present in *H. ebraccata).*

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout rounded to subovoid; snout rounded in profile; canthus rostralis round to distinct; tympanum indistinct, horizontal diameter 1/3-3/5 diameter of eye; male vocal sac single, external; male vocal slits not entirely hidden by tongue, oblique to jaw; vomerine teeth between choanae, transverse; outer finger disks (III, IV) just less than, to 1 1/4 times tympanum; finger webbing formula I 3-3 II 1 2/3-3$^-$ III 2$^+$-2$^+$ IV; white glandular appearing nuptial asperities on thumb of male or absent; ulnus with a low series of warts or absent; tip of prepollex not free; dorsal texture smooth; ventral surface granular; toe disk size from inner to outer I<II<III=IV=V, I<II=III=IV=V, or I<II<III<IV=V; outer toe disks (IV, V) slightly smaller than outer finger disks; toe webbing formula I 1-2$^-$ II 1-2 III 1-2 IV 2-1 V; large oblong inner metatarsal tubercle, outer metatarsal tubercle small and round or absent; distinct inner tarsal fold, no outer tarsal fold; heel smooth; males to 28 mm, females to 30 mm; tibia 56; dorsum reticulated or striped, beige to yellow in life, tan to brown in preservative; dorsolateral stripe always present, extending from nostril through eye at least to mid-body, often to sacrum; dorsal limbs uniform or mottled, upper tibial markings may approach bars; posterior surface of thigh not suffused with melanophores, deep yellow to orange in life; no melanophores under digits I and II, sometimes under digit III, usually under digit IV, always under digit V; iris golden.

DISTRIBUTION: Tropical Caribbean lowlands of Mexico and Central America to Nicaragua, southward on Pacific versant to eastern Panamá, and north and western Colombia.

LOCALITIES: PROV. DE GUANACASTE: Arenal, 520 m; Arenal, laguna, 509 m; 3.2 km W Bagaces, 65 m; Bebedero; 26.9 km N Cañas; 12.3 km S La Cruz; Guayabo de Bagaces, 65 m; 0.8 km W, 1.6 km N Guayabo; Hacienda La Norma, 150 m; 0.8 km E Finca Jiménez on Río Higuerón, 11 m; 7.4, 10.3, 14.3 km N, 9.6, 14.8 km S Liberia; 1.9 km S Nicoya; Peñas Blancas, 44 m; 4.3, 8.6, 21.7 km E Playa del Coco; Finca San Bosco de Tilarán, laguna de Finca Jenkins, 700 m; Santa Cruz, airport; Finca Silencio de Tilarán, laguna, 780 m; Tilarán, 560 m; 3.8 km ENE Tilarán, 620 m; PROV. DE PUNTARENAS: 3.2 km NE Boca del Barranca, 100 m; 11.6 km NW Esparta; 3.2 km SE Golfito;

Palmar Sur, 16 m; Parrita, La Julieta, Finca La Ligia; 6.1 km N mouth Río Grande de Tárcoles, 213 m; 21.8 km. W San Ramón, 410 m; Villa Neily, 75 m; 1.6 km NW Villa Neily, 70 m; 4.2 km NW Villa Neily, 60 m; 7.1 km NW Villa Neily (Fig. 25).

REMARKS: The name *Hyla cherrei* Cope (20) is based on a single specimen, now lost, from Alajuela, Costa Rica, and has never been satisfactorily allocated. The tree-frog fauna of Costa Rica has been extensively collected during the last 30 years and it seems likely that the population represented by this name has been re-sampled. The significant characteristics of the holotype of *H. cherrei* are: vomerine teeth in two patches between very large choanae; snout not prominent, vertical in profile; canthus rostralis sharp, straight, angular; lores vertical; distance from eye to nostril slightly less than diameter of eye; width of interorbital space 1 1/2 times width of upper eyelid; tympanum 1/2 eye and equal in vertical diameter; upper surfaces smooth; fingers almost without web; toes fully palmate; heel of extended leg reaches tip of snout; head and body pigmented above, probably with yellow, in abrupt contrast to the color of rest of body, from which it is separated by a narrow light stripe from eye to sacrum; under surfaces straw-color; upper surfaces of limbs pigmented, except humerus and femur.

The type appears to be a female, since no mention was made of vocal sac, vocal slits or nuptial thumb asperities. Measurements of the type were given as 26 mm in standard length, length of leg 45 mm and length of foot including tarsal segment 20 mm.

The presence of a distinct continuous light stripe from the orbit along the body to the sacrum is found among Costa Rican hylids only in *H. angustilineata, H. colymba, H. ebraccata* and *H. microcephala.* The only other Costa Rican tree-frogs with distinct continuous light stripes are the red-eyed species *H. legleri, H. lythrodes, H. rufioculis* and *H. uranochroa.* In these forms the light stripe runs from the tip of the snout or below the eye to the groin. The red-eyed forms further differ from the type of *H. cherrei* in having the dorsum dark in ground color (bluish or purplish to brown in preservative) and a rounded snout, in profile.

In other aspects of coloration the type of *H. cherrei* differs markedly from *H. angustilineata,* which has a dark green to blackish-brown dorsum and numerous dark flecks on the under surfaces. In these respects the questionable form resembles individuals of *H. microcephala* (for example the type of *H. underwoodi)* and *H. ebraccata* (for example the type of *H. weyerae)* that have a uniform light dorsum and all *H. colymba.* In none of these three forms are the under surfaces marked with dark flecks.

H. angustilineata further differs from Cope's description in having the vomerine teeth extending posterior to the choanae, a rounded snout profile and very little toe webbing. There seems to be ample evidence that the type of *H. cherrei* and *H. angustilineata* represent distinct species.

H. cherrei does not appear to be conspecific with *H. ebraccata* since the

latter has considerable finger webbing, particularly between fingers I-II (webless in *H. cherrei).*

From Cope's nominal form, *H. colymba* differs in having a round canthus and the vomerine teeth forming a broad inverted V -shaped series extending posterior to choanae. The diagnostic prominent mental gland of *H. colymba* is not mentioned in Cope's description of *H. cherrei.*

It is apparent from the above remarks that *H. cherrei* is rather similar to *H. microcephala.* Cope's descriptions of *H. cherrei* agrees with *H. microcephala* in all but two points, the description of toe webbing and lack of pigmentation of the humerus and femur. Taylor (62:853) interpreted the statement "pes fully palmate" to mean that *H. cherrei* had toes webbed to the disks. It seems to us that Cope's statement "Manus almost without web; pes fully palmate". is meant to imply that the webs between the toes were well-developed and not vestigal as on the fingers. It may be noted further that Cope in his remarks on the distinctive characteristics of the frog, after the description, does not mention toe webbing. If the toes were webbed to the disks, an unusual situation in *Hyla,* it is probable that Cope would have emphasized this feature as he does the webless fingers. The amount of pigment on the upper surface of both humerus and femur limb segments in *H. microcephala* is minimal in some individuals and my be further reduced by fading. Since the pigment is light or reduced in many *H. microcephala* it seems likely that Cope's example was similarly colored.

The type locality is given by Cope as Alajuela, which could stand for either the town or province. The collector was apparently Anastasio Alfaro, who later became Director of the Museo Nacional de Costa Rica but who through some error became listed as R. Alfaro (a possible misinterpretation of a Spanish script A as an R). *H. microcephala* is not known from either the city or province of Alajuela, but has been collected from Provincia de Puntarenas, near the boundary with Alajuela (22 km S W of San Ramón).

Since the description of *Hyla cherrei* agrees as nearly as can be determined with *H. microcephala* in all significant features and since the type is lost, it seems appropriate to place the name as a synonym of the latter form. The name *H. cherrei* is available for use as a senior synonym over *H. underwoodi* Boulenger, if the population of *H. microcephala* from northwest Costa Rica is recognized as racially distinct from populations in Panama and southwest Costa Rica. The description of *H. cherrei* agrees in detail with the type description of *H. underwoodi* which is also stated to have toes nearly entirely webbed and thighs lacking pigment.

Hyla phlebodes Stejneger

1906 *Hyla phlebodes* Stejneger: 817 (Holotype: US 29970, Costa Rica: Provincia de Alajuela: Cantón de San Carlos); 1952, Taylor: 888, Fig. 64 (redescription).

1931a *Hyla underwoodi,* Dunn: 413 (misidentification).

DIAGNOSIS: *H. phlebodes* is a small (adults to 26 mm) species that lacks obvious distinctive features. Any small yellowish-brown tree frog with a dark canthal stripe, a dark interorbital stripe, some dark markings on the dorsum, distinct tibial dark bars and a short dorsolateral dark stripe from above eye to axilla is likely to be this form. The only other species with which it might be associated is *H. microcephala.* The latter has a dorsolateral light line in life, bordered below by a dark dorsolateral stripe that extends at least to mid-body (no light stripe, dark stripe if present extends no further posterior than point level with elbow when arm folded against body, Fig. 15, in *H. phlebodes),* usually no interorbital or tibial darks bars (usually present in *H. phlebodes).* Some *H. phlebodes* lack dorsal pattern and resemble similarly colored *H. ebraccata* but never have the light suborbital light area and considerable webbing between fingers I-II as is typical of the latter species.

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout subovoid; snout rounded in profile; canthus rostralis rounded; tympanum moderately distinct, horizontal diameter about 1/3 eye diameter; male vocal sac external, single; male vocal slits not hidden by tongue, parallel to jaw; vomerine teeth lie at level of posterior margins of choanal openings; outer finger disks (III, IV) slightly larger than, to 1 1/2 times tympanum; finger webbing formula I 3-3 II 1 1/2-2 2/3 III 2 1/2-2+ IV; subarticular tubercles double under outer finger (IV), single under thumb (I); white nuptial asperities on thumb of male; ulnar ridge usually absent, sometimes very weakly developed; tip of prepollex not protuberant; dorsum smooth; venter granular; toe disk size from inner to outer $1<II=III=IV=V$ or $1<II<III=IV=V$; outer toe disks (IV, V) equal to or slightly smaller than outer finger disks; toe webbing formula I $1+$-2^{-} II 0-2 III 1-2 IV 2-1 V; large oblong inner metatarsal tubercle; outer metatarsal tubercle indistinct, small, round; definite inner tarsal fold; no outer tarsal fold; heel smooth; males and females to 26 mm; tibia 52; dorsum reticulate or striped, bright salmon-buff to brown in life, tan with light brown markings in preservative; interorbital bar usually present; post orbital stripe present or absent, if present extends no further posterior than point level with elbow when arm folded against body; chest cream, color extending to middle of belly in life; dorsal arm and tibia barred, rest of upper limbs uniform; posterior surface of thigh with or without suffusion of melanophores, yellow to orange in life; scattered melanophores under digits IV and V only, iris golden.

DISTRIBUTION: Lowlands of eastern Nicaragua and Costa Rica to eastern Panamá.

LOCALITIES: PROV. DE ALAJUELA: Los Chiles, 70 m; 14.5 km N Florencia, nr. Muelle de Arenal, 150 m; 3.2 km NE Muelle de Arenal, 50 m; Las Playuelas, 75 m; PROV. DE CARTAGO: 1.6 km NE Río Reventazón bridge on Turrialba-Peralta road; Turrialba, IICA, 602m; PROV. DE GUANACASTE: Arenal, 520 m; Arenal, laguna, 502 m; Guayabo de Bagaces, 550-600 m; 1.6

km N Guayabo, 550 m; Finca San Bosco de Tilarán, laguna de Finca Jenkins, 700 m; 3 km NE Tilarán at divide, 560 m; 6 km NE Tilarán, 490 m; PROV. DE LIMON: Batán; La Castilla; La Lola, 36 m; 0.75, 1.6 km SW Limón (Fig. 26).

Hyla boulengeri (Cope)

1887 *Scytopsis boulengeri* Cope: 12 (Holotype: U.S. 13974, Nicaragua).

1901 *Hyla boulengeri,* Gunther: 267 (redescription); 1952; Taylor: 856, Fig. 55 (redescription): 1958: 21, Fig. 8 (records).

DIAGNOSIS: This species is one of three Costa Rican tree frogs with solid dark bars on the posterior surface of the thighs. It may be easily separated from the other two forms with this feature as follows: from *A. coronata* by lacking knob-like projections on the head, by having a tuberculate dorsum and having the dark bars excluded from the ventral thigh surface (knob-like cephalic projections, smooth dorsum and dark bars or rings on ventral surface of thigh in *A. coronata);* and from *H. lancasteri* by lacking finger webbing and having an elongate snout with the distance from eye to nostril exceeding diameter of orbit (webs between fingers II-III-IV, and snout short, distance from eye to nostril less than diameter of orbit in *H. lancasteri).*

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout subovoid to subelliptical; snout rounded in profile; canthus rostralis round; tympanum fairly distinct, horizontal diameter 1/2-2/3 eye; male vocal sac external, single; male vocal slits not hidden by tongue, oblique to jaw; vomerine teeth between choanae, transverse; finger disks (III, IV) equal to or slightly greater than tympanum; finger webbing not evident; subarticular tubercles single to bifid under outer finger (IV), always single under thumb (I); white glandular appearing nuptial asperities on thumb of male; row of warts along ulnus or not; tip of prepollex not protuberant; dorsal surface tuberculate; chin smooth to tuberculate; belly granular; disk of second toe (II) smaller than all other disks; large disks all subequal; outer toe disks (IV, V) slightly smaller than outer finger disks; toe webbing formula I 2-2+ II 1-2 III 1-2 IV 2+-0 V; distinct oblong inner and outer metatarsal tubercles; no inner tarsal fold; outer tarsus with series of tubercles; heel region tuberculate, in some individuals one tubercle is prominent; males to 48 mm, females to 50 mm; tibia 56; dorsum variable - usually a dark interorbital triangle, elongate postorbital blotch, and/or a reversed dark V on posterior third of back; beige, light brown, or olive in life, tan-brown to dark chocolate-brown in preservative; axilla and groin yellow, yellow-green, or yellow-green with orange cast in life; belly cream or white in life; upper arms and legs faintly to prominently banded, concealed portions of legs strongly banded, bands black, purple-black, or brown with yellow, yellow-green, or pale lemon-yellow interspaces in life; sole of foot suffused with melanophores; iris gold or dull copper.

DISTRIBUTION: From Nicaragua southward on both coasts to Guiana and Colombia.

LOCALITIES: PROV. DE ALAJUELA: Los Chiles, 70 m; 8.9 km N Ciudad Quesada nr. La Florencia, 220 m; 17.6 km N. Florencia, 100 m; 3.2 km NE Muelle de Arenal, 50 m; Las Playuelas, 75 m; PROV. DE CARTAGO: Turrialba, 602 m; PROV. DE GUANACASTE: Arenal, laguna, 509 m; 3.2 km W Bagaces, 65 m; 26.9 km N Cañas; 7.4, 13.7 km N, 20.5 km S Liberia; 21.7 km E Playa del Coco; 4 km NE Tilarán, 700 m; 6 km NE Tilarán, 490 m; PROV. DE HEREDIA: 1 km. NE Puerto Viejo, 100 m; PROV. DE PUNTARENAS: Parrita, 5 m; Rincón de Osa, Camp Seattle, 50 m; 7.1 km NW Villa Neily, 60 m. (Fig. 27).

Hyla elaeochroa Cope

1875 *Hyla elaeochroa* Cope: 105, pl. 26, Fig. 3 (Lectotype: US 30689, Costa Rica: Provincia de Limón: Cantón de Limón: E Foot of mountains near Sipurio); 1952, Taylor: 859, Fig. 56; 1960a, Starrett: 19, Figs. 15-16 (larvae); 1966, Duellman: 270 (synonymy, separates *elaeochroa* from *rubra).*

1886 *Hyla quinquevittata* Cope: 273 (Holotype: US 14187, Nicaragua).

1931b *Hyla rubra* Dunn: 413 (places *elaeochroa* in synonymy); 1932, Dunn and Emlen: 25 (place *elaeochroa* and *quinquevittatus* in synonymy).

1958 *Hyla dulcensis* Taylor: 37, Fig. 17 (Holotype: KU 32166, Costa Rica: Provincia de Puntarenas: Cantón de Golfito: Golfito).

DIAGNOSIS: A species without hand webbing, dark bars on posterior thigh surface or dorsolateral light lines. These features separate it from all other Costa Rican forms without finger webbing except *H. staufferi* and *P. lemur.* From the latter *H. elaeochroa* differs in having a horizontally elliptical pupil, versus vertical; the dorsal ground color dirty gray in life and various shades of pale tan to dark brown in preservative versus bright yellow-green or magenta in life or preservative.

H. staufferi and *H. elaeochroa* are closely related forms. In life they are readily distinguished since *H. elaeochroa* has green bones easily seen through the skin and the bones are colorless in *H. staufferi.* In addition the snout is rounded in dorsal outline in *H. elaeochroa* (pointed in *H. staufferi),* the disks on fingers II-III-IV are larger than the tympanum (equal to or smaller in *H. staufferi),* the dorsum is smooth to granular (tuberculate in *H. staufferi)* and the size is medium, adults to 40 mm (size small, adults less than 30 mm in *H. staufferi).*

SUMMARY OF CHARACTERISTICS: Snout rounded to subovoid in dorsal outline; snout rounded in profile; canthus rostralis round; tympanum rather indistinct, horizontal diameter 1/3-1/2 eye diameter; male vocal sac single,

external; male vocal slits not entirely hidden by tongue, oblique to jaw; vomerine teeth between choanae, transverse; outer finger disks (III, IV) large, about 1 1/4 times tympanum; fingers without web; subarticular tubercles single to almost double under outer finger (IV), always single under thumb; white glandular appearing nuptial asperities on thumb of male; no ulnar ridge; tip of prepollex not protruding; dorsal surface smooth; throat smooth; chest, belly and ventral surface of thigh granular; toe disk size from inner to outer I=II<III=IV=V; outer toe disks (IV, V) equal to or slightly smaller than outer finger disks; toe webbing formula I 2-2+ II 1-2 III 1-2 IV 2-1 V; large oblong outer metatarsal tubercle; inner metatarsal tubercle small, round, indistinct; no inner tarsal fold; series of low warts on outer tarsus or absent; heel smooth; males to 38 mm, females to 40 mm; tibia 51; dorsum almost uniform to striped with interorbital bar, yellow-green, dark olive-green, or bronze in life, tan, gray, or brown in preservative; sides of body and groin bright yellow in life; venter orange, pale yellow, or white in life; upper limb pattern uniform to faintly barred; posterior thigh suffused with melanophores, yellow-green in life; sole of foot suffused with melanophores; iris gold or copper.

DISTRIBUTION: Atlantic lowlands of Nicaragua, Costa Rica and northwest Panamá; southwest Costa Rica and adjacent western Panamá.

LOCALITIES: PROV. DE ALAJUELA: Los Chiles, 70 m; 8.0 km N Ciudad Quesada nr. La Florencia, 220 m; 14.5 km N Florencia, 200 m; 3.2 km E La Fortuna, 150 m; 3.2 km NE Muelle de Arenal, 50 m; Las Playuelas, 11.3 km S Los Chiles, 75 m; PROV. DE CARTAGO: Hacienda Florencia, nr. Turrialba, 500 m; 9 km N La Suiza, 700 m; Turrialba, IICA, 625 m; Turrialba, on road to Pavones, 700 m; PROV. DE GUANACASTE: Finca San Bosco de Tilarán, 700 m; PROV. DE HEREDIA: Finca La Selva, 100 m; PROV. DE LIMON: Bambú, 60 m; 2.4 km E. Los Diamantes, 260 m; La Lola, 39 m; Pandora, 100 m; Tortuguero; PROV. DE PUNTARENAS: Golfito; 3.2 km SE Golfito; Parrita, 5m; Parrita, La Julieta, Finca La Ligia, 5-10 m; Rincón de Osa, Camp Seattle; 21.8 km W San Ramón; Villa Neily, 75 m; 1.6 km NW Villa Neily, 70 m (Fig. 28).

Hyla staufferi Cope

1865b *Hyla staufferi* Cope: 195 (Holotype: US 15317, México: Veracruz: Orizaba); 1952, Taylor: 862 (presumed presence in Costa Rica, redescription); 1954, Taylor: 623, Fig. 8 (Costa Rican records).

1887 *Hyla eximia staufferi,* Cope: 14.

1901 *Hyla eximia.* Gunther (in part): 261.

1932 *Hyla culex* Dunn and Emlen: 24 (Holotype: MCZ 16098, Honduras: Departamento de Atlántida: Tela).

1933 *Hyla altae* Dunn: 1933 (Holotype MCZ 17972, Panamá, Canal Zone: Summit).

DIAGNOSIS: One of the few Costa Rican hylids lacking hand webs. Immediately distinguished from all other species without finger webs as follows: no dark bars on posterior or ventral thigh surfaces (present in *A. coronata* and *H. boulengeri);* no dorsolateral light stripes (present in *H. angustilineata);* dorsum strongly tuberculate (smooth in *A. coronata, H. angustilineata, H. elaeochroa* and *P. lemur).*

The species is most likely to be confused with its close ally *H. elaeochroa,* but they differ in (features for *H. staufferi* in parentheses): outer finger disks (II-III-IV) larger than tympanum (smaller than tympanum), snout rounded in dorsal outline (pointed), and bones green in life (colorless).

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout rounded to subovoid; snout rounded in profile; canthus rostralis round; tympanum distinct, horizontal diameter about 1/2 eye diameter; male vocal sac external, single; male vocal slits hidden by tongue, oblique to jaw; vomerine teeth between choanae; outer finger disks (III, IV) equal to or just larger than tympanum; fingers lack noticeable web; subarticular tubercle single to double under outer finger (IV), always single under thumb; white glandular appearing nuptial asperities on thumb of male; low series of warts present or absent on lower arm; tip of prepollex not protuberant; dorsal surface tuberculate; undersurfaces granular; toe disk size from inner to outer I=II<III=IV=V; outer toe disks (IV, V) slightly smaller than outer finger disks; toe webbing formula I 2+-2 1/2 II 1 2/3-2 1/2 III 1+-2 1/3 IV 2+-1+ V; large oblong inner metatarsal tubercle; outer metatarsal tubercle small, rounded, without melanophores, contrasting with surrounding pigmented foot region; no inner or outer tarsal folds; heel with or without small tubercle; males to 27 mm, females to 28 mm; tibia 49; dorsum striped and/or spotted, dirty gray in life, cream, tan, brown, or dark brown in preservative; sides of body yellowish in life; throat orange to yellow in life; venter dirty white in life; upper limbs blotched or barred; posterior surface of thigh suffused with melanophores, dusky in life; sole of foot suffused with melanophores; iris dark brown with gold flecks.

DISTRIBUTION: Lowlands of tropical Mexico to central Panamá, exclusive of humid forest areas of the Caribbean lowlands and Pacific Panamá and Costa Rica.

LOCALITIES: PROV. DE ALAJUELA: Los Chiles, 70 m; PROV. DE GUANACASTE: 3.2 km W Bagaces, 65 m; 26.9 km N Cañas; 12.3 km S La Cruz; Guardia on the Río Tempisque, 18.1 km W Liberia, 12 m; 1.6 km N Guayabo de Bagaces, 550 m; Hacienda la Norma, 5 km N and 4.5 km W Liberia, 150 m; 7.4, 14.5, 14.7 km N, 14.8 km S Liberia; 5.9 km N, 1.9, 3.2 km. S Nicoya; 8.6 km ESE, 21.7 km E Playas del Coco; Santa Cruz, airport; Tenorio; PROV. DE PUNTARENAS: mouth of Río Barranca. (Fig. 29).

Hyla debilis Taylor

1952 *Hyla debilis* Taylor: 880, Fig. 62 (Holotype: KU 28184, Costa Rica: Provincia de Heredia: Cantón de Heredia: Isla Bonita E slope Volcán Poás, 1700 m).

DIAGNOSIS: A small species (males to 28 mm, females to 29 mm) with a well-developed suborbital light spot and a discontinuous light lateral line or elongate spot on a glandular ridge between groin and midbody. Dorsally this frog is uniform dull green, olive, tan or gray with enamel-like green flecks. The only frogs with which *H. debilis* may be mistaken are the young of its close allies *H. rivularis* and *H. tica, H. ebraccata* or the red-eyed forms *H. lythrodes, H. rufioculis* and *H. uranochroa.*

Neither *H. rivularis* nor *H. tica* have a well developed suborbital light spot and the finger disks are larger than the tympanum (suborbital light spot present and finger disks equal tympanum in *H. debilis). H. rivularis* further differs from *H. debilis* in lacking a white spot in the posterior flank or groin region. *H. tica* frequently has a series of irregular enamel-like white spots along the flank but it has a strongly tuberculate dorsum, snout rounded in profile, canthus rostralis rounded and the upper surface of thigh usually with dark bars (dorsum smooth, snout profile acute, canthus rostralis sharp, and no thigh bars in *debilis).*

From the red-eyed species with a suborbital light spot *(H. lythrodes, H. rufioculis* and *H. uranochroa) H. debilis* may be distinguished by having the sole of the foot heavily suffused with dark pigment (no dark pigment on sole in *H. uranochroa)* venter with a peppering of dark spots and diameter of tympanum 1/3 of orbit (venter immaculate and diameter of tympanum 1/2 of orbit in *H. lythrodes);* and a series of ulnar tubercles and the vomerine tooth patches extending posterior to choanae (an ulnar ridge and vomerine teeth between choanae in *H. rufioculis). H. debilis* has a dull orange iris in life and in the other species the iris is bright red.

H. ebraccata usually has contrasting large dark blotches on the dorsum and a broad dark lateral band from tympanum to groin; and frequently a dorsolateral light line from above eye along the back; in individuals with a uniform dorsum the lateral dark band is bordered above by the dorsolateral light stripe and below by a lateral light stripe from below the tympanum that is usually continuous to groin (in *H. debilis* the dorsum lacks large contrasting dark blotches, and no dark lateral band or dorsolateral light stripe is present).

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout subelliptical to truncate, outline of upper lip nearly semicircular; snout profile acute; canthus rostralis sharp; tympanum distinct, horizontal diameter about 1/3 eye diameter; male vocal sac external, single; male vocal slits not hidden by tongue, oblique to jaw; vomerine teeth extend posterior to choanae; size of outer finger disks (III, IV) moderate, equal to or slightly smaller than tympanum; finger webbing formula I trace II 2⁻-3 III 2 1/2-2 IV; subarticular tubercles single or double under all fingers; brown nuptial asperities on thumb of male; lower arm with weakly de-

veloped ridge or series of low warts; tip of prepollex not protruding; dorsal surface smooth; throat, chest, under surfaces of arm smooth; belly, lower surface of thigh granular, rest of underside of leg smooth; toe disk size from inner to outer I<II=III=IV=V or I<II<III=IV=V; outer toe disks (IV, V) equal to or slightly smaller than finger disks; toe webbing formula I 2⁻-2+ II 1+-2 1/2 III 1 1/2-2 1/2 IV 2 1/2-1+ V; large oblong inner metatarsal tubercle, outer metatarsal tubercle not apparent; inner tarsal fold weakly developed to absent; outer margin of lower leg with or without a low series of warts; heel warty; males to 28 mm, females to 29 mm; tibia 50; dorsum uniform or punctated, dull green, olive, tan, beige, or gray with enamel-green flecks in life, gray-brown, dark tan, red-brown, or dark chocolate with or without blue-gray punctations in preservative; light suborbital spot may extend as upper lip line, cream in life; face and sides of chest green in life; side of body with lateral light elongate spot or line in area from groin to mid-body; upper limb as back; posterior thigh lightly suffused with melanophores or (usually) not, yellow in life, sole of foot suffused with melanophores; iris dull orange or orange-brown.

DISTRIBUTION: Known from two localities on the Atlantic slopes of Costa Rica and from the Pacific slope in western Panamá.

LOCALITIES: PROV. DE CARTAGO: Tapantí, along Río Quiri between road and waterfall, 1280-1320 m; 1 km N of Tapantí, 1300-1400 m; PROV. DE HEREDIA: Volcán Poás, Isla Bonita, 1700 m (Fig. 29).

Hyla pictipes Cope

1875 *Hyla punctariola pictipes* Cope: 106 (Lectotype: US 30652, Costa Rica: Provincia de Limón: Cantón de Limón: E slope Cerro Utyum, misidentified by the collector William M. Gabb as Pico Blanco, 1500-2100 m).
Hyla punctariola moesta Cope: 106 (Costa Rica: Provincia de Limón: Cantón de Limón: E slope Cerro Utyum, erroneously cited as Pico Blanco, 1500-2100 m).
Hyla punctariola monticola Cope: 106 (Costa Rica: Provincia de Limón: Cantón de Limón: E slope Cerro Utyum, erroneously cited as Pico Blanco, 1500-2100 m).

1952 *Hyla moesta,* Taylor: 855 (quotation of Cope description).
Hyla monticola, Taylor: 855 quotation of Cope description).
Hyla pictipes, Taylor: 878 (redescription of syntypes).

1966 *Hyla pictipes,* Starrett: 17, Figs. 1-2 (redescription).

DIAGNOSIS: Unique among Costa Rican hylids in having the posterior surface of the thigh dark with a series of discrete light (yellow in life) spots. In most specimens similar light dots are present on the anterior thigh surface, in the groin and forward along the flank. Some individuals tend to have the number of thigh spots reduced due to a heavy suffusion of dark pigment; in these individuals the under surfaces of the body and limbs are heavily marked with dark pigment.

The only other tree-frog that approaches *H. pictipes* in coloration is the highly variable *H. pseudopuma.* Most examples of the latter form have yellow spots in the groin and along the flank, but the posterior surface of the thigh is without spotting and the venter is never heavily suffused with dark pigment as in *H. pictipes.*

All of the species of *Smilisca* usually have a reticulum of narrow purple to brown lines on the light ground color of the groin and flank and sometimes the light areas form light spots. The posterior surface of the thigh is reticulated with purple to brown and light pigment in many *S. baudinii, S. sila, S. sordida,* and *S. puma* or it is uniformly dark in some examples of these species and all *S. phaeota* and does not show the discrete light spotting typical of *H. pictipes.*

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout truncate, outline of upper lip semicircular; snout profile acute; canthus rostralis sharp; tympanum indistinct, horizontal diameter about 1/3 diameter of eye; male vocal sac internal, single; vocal slits of male hidden by tongue, oblique to jaw; vomerine teeth extend posterior to choanae, transverse; outer finger disks (III, IV) large, 1 1/3-2 times tympanum; finger webbing formula I trace II 2⁻-3 1/2 III 3⁻-2 1/2 IV; subarticular tubercles double under outer finger (IV), single under thumb; brown nuptial asperities on thumb of male; warty fold along lower arm; tip of prepollex not protruding; dorsal surface smooth to slightly tuberculate; chin surface smooth, chest and under surface of arm smooth to smooth-granular, belly and lower surface of thigh granular, rest of leg under surface smooth; toe disk size from inner to outer I<II=III=IV=V or I<II<III=IV=V; outer toe disks (IV, V) large, just smaller than outer finger disks; toe webbing fomula I 1 1/2-2 1/2 II 1+-2 1/2 III 1+-2 1/2 IV 2 1/2-1+ V; large oblong inner metatarsal tubercle, outer metatarsal tubercle small, round; no inner tarsal fold, series of low warts on outer tarsus; warts on heel, some pronounced into low flap; males to 36 mm, females to 42 mm; tibia 52; back and head uniform or faintly mottled, leaf-green or olive-green with black or green-black marbling in life, gray blue, tan, chocolate or brown-black in preservative; sides of body with contrasting light spots on a dark field; lip line yellow, gray, or absent in life; ventral surface uniform cream, with dark marbling on light ground, or almost uniform dark; dorsal limb pattern and color same as back; all concealed portions of leg with same pattern as side of body; white frosting on outer edges of arms, legs, and over vent in life; posterior thigh suffused with melanophores, dusky yellow with bright yellow spots, dusky with yellow spots, black with yellow spots, or olive with yellow spots in life; sole of foot suffused with melanophores; iris yellow, green-gold, green, green-brown, brown or dark brown (Figs. 17-18).

DISTRIBUTION: High altitudes of the Cordilleras Central and de Talamanca of Costa Rica, between 1900 to 2500 m.

LOCALITIES: PROV. DE ALAJUELA: Río Poasito, 1 km W Poasito, 2000 m; Volcán Poás, SE slope, 1980 m; PROV. DE CARTAGO: 0.5 km E Tierra Blanca, 2220 m; Volcán Turrialba, S slope, 2350 and 2470 m; PROV. DE HEREDIA: Alto del Roble, 0.4 km N of Cerro Chompipe, 2020-2040 m; Volcán Barba, 2290 m; PROV DE SAN JOSE: Cerro de la Muerte, S side, 2499 m; 3 km SE Rancho Redondo, 2050 m; on Inter-American Highway to San Isidro from San Jose, 2800 m (Fig. 30).

Hyla rivularis Taylor

1952 *Hyla rivularis* Taylor: 847, Fig. 53 (Holotype: KU 28197, Costa Rica: Provincia de Heredia: Cantón de Heredia: Isla Bonita, E slope Volcán Poás, 1600 m); 1960a, Starrett: 23, Figs. 21-22 (larvae).

DIAGNOSIS: A medium-sized species (adult males to 34 mm, females to 37 mm) without any striking features of coloration (no light or dark dorsolateral or lateral stripes or bands, no light suborbital light spot, no dark bars or discrete light spots on surfaces of hind limbs) except that the dorsum is usually marked with dark blotches and the venter with a peppering of dark spots. The presence of finger webs, vomerine teeth in linear series and not bordering margin of choanae, acute snout profile and vertical tympanum 1/3 eye and absence of paired odontoids at tip of lower jaw will separate *H. rivularis* from all other Costa Rican hylids with similar color patterns.

Individual specimens of *H. rivularis* may be confused with *H. pseudopuma, H. tica* or *S. sordida,* particularly the juveniles of the latter three species. From *H. pseudopuma* the present species differs in having the diameter of the tympanum 1/3 of eye diameter and an acute snout profile (tympanum 1/2 or more of eye and snout rounded in *H. pseudopuma).* In some *H. pseudopuma* the upper surfaces of the thigh are barred with dark, and yellow groin and flank spots (white in preservative) are usually present (no thigh bars or yellow spots in groin in *H. rivularis).*

H. rivularis and *H. tica* are close allies but the latter has a rounded or vertical snout profile, usually barred dorsal surface of the thigh, a moderate sized tympanum (1/2 diameter of eye) and a strongly tuberculate dorsum *(versus* acute snout, unbarred thigh, small tympanum 1/3 eye and smooth to weakly granular dorsum).

S. sordida has considerable hand webbing, formula II 1+-2+ III 2⁻-1+ IV, rounded snout profile and the vomerine tooth patches between the choanae, while *H. rivularis* has vestigial hand webbing, formula II 2+-3+ III 2 2/3-2+ IV, an acute snout and vomerine tooth patches that project posterior to the choanae. *S. sordida* usually has the flank and posterior thigh surface mottled with light (yellow or white) and dark (bluish to purple in life) and the upper thigh barred (never any thigh or groin mottling and no thigh bars in *H. rivularis).*

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout subelliptical to truncate, upper lip outline nearly semicircular; snout acute in profile; canthus rostralis sharp; tympanum hidden, horizontal diameter 1/4 to 1/3 eye; male with single, external vocal sac; vocal slits of male not hidden by tongue, oblique to jaw; vomerine teeth project posterior to choanae, transverse; outer finger disks (III, IV) 1 1/2 to 2 times the tympanum; finger webbing formula I trace II 2+-3 III 2 2/3-2+ IV; subarticular tubercles double under all fingers; tan to brown nuptial asperities on thumb of male; ulnus with warty ridge; tip of prepollex not protuberant; dorsal texture smooth to granular; throat, chest, lower surface of arm smooth-granular, belly and under surface of thigh granular; rest of leg under surface smooth; ventrolateral glands in breeding males; toe disk size from inner to outer I<II=III=IV=V or I<II<III=IV=V; outer toe disks (IV, V) almost equal to or just slightly smaller than outer finger disks; toe webbing formula I 2⁻-3 II 1+-2 2/3 III 1 1/4-2 2/3 IV 2 1/3-1 1/4 V; large oblong inner metatarsal tubercle, outer metatarsal tubercle very small, rounded; inner tarsal fold weakly developed to absent; ridge of warts on outer tarsus; heel with transverse row of warts usually produced into a dermal flap; males to 34 mm, females to 37 mm; tibia 51; dorsum uniform, punctate, or blotched, gray, yellow-brown, or tan in life, ash, tan, brown, chocolate, or brown-black in preservative; dark eye stripe usually present in life; some specimens with blue-green or dull gray-turquoise on side of head in life; belly dirty white in life; dorsal limb pattern similar to dorsum pattern; posterior surface of thigh suffused with melanophores or not, yellow to green in life; sole of foot suffused with melanophores; iris dull gold.

DISTRIBUTION: The upper slopes of the Cordilleras de Tilarán, Central and Talamanca in northern and central Costa Rica, at elevations between 1200 and 2100 m.

LOCALITIES: PROV. DE ALAJUELA: 0.3 km N Angel Falls, 1490 m; between Angel Falls and La Cinchona, 1370 m; La Cinchona, 1372 m; La Cinchona, S end, in a mountain stream, 1250 m; 1.6 km S of Zapote on Zarcero Ciudad Quesada road, 1280 m; 8 km N of Zarcero, 1680 m; PROV. DE CARTAGO: 1.6 km NE of Casa Mata on Inter-American Highway, 1900 m; 8 km. SE of Lechería Central on road to Santa Cruz, 2011 m; 1 km E of Pacayas, 1600 m; 3.2 km. SE of Tres Ríos, El Alto de Ochomogo, 1494; PROV. DE HEREDIA: Alto del Roble 0.4 km N of Cerro Chompipe, 2020-2040 m; 1.6 km NNE Uvita, watershed of the Río de la Hoja, 1720 m - 1740 m; Volcán Barba, nr. Cinco Esquinas, 9.8 km S Vara Blanca, 1524 m; Volcán Barba, 2.7 km N San José de la Montaña, 1828 m; Volcán Poás, Isla Bonita, 1675 m; PROV. DE PUNTARENAS: 0.8 km NE of Monteverde, 1450 m; 0.8 km W of Monteverde, 1350 m; 1.2 km ENE Monteverde, 1500 m; 2.4 km NE Monteverde, 1520 m; PROV. DE SAN JOSE: El Copey; 3.2 km WSW of Escazú, 1500 m; Inter-American Highway to San Isidro del General, southern slopes, 2000 m; 19.2 km N San Isidro del General (Fig. 31).

Hyla tica Starrett

1966 *Hyla tica* Starrett: 23, Fig. 5 (Holotype: UM 122482, Costa Rica: Provincia de Cartago: Cantón de Turrialba, stream on Volcán Turrialba, 1300 m).

DIAGNOSIS: One of a few species with a strongly tuberculate dorsum, readily distinguished from other forms with this feature by lacking arm and limb fringes and a protuberant spine-tipped prepollex in males (fringe and prepollex spine present in *H. fimbrimembra, H. immensa* and *H. richardtaylori),* lacking dark bars on the anterior and posterior surfaces of the thigh (dark thigh bars present in *H. boulengeri* and *H. lancasteri),* having considerable finger webbing (no finger webs in *H. staufferi),* vomerine tooth patches extending posterior to choanae and subarticular tubercles under thumb double (vomerine tooth patches between choanae and subarticular tubercles under thumb single in *S. sila).*

From its closest non-tuberculate allies *H. debilis, H. pictipes* and *H. rivularis, tica* further differs in having a snout rounded in profile, canthus rostralis rounded, upper surface of thigh usually barred with dark and tympanum moderate, diameter 1/2 diameter of eye (in the other three species the snout profile is acute or vertical, canthus rostralis sharp, upper thigh surface without dark bars and tympanum small, diameter 1/3 eye). Occasional granular *H. rivularis* may be confused with *H. tica,* but the former have outer finger disks smaller than the tympanum (about equal to tympanum in *H. tica).*

H. tica may sometimes be difficult to separate from individuals of *H. pseudopuma.* In *H. tica* dark bars are usually present on the dorsal surface of the thigh, the posterior surface of the thigh is yellow although usually suffused with dark pigment and never mottled with light and dark (the upper surface of thigh usually is not barred and the posterior surface of the thigh is a solid dark color in *H. pseudopuma).*

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout subelliptical to truncate, outline of upper lip semicircular; snout rounded to vertical in profile; canthus rostralis rounded to sharp; tympanum distinct, horizontal diameter about 1/2 diameter of eye; vocal sac in male single, external, not large when expanded; vocal slits in male not hidden by tongue, oblique to jaw; vomerine teeth extend posterior to choanae, transverse; outer finger disks (III, IV) large, from equal to 1 1/2 times tympanum; finger webbing formula I trace II 1 3/4-3 III 2 1/3-2 IV; subarticular tubercles double under all fingers; tan to brown nuptial asperities on thumb of male; series of low warts along ulnus; tip of prepollex not protuberant; dorsal texture moderately to very warty; throat surface smooth to granular; under surface of arm, chest, belly, and thigh granular; rest of lower surface of leg smooth; toe disk size from inner to outer I<II=III=IV=V or I<II<III=IV=V; outer toe disks (IV, V) equal to or slightly smaller than outer finger disks; toe webbing formula I 1+-2 II 1-2 III 1-2 IV 2-1 V; large inner metatarsal tubercle, outer metatarsal tubercle small, round, usually lighter than surrounding area; inner tarsal fold weakly developed to absent; low series of

warts on outer tarsus evident or not; heel warty, often with a single prominent wart; males to 33 mm, females to 38 mm; tibia 53; dorsum uniform, mottled, or with distinct blotches, brown, greenish-gray or tan with gold-gray, green, dark brown, ot black markings in life, gray-brown, tan chocolate, or brown-black in preservative; sides of body mottled to almost spotted, light aspects yellow in life; ventral surface of body dirty white in life; underlegs yellow in life; upper limbs uniform or with bars; posterior surface of thigh suffused or not with melanophores, yellow-green or yellow in life; sole of foot suffused with melanophores; iris pale gold, brown-gold, red-gold, gray, or dark brown.

DISTRIBUTION: Slopes of the Cordilleras de Tilarán, Central and Talamanca in northern and central Costa Rica and the Pacific slope of western Panamá, from 1100 to 1600 m.

LOCALITIES: PROV. DE ALAJUELA: La Cinchona, 1372 m; 4.8 km S Ciudad Quesada; E slope Volcán Poás, 10.5 km N Vara Blanca; 1.6 km S of Zapote on Zarcero Ciudad-Quesada Road, 1280 m; PROV. DE CARTAGO: Río Playas where it crosses the Pacayas-Santa Cruz Road, 1650 m; Tapantí, along Río Quiri between road and waterfall, 1280-1320 m; 1 km N Tapantí, 1300-1400 m; Volcán Turrialba, 1370 m; PROV. DE HEREDIA: San José de la Montaña; PROV. DE PUNTARENAS: 0.8 km NE Monteverde, 1433-1493 m; 0.8 km. W Monteverde, tributary to Río Guacimal, 1372 m; PROV. DE SAN JOSE: area 0.4 km above (SW) and 0.4 km below confluence of Río Claro and Río La Hondura, 1128-1189 m; 1 km S of San Cristóbal Sur in Río Tarrazú (Fig. 32).

REMARKS: In general the females of this form tend to have a more complicated dorsal pattern and considerably more enamel-like white areas within the dorsolateral ground color along the flanks, than are found in males. One population sample (four specimens from Río Playas on Volcán Turrialba) is distinctive. These individuals, all males, are extremely rugose, very dark and nearly uniform in coloration. In addition there is very little peppering of dark flecks ventrally and the bars on the dorsal surface of the thighs are faintly suggested or absent altogether. The snout appears to be slightly longer and deeper and the profile more nearly vertical than in most *H. tica* populations.

A single specimen from the Tarrazú region is somewhat intermediate in coloration and head shape between the Río Playas sample and typical *H. tica*. Another example from near Ciudad Quesada approaches the Playas frogs in rugosity but otherwise resembles other samples of *H. tica*.

Hyla legleri Taylor

1958 *Hyla legleri* Taylor: 33, Figs. 15-16 (Holotype: KU 32982, Costa Rica: Provincia de San José: Cantón de Pérez-Zeledón: 15 km WSW San Isidro de El General on road to Dominical, approximately 800 m).

DIAGNOSIS: A species of red-eyed *Hyla* with a brown dorsum in life and preservative. The red iris color separates this form from all but its closest allies in life. In both living and preserved specimens *H. legleri* has a continuous white lateral stripe from below tympanum to groin (Fig. 13), a feature shared only with the other red-eyed species and some *H. ebraccata* (Fig. 12) in Costa Rica. From the red-eyed hylas, *H. lythrodes, H. rufioculis* and *H. uranochroa* *H. legleri* differs in having the throat heavily suffused with dark pigment to form a fine mottling of dark and light colors at least anteriorly and in lacking a suborbital light spot (throat immaculate in *H. lythrodes, H. uranochroa* and most *H. rufioculis,* occasionally a few large dark throat spots in the latter, and an expanded light suborbital spot in all three forms). *H. ebraccata* has a prominent light suborbital spot and an immaculate throat in contradistinction to *H. legleri.*

Occasional juvenile specimens of the genus *Phyllomedusa* may be mistaken for *H. legleri,* but no members of the former genus have a dark throat or lateral light line from below tympanum to groin and all have a vertical rather than horizontal pupil.

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout truncate to subovoid, outline of upper lip semicircular; snout profile rounded; canthus rostralis round; tympanum distinct, horizontal diameter 1/3 to 1/2 diameter of eye; male vocal sac internal, single; male vocal slits not hidden by tongue, almost parallel to jaw; vomerine teeth between choanae, transverse; outer finger disks (III, IV) large, equal to or larger than tympanum; finger webbing formula I 3-3+ II 1 1/2-2 1/4 III 2+-2 IV; subarticular tubercles usually double under outer finger (IV), sometimes single, always single under thumb; brown nuptial asperities on thumb of male; ulnar fold or ridge; tip of prepollex not protuberant; dorsal surface smooth; throat, chest, under surface of arm smooth-granular to granular; belly and under surface of thigh granular; lower surface of tibia smooth; inner toe disk (I) smaller than outer disks; outer toe disks (IV, V) slightly smaller than outer finger disks; toe webbing formula I 1-2 II 1-2 III 1-2 IV 2-1 V; large oblong inner metatarsal tubercle, outer metatarsal tubercle small, round; inner tarsal fold weakly to moderately developed, distinct outer tarsal fold; series of warts along heel stripe often produced into flap; males to 35 mm, females to 39 mm; tibia 51; dorsum uniform, mottled, or with small light flecks, brown, mottled with bronze or dark green in life, brown or brown mottled with small white flecks in preservative; light stripe along upper lip, not expanded below eye, ivory in life; lateral stripe on body from arm to groin and over anus, ivory in life; under surfaces of abdomen and groin yellow in life; rest of underside dirty white in life; chin smoky in life; upper limbs mottled; outer margin of arm with light stripe, ivory in life; upper legs dark brown with green bands on tibia in life; heel and outer tarsal segment with light stripe, ivory in life; under surfaces of hind leg yellow in life; posterior thigh suffused with melanophores, smoky in life; sole of foot suffused with melanophores; iris red.

DISTRIBUTION: Known from several localities on the Pacific versant of southern Costa Rica, between 700-1600 m.

LOCALITIES: PROV. DE PUNTARENAS: Finca Helechales, 15 km NE Potrero Grande, 1050 m; Finca Loma Linda, 2 km SSW Cañas Gordas, 1170 m; PROV. DE SAN JOSE: Cerro de la Muerte, S side, 1524 m; 16 km SW San Isidro de El General on Dominical road, 880 m (Fig. 33).

Hyla lythrodes Savage

1968 *Hyla lythrodes* Savage: (Holotype: LA 26766, Costa Rica: Provincia de Limón: Cantón de Limón: Alta Talamanca: 21 km SW Amubri at confluence of Río Lari and Río Dipari, 800 m).

DIAGNOSIS: A species of red-eyed hyla (Fig. 13) readily distinguished from its close relatives as follows: (characteristics for compared species in parentheses) from *H. uranochroa* in having a light brown dorsum in life and preservative, an expanded suborbital spot and the sole of the foot suffused with dark pigment (dorsum bright green in life, bluish to purple in preservative; an unexpanded suborbital spot and sole of foot without dark pigment); from *H. legleri* in the expanded light suborbital spot, immaculate throat and posterior surface of thigh without a suffusion of dark pigment (no suborbital light spot, throat dark and thigh suffused with dark pigment); and from *H. rufioculis* in having the tympanum 1/2 orbit, larger than finger disks and the posterior surface of thigh without dark pigment suffusion (tympanum 1/3 diameter of orbit, smaller than finger disks and posterior surface of thigh suffused with dark pigment).

The only other Costa Rican *Hyla* in which some individuals have a white lateral stripe is *H. ebraccata.* The latter form differs from *H. lythrodes* in having the dorsum marked with large dark blotches or numerous punctations and a broad dark lateral band along the side (dorsum uniform and no lateral dark band in the red-eyed form).

Some juvenile or recently transformed *Phyllomedusa* might be confused with *H. lythrodes,* but the former have vertical pupils, no lateral light stripe, although a dorsolateral light stripe may be present and lack an expanded white suborbital spot (horizontal pupil, lateral light stripe and enlarged white suborbital spot in the latter).

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout truncate from above, upper lip semicircular in outline; snout rounded in profile; canthus rostralis rounded; tympanum distinct, horizontal diameter 3/5 eye diameter; male vocal sac single, internal; male vocal slits not entirely hidden by tongue, obliquely parallel to jaw; vomerine teeth lie near level of posterior margin of choanal openings; outer finger disks (III, IV) smaller than tympanum; finger webbing formula I 3-3 II 2 1/4-3 1/2 III 3-2 1/4 IV; subarticular tubercles single under

all fingers; light tan nuptial asperities on thumb of male; no ulnar ridge; tip of prepollex not free and protuberant; dorsum smooth; ventral surface strongly granular; inner toe disk (I) smaller than outer disks; outer toe disks (IV, V) slightly smaller than outer finger disks; toe webbing formula I 2-2 1/2 II 1 1/2-2 1/2 III 1 3/4-2+ IV 2 1/2-1 1/2 V; inner metatarsal tubercle oblong, large; outer metatarsal tubercle not apparent; no apparent tarsal folds; heel smooth; male 30 mm; tibia 52; dorsum uniform, light brown in life and preservative; eyelid and top of head with scattered green or bronze flecks in life; light upper lip stripe extends to groin and greatly expanded under eye, ivory in life; light stripe over anus, white in life; venter pale yellow in life, white in preservative; light line on outer arm, knee and foot, white in life; posterior thigh lacking melanophores, pale yellow in life; sole of foot heavily suffused with melanophores; iris red.

DISTRIBUTION: Known only from the type locality.

LOCALITY: PROV. DE LIMON: Alta Talamanca, confluence of Río Lari and Río Dipari about 21 km SW of Amubri, 800 m (Fig. 33).

Hyla rufioculis Taylor

1952 *Hyla rufioculis* Taylor: 827, Fig. 47 (Holotype: KU 28216, Costa Rica: Provincia de Heredia: Cantón de Heredia: Isla Bonita, E slope Volcán Poás).

DIAGNOSIS: One of four lower Central American *Hyla* with the iris of the eye bright red and a continuous white lateral stripe from below tympanum to groin (Fig. 13). Distinguished from the other red-eyed species by having a brown dorsal ground color (in life and preservative), small tympanum (diameter of tympanum 1/3 diameter of orbit), and the posterior surface of thigh and sole of foot suffused with dark pigment (dorsum leaf green in life, bluish to purple in preservative, tympanum 1/2 orbit and thigh and sole of foot without dark pigment in *H. uranochroa);* the characteristics of tympanum size and thigh pigmentation also separate *H. rufioculis* from *H. lythrodes,* a species that agrees with *H. uranochroa* in these regards; and differing from *H. legleri* in having the white lip stripe expanded into a suborbital light spot, the throat immaculate or occasionally with a few large dark spots and the small tympanum (no suborbital light spot, throat heavily suffused with dark pigment to form a fine mottling and the tympanum 1/2 of orbit in *H. legleri). H. rufioculis* often has some evidence of dark dorsal markings and rarely the lateral light stripe may be broken up into a linear series of white spots.

The only other Costa Rican frogs that might be mistaken for *H. rufioculis* are juvenile *Phyllomedusa* or some individuals of *H. ebraccata. Phyllomedusa* is distinguished from all *Hyla* by having a vertical pupil (horizontal in *Hyla)* and none of the species have a lateral light stripe, although *P. callidryas* may

have a dorsolateral light line from above the shoulder posteriorly to the level of the groin.

H. ebraccata may have a light lateral stripe, but it has a definite broad dark band from tympanum posteriorly (Fig. 12) and the posterior surface of the thigh is light and without a suffusion of dark pigment. No dark lateral band that contrasts with the dorsal pattern is found in *H. rufioculis* and the posterior surface of the thigh is always suffused with dark pigment.

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout truncate, outline of upper lip semicircular; snout rounded in profile; canthus rostralis sharp; tympanum distinct, horizontal diameter 1/3-3/7 eye diameter; male vocal sac single, internal; male vocal slits not completely hidden by tongue, oblique to jaw; vomerine teeth between choanae, transverse; outer finger disks (III, IV) large, equal to or (usually) larger than tympanum; finger webbing formula I trace II 2^{-}-3 III 2 1/2-2^{+} IV; subarticular tubercle under outer finger (IV) usually double, sometimes single, always single under thumb; brown nuptial asperities on male thumb; fold or warty fold along lower arm; tip of prepollex not free and protruding; dorsal surface finely granular; ventral surfaces granular except for smooth lower leg surfaces; toe disk size from inner to outer I<II=III=IV=V or I<II<III=IV=V; outer toe disks (IV, V) equal to or just smaller than outer finger disks; toe webbing formula I 1 2/3-2^{+} II 1-2 1/2 III 1-2 IV 2-1 V; large inner metatarsal tubercle, small round outer metatarsal tubercle; inner and outer tarsal folds; series of warts along heel stripe present or absent; males to 31 mm, females to 40 mm; tibia 53; dorsum uniform or mottled, olive or brown mottled with bronze, tan, or brown in life, dark brown mottled with brown and tan in preservative; light suborbital spot often confluent with light upper lip line, white or cream in life; lateral light stripe on body complete or rarely broken into spots, white or cream in life; light stripe above vent, white or cream in life; venter white or cream in life, males usually with a ventral suffusion of melanophores; light spot on shoulder, remainder of upper arm surface uniform or mottled; light stripe along outer arm, white or cream in life; upper leg surfaces uniform or mottled; light stripe along outer edge of tarsal segment extending across heel, white or cream in life; ventral limb surfaces yellow in life; posterior thigh profusely suffused with melanophores, yellow, covered with gray in life; sole of foot suffused with melanophores; iris bright red.

DISTRIBUTION: Along both Atlantic and Pacific slopes of the Costa Rican cordilleras at elevations between 650-1600 m.

LOCALITIES: PROV. DE ALAJUELA: Cinchona; 4.8 ks S Ciudad Quesada; PROV. DE CARTAGO: Moravia de Chirripó, 1116 m; Morehouse Finca, 7.2 km S Turrialba, 600 m; Río Chitaría on Turrialba-Peralta Road, 775 m; PROV. DE GUANACASTE: Finca Silencio de Tilarán, 850-880 m; PROV. DE HEREDIA: Volcán Poás, Isla Bonita, 1300 m; PROV. DE LIMON: El Tigre,

680 m; PROV. DE PUNTARENAS: Finca Loma Linda, 2 km SSW Cañas Gordas, 1170 m; PROV. DE SAN JOSE: Cerro de la Muerte, S side, 1524 m; nr. confluence of Río Claro and Río La Hondura, 1130-1190 m; 12.9 km N San Isidro de El General, 1500 m; 15 km SW of San Isidro de El General on Dominical road, 880 m (Fig. 34).

Hyla uranochroa Cope

1875 *Hyla uranochroa* Cope: 103, pl. 27, Fig. 4 (Holotype: US 30651, Costa Rica: Provincia de Limón: Cantón de Limón: near Sipurio, approximately 60 m); 1924, Dunn: 2, pl. 1, Fig. 1-1ª; 1952, Taylor: 834, Fig. 49 (synonymy, description); 1966, Duellman: 276 (places *alleei* in synonymy).

1952 *Hyla alleei* Taylor: 831, Fig. 48 (Holotype: RCT 775, Costa Rica: Provincia de Heredia: Cantón de Heredia: Isla Bonita, E slope Volcán Poás).

DIAGNOSIS: In life, unique among lower Central American tree-frogs in having a uniform leaf-green dorsum, red eyes and a continuous enamel-like white stripe along upper lip under tympanum to groin (Fig. 13). The only other species with which it might be confused in life are *Phyllomedusa callidryas, P. saltator* and *P. spurrelli* which have vertical pupils (horizontal in *Hyla)* and lack the lateral light stripe, although some *callidryas* have a dorsolateral light stripe from above the axilla to level of hind limbs. The only other red-eyed species, *H. legleri, H. lythrodes* and *H. rufioculis,* differ from *H. uranochroa* in having the sole of the foot suffused with dark pigment, the dorsal ground color brown in life and preservative and a short snout (distance from eye to nostril less than diameter of orbit); in *H. uranochroa* the dorsum is leaf-green in life, bluish to purple in preservative, the sole of the foot lacks dark pigment and the snout is moderately long (distance from eye to nostril equal to diameter of orbit).

Hyla ebraccata frequently has a lateral light stripe but unlike *H. uranochroa* has a brown dorsal ground color (Fig. 12), in life and preservative, and usually has large contrasting dark dorsal blotches and a broad dark lateral band from tympanum along the flank.

SUMMARY OF CHARACTERISTICS: Snout truncate in dorsal outline, upper lip semicircular in outline; snout rounded in profile; canthus rostralis rounded; tympanum distinct, horizontal diameter 3/5 to 4/5 diameter of eye; male vocal sac single, internal; male vocal slits not entirely hidden by tongue, almost parallel to jaw, vomerine teeth between choanae, transverse; outer finger disks (III, IV) moderate, about 3/5 tympanum; finger webbing formula I trace II 2-3 III 2 1/2-2+ IV; subarticular tubercles single to double under outer finger (IV), always single under thumb (I); light tan nuptial asperities on thumb of male usually present; distinct ulnar ridge; tip of prepollex not protruding; dorsal texture smooth-granular; chin, chest, under surface of arm smooth to smooth-granular, belly and underside of thigh granular, lower surface of tibia smooth; inner toe disk (I) smaller than outer disks; outer toe disks (IV, V) equal to or slightly smaller than outer finger disks; toe webbing formula

I 2⁻-2+ II 1+ -2+ III 1+ -2+ IV 2+ -1+ V, large oblong inner metatarsal tubercle, outer metatarsal tubercle absent; weak inner tarsal fold, moderately developed outer tarsal fold; warts along heel stripe, often produced into a flap; males to 35 mm, females to 39 mm; tibia 51; dorsum uniform, enamel-green in life, bluish to purple in preservative; light upper lip line extends to groin, yellow-white in life; suborbital light spot usually not expanded; light stripe over anus, enamel white in life; upper surface of limb uniform; light stripe on outer arm and on heel, outer tarsus and foot enamel white in life; belly and throat bright yellow in life; undersides of limbs dull yellow in life; posterior thigh not suffused with melanophores, apricot or rich dull yellow in life; no melanophores under toes I and II, few scattered melanophores under digits III, IV, V; iris red.

DISTRIBUTION: Along both Atlantic and Pacific slopes of the Cordilleras de Tilarán, Central and Talamanca of Costa Rica to the Caribbean slopes of Provincia de Bocas del Toro, Panamá, at elevations from 650-1750 m.

LOCALITIES: PROV. DE ALAJUELA: between Angel Falls and La Cinchona, 1370 m; La Cinchona, 1372 m; La Cinchona, S end in a mountain stream, 1250 m; N limits of Ciudad Quesada, 656 m; 1.6 km S Zapote on Zarcero-Ciudad Quesada Road, 1280 m; PROV. DE CARTAGO: La Estrella, 1525 m; 1 km E of Pacayas, 1600 m; Río Izarquito, nr. Pavones on Turrialba-Peralta road, 819 m; 1 km N of Tapantí, 1300-1400 m; PROV. DE GUANACASTE: Finca Silencio de Tilarán, 880 m; PROV. DE HEREDIA: 1.6 km NNE Uvita, watershed of the Río de la Hoja, 1720-1740 m; 1 km E Uvita above San Rafael de Heredia, 1600 m; PROV. DE LIMON: El Tigre, 680 m; nr. Sipurio; PROV. DE PUNTARENAS: 0.8 km W Monteverde, tributary to Río Guacimal, 1372 m; 0.8 km NE Monteverde, 1433-1494 m; 1.2 km ENE Monteverde, 1500 m; 2.4 km NE Monteverde, 1520 m; 3.6 km E Monteverde, 1550-1580 m; PROV. DE SAN JOSE: Cerro de la Muerte, S side, 1585 m; 1.1 km W La Hondura, 1128 m; 0.5 km E,N,S La Palma, 1500 m; La Palma, Río Sucio, 1600 m; 1.4 S Alto La Palma, 1500 m; 14 km N San Isidro de El General, 1420 m; 15 km N San Isidro de El General, 1490 m (Fig. 35).

Hyla picadoi Dunn

1937 *Hyla picadoi* Dunn: 163 (Holotype: MCZ 16002, Costa Rica: Provincia de Heredia: Cantón de Santa Bárbara: Volcán Barba, 2140 m; probably near Los Cartagos SW slope of Volcán Barba); 1952, Taylor: 824, fig. 46 (redescription).

DIAGNOSIS: Immediately distinguished from all other Central American hylids by possessing a large pair of odontoids (bony denticles) at tip of lower jaw. Young *H. picadoi* may occasionally be confused with adult *H. zeteki* since both species apparently are bromeliad-breeders and similar in coloration. In *H. picadoi* the tympanum is vertical, directed laterally and obscure or hidden;

in *H. zeteki* the tympanum is oblique, directed dorsolaterally and well-developed (Figs. 8-9).

SUMMARY OF CHARACTERISTICS: Snout truncate in dorsal outline with a median point and two lateral protuberances for nostrils; snout overhangs jaw, upper lip semicircular in outline; snout acute in profile; canthus rostralis sharp; tympanum usually hidden, horizontal diameter about 1/3 diameter of eye; male vocal sac internal, single; male vocal slits not hidden by tongue, oblique to jaw; vomerine tooth patches almost entirely posterior to choanae, in straight series; outer finger disks (III, IV) large, 2/5 - 1/2 eye; finger webbing formula I 2+ -3+ II 2⁻-3 III 3⁻-2+ IV; subarticular tubercles single to double under all fingers; white glandular nuptial asperities on thumb of male; low ridge of warts on ulnus slightly developed or absent; tip of prepollex not protruding; dorsal texture smooth-granular; throat texture smooth-granular; chest, under surface of arm, belly, and thigh granular; toe disk size from inner to outer I<II=III=IV=V; outer toe disks (IV, V) large, slightly smaller than outer finger disks, about equal to outer finger disks; toe webbing formula I 2-3 II 2⁻-3 1/2 III 1 2/3-3 IV 3-2⁻ V; large inner metatarsal tubercle, no apparent outer metatarsal tubercle; inner tarsal fold weakly developed to absent; no outer tarsal fold; ventral surface of tarsal segment granular; heels weakly tuberculate; males to 33 mm, females 34 mm; tibia 51; dorsum olive-brown or metallic golden-orange with olive cast or brown with heavy yellow fleckings in life, tan with brown markings in preservative; usually with eye mask and a thin dorsolateral dark stripe continuing to sacrum; head metallic gold above in life; throat pale yellow in life; upper limb surfaces uniform to barred, light non-metallic yellowish above or with a reticulum of brown and yellow in life; posterior thigh heavily suffused with melanophores; sole of foot heavily suffused with melanophores; iris red-brown to rusty red.

DISTRIBUTION: The higher regions of the cordilleras of Costa Rica.

LOCALITIES: PROV. DE ALAJUELA: Volcán Poás, nr. Poasito, 2130 m; Volcán Poás, 12.9 km NW Poasito, 2070 m; PROV. DE CARTAGO: Cerro de La Muerte, Inter-American Highway, 2.4 km N Los Cruces, 2770 m; 1 km SE of La Chonta, between La Chonta and Santa María, 2510 m; Volcán Turrialba S slope, 2620 m; PROV. DE HEREDIA: Volcán Barba, 2140 m; E end Volcán Barba, El Gallito, 1900 m; PROV. DE SAN JOSE: nr El Empalme, 2200 m (Fig. 36).

Hyla zeteki Gaige

1929 *Hyla zeteki* Gaige: 4 (Holotype: UM 63875, Panamá: Provincia de Chiriquí: Valle de Caldera, above Boquete); 1937, Dunn: 164 (records, eggs and larvae); 1952, Taylor: 876, Fig. 61 (redescription) ; 1960a, Starrett: 26, Figs. 23-25 (redescription of larvae).

DIAGNOSIS: This frog is a small species, males to 23 mm, females to 27 mm, separated from all other hylids in Costa Rica by having the tympanum oblique and directed dorsolaterally (Figs. 8-9). Its larger (males to 33 mm; females to 34 mm) ally *H. picadoi* has an obscure vertical tympanum that is directed laterally and paired odontoids at the tip of the lower jaw (absent in *H. zeteki).*

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout truncate; snout acute in profile; canthus rostralis moderately sharp; tympanum not clearly distinct, horizontal diameter about 1/3 eye; single internal vocal sac in males; vocal slits in males not entirely hidden by tongue, oblique to jaw; vomerine tooth patches almost entirely posterior to choanae, in transverse series; outer finger disks (III, IV) moderately large, from equal to 1 1/2 times the tympanum; finger webbing formula I trace II 2-3 III 3^{-}-2^{+} IV; subarticular tubercles single to double under all fingers; white glandular nuptial asperities in males; low series of warts along lower arm weakly developed to absent; tip of prepollex not protruding; dorsal texture smooth, granular on sides of body; chin texture smooth to smooth-granular; chest, lower surfaces of arm, belly, and thigh granular; underside of tibia smooth to smooth-granular; inner toe disk (I) smaller than outer disks; outer toe disks large, equal to or slightly smaller than outer finger disks; toe webbing formula I 2-3 II 2^{-}-3^{+} III 2-3 IV 3^{-}-2 V; large oblong inner metatarsal tubercle; outer metatarsal tubercle small, rounded, raised; low inner tarsal fold; low series of warts on outer tarsal segment; heel warty-tuberculate; males to 23 mm, females to 27 mm; tibia 56; dorsum lacking distinct pattern, straw in life, tan-brown in preservative; concentration of melanophores on head, brown in life; some specimens with dark stripe from under nostril to under eye; ventral area white in life; lower surfaces of arms and legs yellow in life; all specimens with a dark wrist stripe, remainder of dorsal limbs uniform, straw in life; posterior thigh heavily suffused with melanophores; sole of foot suffused with melanophores; iris red-brown.

DISTRIBUTION: Mountains of central Costa Rica and western Panamá.

LOCALITIES: PROV. DE CARTAGO: La Estrella, 1525 m; PROV. DE HEREDIA: E slope Volcán Poás, Isla Bonita, 1675 m; PROV. DE SAN JOSE: La Hondura, 1200 m; 0.5 km E, N, S, 1.4 km S of Alto La Palma, 1500 m (Fig. 36).

Hyla angustilineata Taylor

1952 *Hyla angustilineata* Taylor: 850, Fig. 54 (Holotype: US 75060, Costa Rica: Provincia de San José: Cantón de Coronado, La Palma, 1500 m).

DIAGNOSIS: The only species in the region without hand webbing, with a narrow dorsolateral light stripe from above tympanum to level of hindlimbs (Fig. 10) and the under surfaces peppered with dark spots. The only other

hylids with a dorsolateral light stripe *(H. colymba, H. ebraccata, H. microcephala, H. phlebodes* and *P. callidryas)* have considerable finger webbing and the lower surfaces without dark spotting.

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout subelliptical to pointed, upper lip outline rounded; snout rounded in profile; canthus rostralis sharp; tympanum moderate, horizontal diameter 2/5-1/2 diameter of eye; male vocal sacs internal, paired, lateral; male vocal slits not completely hidden by tongue, oblique to jaw; vomerine teeth at level of posterior margins of choanal openings; outer finger disks large, 1-1 1/4 times the tympanum; fingers without distinct webbing; subarticular tubercle double under outer finger (IV), single to double under remaining fingers; brown nuptial asperities on males extending to disk of thumb (I); ulnar ridge absent to weakly developed; tip of prepollex not protruding externally; dorsum smooth; chin surface smooth-granular, chest, under surface of arm and belly granular; rest of underside of leg smooth; toe disk size from inner to outer I<II<III=IV=V; outer toe disks (IV, V) slightly smaller than outer finger disks; toe webbing formula I 2^{+}-3^{--} II 2^{--}-3 1/3 III 2-3 1/4 IV 3-2^{--} V; large oblong inner metatarsal tubercle, outer metatarsal tubercle not apparent; inner tarsal fold weak, outer tarsal region warty; heel slightly to very warty, often one prominent wart; males to 31 mm; tibia 56; dorsum uniform or with a few dark punctations, beige-bronze or green with streak of green behind eye and above lateral stripe (if dorsum not green) or with bronze flecks in life, light gray with a hint of brown to dark chocolate in preservative; dorsolateral line from tip of snout through nostril, eye, over tympanum to sacrum, silver white bordered below by dark brown which is bordered below by light brown or chocolate bordered with thin white lines in life; upper lip and lore golden bronze in life; entire ventral surface with dark spots, yellow with green cast to yellow cream with brown flecks in life; dorsal limb pattern uniform with small dark spots, brown or beige with dark brown flecks in life; posterior thigh suffused with melanophores, yellow with green cast in life; sole of foot suffused with melanophores; iris orange-bronze with central dark brown band.

DISTRIBUTION: Lower montane zone of the Cordilleras de Tilarán and Central of Costa Rica.

LOCALITIES: PROV. DE HEREDIA: S fork of Río Las Vueltas nr. Cerro Chompipe, 2000 m; PROVS. DE PUNTARENAS - ALAJUELA: 3.2 km ENE of Monteverde, 1590 m; PROV. DE SAN JOSE: La Palma, 1520 m (Fig. 37).

Hyla colymba Dunn

1924 *Hyla albomarginata,* Dunn: 3, pl. 1, figs. 2-2a (misidentification, description of larvae).

1931a *Hyla colymba* Dunn: 400 (Holotype: MCZ 10234, Panama: Provincia de Bocas del Toro: La Loma, 450 m); 1966 Duellman: 267 (*alvaradoi* synonymized).

1952 *Hyla alvaradoi* Taylor: 882, Fig. 63 (Holotype: KU 30886, Costa Rica: Provincia de Cartago: Cantón de Turrialba: Moravia de Chirripó); 1958, Taylor: 30, fig. 12 (life colors, eggs).

DIAGNOSIS: Readily separated from other Costa Rican hylids by having the following combination of features: dorsolateral light stripe and circular mental gland. The latter feature is unique to *H. colymba* among the species considered in the present paper.

H. colymba may be confused with juvenile *H. rufitela* in preservative on superficial examination. In life the latter has a dark green ground color, green bones and bright red webs and could not be mistaken for the pale yellowish-green, white-boned *colymba. H. rufitela* has a free protuberant prepollex, with a terminal spine in males, a large heel tubercle and no white mental gland (prepollex without protuberant free tip, no heel tubercle and a mental gland present in *colymba).*

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout truncate, upper lip semicircular; canthus rostralis distinct, slightly rounded; circular mental gland; tympanum evident, covered with skin, less than 1/2 eye; vocal sac in male scarcely discernible externally, seemingly paired; male vocal slits some distance from jaw bones, mostly behind tongue; vomerine teeth in 2 rather high fasciculi, extending posterior to choanal openings, acute angulate; finger webbing formula I trace II 2-3 III 2-2 IV; subarticular tubercles single under finger IV; ulnar ridge; dorsum smooth; venter granular; toe webbing formula I 3-3 II 2-2 III 1-2 IV 2-1 V; inner metatarsal tubercle indistinct, outer not apparent; male 31 mm; tibia 58; dorsal pattern uniform with clusters of chromatophores; dorsal limb pattern uniform; color in preservative white with sparse peppering of fine black pigment and a scattering of minute rounded cream dots on the dorsal surfaces; color in life green-yellow above, yellow predominating; hands and feet yellow, legs yellow with a slight green wash on toe pads but not under fingers; cream-yellow line from eye back on shoulder; venter cream; under legs flesh with a slight yellow tinge; sides yellow-cream, nearly uniform with a slight brownish wash dorsolaterally; an ochre yellow line borders the anal flap.

DISTRIBUTION: Subtropical areas from Costa Rica to the Darién region of eastern Panamá.

LOCALITY: PROV. DE CARTAGO: Moravia de Chirripó, 1220 m (Fig. 38).

REMARKS: DUELLMAN (25) reported this species from La Lola, Provincia de Limón, Costa Rica. This locality is in the lowland tropical belt in a very different vegetational association than other sites for the species. All other records

for *colymba* lie in subtropical situations above 700 m. in elevation. Dr. Duellman (pers. comm.) has informed us that the La Lola record is based upon UM 118424. Examination of the specimen indicates that it is a somewhat faded juvenile or subadult *Smilisca sordida.* It differs most obviously from *colymba* in having extensive finger and toe webbing: I trace II 1 1/4-2 1/4 III 2⁻-1 1/2 IV; I 1-1+ II 1-1 1/4 III 0-1/2 IV 1-1 V; and the vomerine tooth patches far anterior between the choanae. In all other features this frog agrees with *S. sordida.*

Hyla lancasteri Barbour

1928 *Hyla lancasteri* Barbour: 31, Pl. 4, fig. 2 (Holotype: MCZ 13062, Costa Rica: Provincia de Cartago: Cantón de Turrialba: Peralta, 368 m); 1966, Duellman: 271.

1932 *Hyla boulengeri,* Dunn and Emlen (in part): 25.

1952 *Hyla moraviensis* Taylor: Taylor: 865, fig. 57 (Holotype: KU 30284, Costa Rica: Provincia de Cartago:Cantón de Turrialba: Moravia de Chirripó, 1116 m); 1960a, Starrett: 21, figs. 17-18 (larvae).

DIAGNOSIS: *H. lancasteri* differs from all other Costa Rican species, except *H. boulengeri* and *A. coronata,* in having the posterior surface of the thigh marked with solid dark bars that alternate with lighter color. The dark thigh bars are restricted to the anterior, upper and posterior surfaces of the thigh in *H. lancasteri* but continue as rings, bars or spots onto the ventral thigh surface in *Anotheca. H. lancasteri* has a weak but conspicuous web between fingers II-III-IV but *H. boulengeri* and *A. coronata* lack hand webs. This moderate sized species further differs from *H. boulengeri* in having a short, blunt snout (distance from eye to nostril less than diameter of orbit)versus snout elongate (distance from eye to nostril exceeding diameter of orbit). In both *H. lancasteri* and *H. boulengeri* the light areas between the dark bars are bright yellow in life (white in preservative). They are the only species in the region with alternating dark bars and yellow interspaces on the posterior thigh surfaces.

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout truncate, upper lip semicircular in outline; snout acute in profile; canthus rostralis sharp; tympanum hidden to distinct, horizontal diameter approximately 1/2 eye diameter; vocal sac single, internal in males; vocal slits of males not hidden by tongue, oblique to jaw; vomerine tooth patches extend posterior to choanae, transverse to obtuse angulate; outer finger disks (III, IV) slightly smaller to a little larger than tympanum; finger webbing formula I 3-3+ II 1 2/3-2 2/3 III 2 1/3-2 IV; subarticular tubercles single to double under all fingers; males with brown nuptial asperities; moderately to well developed row of warts along lower arm; tip of prepollex not projecting; dorsum moderately to strongly tuberculate; chin surface smooth, belly granular; toe disk size from inner to outer I<II=III=IV=V or I<II<III=IV=V; outer toe disks (IV, V) large, slightly smaller than outer

finger disks; toe webbing formula I 1 1/2-2+ II 1-2+ III 1 1/4-2 IV 2-1 V; large inner metatarsal tubercle, no outer tubercle; weak inner tarsal fold, series of warts on outer tarsal area; heel weakly to strongly tuberculate; males to 32 mm, females to 33 mm; tibia 54; dorsum uniform to darkly spotted, cream, lavender, or gray-brown with brown splotches and varying amounts of green flecking in life, tan to deep brown in preservative; sides of body with several dark spots; a prominent dark spot in groin; chin and chest white to pearl gray posteriorly in life; venter cream in life; dorsal arms with faint cross bars; upper legs with faint bars; concealed portions of upper and lateral surfaces of legs with markedly contrasting dark bars, areas between bars bright yellow in life, white in preservative; sole of foot lightly suffused with melanophores; iris brown.

DISTRIBUTION: Caribbean foothills and slopes of the mountains of Costa Rica and northwestern Panamá.

LOCALITIES: PROV. DE CARTAGO: 7.4 km. W Juan Viñas; Moravia de Chirripó, 1160 m; Peralta, 350 m; Quebrada Bóveda, on Pavones Road, 700 m; Río Chitaría, on Pavones Road, 775 m; Volcán Turrialba, S slope, 914 m; PROV. DE LIMON: El Tigre, 680 m. (Fig. 37).

Hyla pseudopuma Gunther

1898 *Hyla puma,* Boulenger: 478 (misidentification).

1901 *Hyla pseudopuma* Gunther: 274, pl. 72, Figs. A. B. (Syntypes: BM 1947. 2. 23 16-23, 2.2.23.2-3, Costa Rica: Provincia de San José: Cantón de Coronado: La Palma, 1500 m), 1952, Taylor: 817, Figs. 59-60; 1958: 31, Figs. 13-14 (records, color variation, redescription); 1960a, Starrett: 22, Figs. 19-20 (larvae).

DIAGNOSIS: A medium (males to 45 mm) to large (females to 52 mm) tree-frog that exhibits a considerable amount of variation in structural and color characteristics. Although most specimens are easy to identify, extremes in the variation and juveniles frequently may be mistaken for other species. *H. pseudopuma* never has the following striking features of coloration, typical of certain other Costa Rican forms: dark bars on anterior, posterior or ventral thigh surfaces; lateral or dorsolateral light stripes; suborbital white spot; discrete light spots on posterior surfaces of thigh, or the venter nearly completely dark in color. The species always lacks fleshy fringes on the posteroventral margins of lower arm and leg, a protuberant prepollex, curved vomerine tooth series, odontoids at tip of lower jaw, and a strongly oblique tympanum. The hands have a considerable amount of webbing and the toe webbing is reduced.

Individuals of *H. pseudopuma* are most likely to be confused with large individuals of *S. puma,* juvenile or male *Smilisca sordida,* and adult female *H. rivularis* and *H. tica.*

Superficially, *S. puma* and *H. pseudopuma* resemble one another in form and coloration. *S. puma* has the groin and flank marked with a fine dark

reticulum, a distinct light stripe bordered below by a dark stripe along the posterior margin of the tarsal and foot segments of the hind limb and paired elongate dorsal blotches running from head to sacrum that anastomose at one to several points across the mid-line. In *H. pseudopuma* the groin and flank are marked with bright yellow spots in life but no fine dark reticulum is present, no distinct light and dark tarsal to foot stripe is present and while the dorsum may be uniform or marked with large dark blotches the pattern does not approach the condition described for *S. puma.* In addition the vomerine tooth patches lie near the level of the middle of the choanae in *S. puma* (Fig. 1) and at the level of posterior margin of the choanae and extending posterior to them in *H. pseudopuma* (Fig. 2). *S. sordida* is also among the most variable species in Costa Rica but the two may be distinguished by vomerine tooth position (in *H. pseudopuma* the patches lie at the level of the posterior margin of the choanae and extend slightly posteriorly, in *S. sordida* the patches are near the level of the middle of the choanae) and flank and thigh coloration (in *H. pseudopuma* the groin and lower edge of lateral ground color is marked with bright yellow spots in life, the spots are faded and obscure in preservative; in *S. sordida* the groin and flanks are pale dirty-yellow to white, reticulated with purplish-brown, the reticulum is obvious in preserved specimens, the posterior surface of the thigh is uniform brown or yellow in *H. pseudopuma* and purple or brown usually mottled with light in *S. sordida*). The amount of toe webbing is also diagnostic. In *H. pseudopuma* the modal formula is I 1 1/2-2+ II 1+-2 1/2 III 1 1/2-2 1/2 IV 2 1/2-1+-V, in *S. sordida* I 0-1+ II 0-1 1/4 III 0-1½ IV 1 1/2-0 V; the web between toes I-II does not reach the base of the disk on toe I and at least two phalanges of toe II free of webbing in *H. pseudopuma;* the web almost always reaches the base of the disk on toe I and only the first phalange is free of webbing on toe II in *S. sordida.*

H. rivularis and *H. tica* may be occasionally confused with immature *H. pseudopuma,* but the acute snout profile, tympanum 1/3 diameter of eye and usually heavy dark ventral peppering will separate the former from the latter (rounded snout profile, tympanum at least 1/2 diameter of eye and never more than a few ventral dark flecks). *H. tica* has a strongly tuberculate dorsum and a series of warts along the outer margin of the lower arm while the dorsum is smooth to granular and there is no series of warts along the lower arm in *H. pseudopuma.*

Occasional specimens of *H. pseudopuma* have the entire flank blue-purple in life, but this color changes to brown in preservative. Preserved individuals with dark flanks might be erroneously associated with *S. baudinii, S. phaeota* or *H. ebraccata,* which have distinct dark lateral bands. In the former two species the bands extend from the tympanum to axilla as dark brown areas on a slightly lighter green, gray or brown ground color. In *H. ebraccata* the lateral brown band may extend to mid-body and is usually delimited above and below by a light stripe. In the examples of *H. pseudopuma* with dark flanks the entire flank is unicolor purplish (brown) invaded below by yellow spots and not delimited by a light stripe.

SUMMARY OF CHARACTERISTICS: Snout truncate with a median projection in dorsal outline; snout rounded in profile; canthus rostralis sharp; tympanum distinct, horizontal diameter 1/2-2/3 eye diameter; male vocal sacs internal, paired, lateral; vocal slits of male not entirely hidden by tongue, oblique to jaw; vomerine teeth extend posterior to choanal openings; outer finger disks (III, IV) equal to or smaller than tympanum; finger webbing formula I trace II 2⁻-3⁻ III 2 1/3-2 IV; subarticular tubercles single to double under all fingers; brown nuptial asperities on male thumb extend to disk; warty fold or series of warts along lower arm; tip of prepollex not protuberant; dorsal texture smooth to slightly granular; chin surface smooth granular to granular; chest, under surface of arm and thigh, and belly granular; rest of lower leg surface smooth; toe disk size from inner to outer I < II = III = IV = V or I < II < III = IV = V; outer toe disks large, equal to or slightly smaller than outer finger disks; toe webbing formula I 1 1/2-2+ II 1+-2 1/2 III 1 1/2-2 1/2 IV 2 1/2-1+ V; inner metatarsal tubercle oblong, large; outer metatarsal tubercle small, round, or absent; inner tarsal fold usually distinct, outer tarsal fold absent; heel sometimes with series of warts; males to 45 mm, females to 52 mm; tibia 51; dorsal pattern variable-uniform, spotted, or blotched, brown blotched or spotted with tan in life, gray, tan, brown or chocolate in preservative; flank spotted, mottled, or solid blue-purple in life in some; groin spots yellow in life if present; ventral surfaces yellow in life; upper limb pattern variable-uniform to definitely barred; light heel and seat stripe, ivory in life; posterior thigh with scattered to profuse suffusion of melanophores, yellow or brown (anterior surface also) in life; sole of foot suffused with melanophores; iris gold.

DISTRIBUTIONS Moderate altitudes in the Costa Rican cordilleras, to northwestern Panamá.

LOCALITIES: PROV. DE ALAJUELA: Between Angel Falls and La Cinchona, 1370 m; 0.3 km N Angel Falls on Vara Blanca-Cariblanco road, 1494 m; La Cinchona, 1372 m; S slopes of Volcán Poás; 1.6 km S of Zapote on Zarcero-Ciudad Quesada road, 1280 m; PROV. DE CARTAGO: 28.8 km S Cartago on Inter-American Highway, 2115 m; 1.3 km SE La Chonta, 2340 m; 1 km SE La Chonta, between La Chonta and Santa María, 2510 m; El Empalme, 2290 m; Moravia de Chirripó; 1116 m; Río Playas at Pacayas-Santa Cruz road, 1650 m; PROV. DE HEREDIA: Alto del Roble, 2020-2040 m; Volcán Barba, nr. Cinco Esquinas, 9.8 km S Vara Blanca, 1524 m; Volcán Barba, Finca Montecristo, 1860 m; Volcán Poás, Cinchona, 1220-1680 m; Volcán Poás, Vara Blanca; PROV. PUNTARENAS: 0.8 km NE Monteverde, 1433-1494 m; 1.2 km ENE Monteverde, 1500 m; 2.4 km NE Monteverde, 1520 m; 3.2 km ENE Monteverde, (on Puntarenas-Alajuela Boundary), 1590 m; 3.6 km E Monteverde, 1550-1580 m; PROV. DE SAN JOSE: Empalme, 2290 m; 0.5 km S La Palma, 1500 m; 1.4 km S of La Palma, 1500 m; Rancho Redondo, 2000 m; nr. confluence of Río Claro and Río La Hondura, 1130-1190 m; San Pedro de Montes de Oca, Ciudad Universitaria, 1160 m (Fig. 39).

Phrynohyas venulosa (Laurenti)

1768 *Rana venulosa* Laurenti; 31 (based on Seba, 1734: 115, pl. 72, Fig. 4); validated by fiat, International Commission of Zoological Nomenclature, 1958: 169.

1803 *Hyla venulosa* Daudin: 35.

1824 *Hyla zonata* Spix: 41, pl. 12, Fig. 1 (Holotype: apparently lost, Brazil: Amazonas: Río Teffe); rejected by fiat, International Commission of Zoological Nomenclature, 1958: 169).

1843 *Phrynohyas zonata,* Fitzinger: 30.
Acrodytes venulosa, Fitzinger: 30.

1877 *Hyla spilomma* Cope (Holotype: apparently lost, Mexico: Veracruz: Cosamaloapam).

1945 *Acrodytes modesta* Taylor and H. M. Smith: 594, pl. 27, Fig. 2, pl. 28, Figs. 2-3 (Holotype: US 115013, México: Chiapas: Cruz de Piedra, near Acacoyagua).

1958 *Phrynohyas venulosa* International Commission of Zoological Nomenclature: 169 (validation by fiat; rejection of *Acrodytes* Fitzinger). For complete synonymy see DUELLMAN (22).

DIAGNOSIS: A very large species (males to 90 mm, females to 96 mm) with a very warty dorsum, green bones in life and paired external lateral vocal sacs in males. The species lacks fringes along the lower arm and leg, a protuberant prepollical tip and the distinctive features of coloration (lateral or dorsolateral dark or light stripes or bands, barred or spotted posterior thigh surfaces, mid-dorsal dark stripe, suborbital light stripe, or flank bars). Small specimens of *P. venulosa* might rarely be mistaken for other similarly colored forms with strongly tuberculate or warty dorsal surfaces *(H. tica* and *S. sila).* Both of these forms have a well-developed series of warts along the outer edge of the lower arm and are never larger than 41 mm (versus no series of warts along lower arm and much larger, to 96 mm).

Smilisca baudinii and *S. phaeota* agree with *Phrynohyas* in having paired external lateral vocal expansions in males. These forms have a smooth dorsum, *S. baudinii* has a well-developed series of warts along the forearm (absent in *P. venulosa*) and *S. phaeota* has a reticulum of narrow dark lines in groin and along the flank (the groin and flank coloration is an extension of the dorsal pattern in *P. venulosa*).

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout rounded to nearly semicircular; snout rounded in profile; canthus rostralis round; tympanum large, horizontal diameter 1/2 to 2/3 eye diameter, tympanum may be partially overhung by enlarged parotoid glands; male vocal sacs external, paired, lateral; male vocal slits not entirely hidden by tongue, oblique to jaw; vomerine teeth lie at level of posterior margins of choanal openings, transverse; outer finger disks (III, IV) large, 1-1 1/4 times tympanum; finger webbing formula I 2^{+}-3^{--} II 1 1/2-2 1/2 III 2 1/3-2^{+} IV: subarticular tubercles single to double under

outer finger (IV), always single under thumb (I); tan nuptial asperities on thumb of male; lower arm without ridge or scattered series of warts; tip of prepollex not protuberant; dorsum strongly tuberculate, glandular; chin, chest, belly, under surface of thigh granular; underside of arm smooth-granular; underside of ventral tibia area smooth; toe disk size from inner to outer I < II = III = IV = V or I < II < III = IV = V; outer toe disks (IV, V) slightly smaller than outer finger disks; toe webbing formula I 0-2⁻ II 0-2 III 1-2 IV 2⁻ -0 V; large oblong inner metatarsal tubercle; outer metatarsal tubercle small, distinct, round; weakly developed inner tarsal fold, no apparent outer tarsal fold; heel slightly warty; males to 90 mm, females to 96 mm; tibia 48; dorsum uniform or blotched, dark yellow-brown with or without yellow-brown spots in life, tan, brown, chocolate, or brown-black in preservative; venter dirty light brown or cream in life; upper limbs uniform with or without dark punctations or barred; heels and fingers I, II clay in life; posterior surface of thigh suffused with melanophores, clay in life; sole of foot suffused with melanophores.

DISTRIBUTION: Lowlands of tropical México to southern Brasil.

LOCALITIES: PROV. DE ALAJUELA: Los Chiles, 70 m; PROV. DE GUANACASTE: Bebedero: Las Hurras (sic); 0.8 km E Finca Jiménez on Río Higuerón, 11 m; 17.1, 19.8, 20, 20.3, 33.1 km N Liberia; PROV. DE PUNTARENAS: Palmar, 16 m; Parrita, 5 m; Parrita, La Julieta, Finca La Ligia; 3.2 km SW Rincón de Osa, 30 m (Fig. 40).

REMARKS: In his review of the genus DUELLMAN (22) recognized three species in Central America, *P. venulosa* (this name fixed by fiat of the International Commission of Zoological Nomenclature in 1958 to the form called *zonata* in Duellman's paper), *P. modesta* and *P. spilomma.* Subsequently, he (DUELLMAN, 25) placed *modesta* in the synonymy of *spilomma,* because the former appears to represent a genetic variant with a uniform dorsum of the latter, which was based on specimens having bold dark dorsal blotches.

According to Duellman *P. spilomma* ranges along the Atlantic lowlands of Middle America from Veracruz, México, to central Nicaragua and along the Pacific coast from the Isthmus of Tehuantepec to El Salvador; and *P. venulosa* is an essentially South American species ranging northward along the Pacific versant of Central America to Nicaragua. The two species were distinguished solely on differences in coloration. *P. venulosa* usually has a large dark, light-bordered patch on the back and was differentiated from *spilomma* on the basis of having the leg bands outlined by dark. Most *spilomma* also have a dark, light-bordered dorsal patch but according to Duellman the leg bands are usually not outlined by a dark line, or if they are the center of the band is stippled with dark pigment. That the leg band differences do not provide a guide to separating the two forms is suggested by Duellman's own figures: Pl. 5, Fig. 2 of a *venulosa* from Costa Rica and Pl. 6, Fig. 2 of another from Venezuela agree with

spilomma. In addition to the blotched and banded individuals, some examples of both forms are uniform brown above or with small dark flecks.

The Costa Rican specimens at hand contribute to the solution of this problem. The Atlantic slope examples are all uniform brown above, but since there are only four frogs all from the same locality, Los Chiles, this sample probably indicates local variation. The specimens from the Pacific lowlands are blotched and banded. In terms of leg bands the sample is variable. One specimen from Guanacaste; near Finca Jiménez, near Cañas (CRE 842) has leg bands of *venulosa.* All others have the bands outlined with dark and heavily speckled with dark punctations, the pattern presumably characteristic of *spilomma.* Apparently the populations along the Pacific coast of Costa Rica are variable in the supposedly diagnostic pattern characteristics and suggest an intermediate gene pool. For this reason we regard all Central American *Phrynohyas* as representative of a single species population for which the name *venulosa* must apply.

Phyllomedusa annae Duellman

1865a *Agalychnis moreletii,* Cope: 110 (misidentification with *moreletii,* A. Dumeril).

1867 *Hyla moreletii,* Keferstein: 256 (misidentification).

1957 *Phyllomedusa moreletii,* Funkhouser: 40 (in part).
Phyllomedusa dacnicolor, Funkhouser: 37 (in part; Costa Rican specimens = *annae).*

1963 *Phyllomedusa annae* Duellman: 1, Figs. 1-4 (Holotype: KU 64020, Costa Rica: Provincia de Cartago: Cantón de Paraíso: Tapantí, 1200 m).

DIAGNOSIS: A large (males to 63 mm, females to 84 mm) tree-frog, with dorsum green in life, bluish-purple in preservative and the flank blue to purple in life and dark in preservative, without contrasting light markings. *P. annae* resembles most closely *P. saltator* which has less toe webbing, web between toes IV-V originating at or proximal to proximal (3rd from toe tip) subarticular tubercle of toe IV and has bright red eyes in life (web between toes IV-V originating distal to proximal subarticular tubercle of toe IV and eyes yellow to yellow-orange in life, in *P. annae).* The species differs most obviously from *P. spurrelli* which also lacks contrasting dark and light lateral areas in flank color since the flank is orange in life in the latter (light in preservative).

Small *P. annae* might rarely be confused with preserved *H. uranochroa* since the latter may be deep bluish purple in coloration. The two differ in: a lateral light stripe, a suborbital light spot and posterior surface of thigh without dark pigment in *H. uranochroa* versus no lateral light stripe, no suborbital light area and posterior surface of thigh suffused with dark pigment in *P. annae.*

DISTRIBUTION: Pacific and Atlantic slopes of the Cordilleras de Talamanca, Central and Tilarán of Costa Rica at intermediate elevations.

LOCALITIES: PROV. DE CARTAGO: Cartago, 1376 m; 2 km S of Cartago; Chirripó; Moravia de Chirripó, 1116 m; Tapantí, Tapantí bridge over Río Grande on S bank of river; PROV. DE GUANACASTE: Finca Silencio de Tilarán, laguna, 780 m; PROV. DE HEREDIA: Cinchona; PROV. DE SAN JOSE: S margin of Río María Aguilar; Ciudad Universitaria; Guadalupe; La Palma; San José, 1160 m; San Pedro de Montes de Oca (Fig. 41).

Phyllomedusa calcarifer (Boulenger)

1902 *Agalychnis calcarifer* Boulenger: 52 (Holotype: BM 1947. 2. 24. 22; Ecuador: Provincia de Esmeraldas: Río Durango, 100 m).

1957 *Phyllomedusa calcarifer,* Funkhouser: 24, Fig. 11 (redescription)

DIAGNOSIS: The only species of Costa Rican tree-frog with a green dorsum (bluish to purple in preservative), a series of dark vertical bars along flank on a light ground color and a series of transverse dark bars on upper surface of thigh. The only other member of the family in the region with dark flank bars is *H. rosenbergi* which is light brown in color, has a mid-dorsal dark stripe on head and the dark lateral bars are narrow brown wavy lines.

P. callidryas has the flanks dark with a series of light vertical lines or bars and cannot be confused with *P. calcarifer.*

DISTRIBUTION: Lowlands of northwestern Ecuador through the Colombian Chocó, to the Caribbean versant of Panamá and Costa Rica.

LOCALITY: PROV. DE HEREDIA: Finca La Selva, 100 m (Fig. 42).

Phyllomedusa callidryas (Cope)

1862 *Hyla callidryas* Cope: 359 (Holotype: AP 2091, Panamá).

1865a *Agalychnis callidryas,* Cope: 110 (generic features).

1885 *Agalychnis helenae* Cope: 182 (Holotype: US 13737, Nicaragua).

1957 *Phyllomedusa helenae,* Funkhouser: 32, Fig. 20 (redescription).
Phyllomedusa callidryas callidryas Funkhouser: 33, Fig. 21 (redescription).
Phyllomedusa callidryas taylori Funkhouser: 34, Fig. 22 (Holotype: FM 100166, México: Veracruz: Tierra Colorada).
Phyllomedusa dacnicolor, Funkhouser: 37 (in part; Honduras example).

1967 *Phyllomedusa callidryas,* Savage and Heyer: (synonymize *helenae* and *taylori* with *callidryas).*

DIAGNOSIS: Immediately recognizable in life as the only green, red-eyed tree-frog in lower Central America with vertical light lines or bars on dark flanks. In preservative the dorsum is bluish to purple but the flank pattern will separate the species from all other forms.

DISTRIBUTION: Caribbean lowlands from Panamá to central Veracruz, México; Pacific lowlands of the Golfo Dulce region of Costa Rica and western Panamá.

LOCALITIES: PROV. DE ALAJUELA: Laguna Monte Alegre; 3.2 km NE Muelle de Arenal; San Carlos; PROV. DE CARTAGO: Tunnel Camp nr. Peralta; Turrialba, 646 m; 3.2 km. SW Turrialba; PROV. DE GUANACASTE: Finca San Bosco, 700 m; 2 km E Tilarán; 4 km ENE of Tilarán; Finca Silencio de Tilarán, laguna 780 m; 3.8 km from Tilarán toward Arenal; PROV. DE LIMON: Batán; confluence of Ríos Lari and Dipari about 20.8 km SW of Amubri; La Lola; Pandora; Puerto Viejo, 100 m; Suretka; El Tigre, 9 km SW of Siquirres; PROV. DE PUNTARENAS: 3 km NW Buenos Aires; Golfito; 4 km ESE Palmar Sur; Parrita; Potrero Grande; Río Ferruviosa, 7.2 km S of Rincón de Osa; 21.8 W of San Ramón; Villa Neily; PROV. DE SAN JOSE: San Isidro de El General; 5 and 1.5 km NE Alfombra (Fig. 43).

Phyllomedusa saltator (Taylor)

1955 *Agalychnis saltator* Taylor: 527, Fig. 10 (Holotype: KU 35615, Costa Rica: Provincia de Guanacaste: Cantón de Tilarán: 4 km NNE Tilarán: Laguna at Finca de Jenkins, 780 m.

1957 *Phyllomedusa saltator,* Funkhouser: 36, Fig. 23 (redescription).

DIAGNOSIS: The only member of the genus in Costa Rica, except *P. annae,* with considerable finger and toe webbing and dark flanks without contrasting light areas. From *P. annae* it may be distinguished by having red eyes in life and reduced toe webbing (web between toes IV-V originates at or proximal to 3rd subarticular or proximal tubercle of toe IV). In *P. annae* the iris is yellow to orange in life and the web on toe IV originates distal to the proximal subarticular tubercle on the outer side.

Sometimes *P. saltator* might be confused with adult *H. uranochroa* which are also green dorsally and have red eyes. *P. saltator* never has a lateral light stripe or suborbital light spot and the posterior surface of thigh is suffused with dark pigment. In *H. uranochroa* a light lateral stripe and suborbital light area are present and the posterior surface of the thigh is without dark pigment.

DISTRIBUTION: Atlantic versant of northern Costa Rica.

LOCALITIES: PROV DE GUANACASTE: Finca Jenkins - Finca San Bosco de Tilarán, 780 m; PROV. DE HEREDIA: Finca La Selva, 100 m (Fig. 44).

Phyllomedusa spurrelli (Boulenger)

1913 *Agalychnis spurrelli* Boulenger: 1024, text-Fig. 177, pl. 103 (Syntypes: BM 1913. 11. 12. 127-128, 1947. 2. 24. 24-25, Colombia: Provincia de Chocó: Peña Lisa near Condoto, 100 m).

1957 *Phyllomedusa spurrelli,* Funkhouser: 39, Fig. 8 (redescription).

DIAGNOSIS: Unique among Costa Rican tree-frogs in life by having bright red eyes, green dorsal color and the flanks uniform orange. In preservative distinguished from *P. annae* and *P. saltator* by the light flanks (flanks dark in the latter two species) and from *H. uranochroa,* another green tree-frog with red eyes in life, by lacking a lateral white stripe and white spot under eye and having more finger webbing (web between fingers II-III leaving less than two phalanges of finger III free of web). In *H. uranochroa* a lateral light stripe and suborbital light spot are present and more than two phalanges are free of webbing on finger III.

DISTRIBUTION: Lowlands of the Colombian Chocó; Barro Colorado Island, Panamá; and the Golfo Dulce region of Costa Rica.

LOCALITIES: PROV. DE PUNTARENAS: Rincón de Osa; Río Ferruviosa, 7.2 km S of Rincón de Osa; PROV. DE SAN JOSE: 16 km SW San Isidro de El General, 884 m (Fig. 42).

Phyllomedusa lemur (Boulenger)

1882 *Phyllomedusa lemur* Boulenger: 425 (Holotype: BM 74-8-11-9, Costa Rica); 1952, Taylor: 809, Fig. 41.

1887 *Agalychnis lemur,* Cope: 15 (list).

DIAGNOSIS: The only tree-frog in Costa Rica lacking finger and toe webs.

DISTRIBUTION: Intermediate elevations on both slopes of the Cordilleras de Talamanca, Central and Tilarán of Costa Rica; extending into Panamá.

LOCALITIES: PROV. DE ALAJUELA: Cinchona; 4.8 km S. Ciudad Quesada; PROV. DE CARTAGO: Moravia de Chirripó; bridge over Río Grande at Tapantí; road from Turrialba to Peralta at Río Chitaría; El Silencio de Sitio Mata, La Suiza; Tapantí; PROV. DE HEREDIA: Cariblanco; PROV. DE LIMON: El Tigre, 9 km SW of Siquirres; confluence of Río Claro and Río La Hondura; 1.1 km W La Hondura; La Palma; 0.8 and 1.4 km S La Palma (Fig. 44).

Smilisca baudinii (Duméril and Bibron)

1841 *Hyla baudinii* Duméril and Bibron: 564 (Holotype: PM 401, México).

1865b *Smilisca baudinii,* Cope: 65; 1952, Taylor: 794 (specimens from Costa Rica); 1960b, Starrett: 302 (redefines genus).

1954 *Hyla manisorum* Taylor: 630, Fig. 11 (Holotype: KU 34927, Costa Rica: Provincia de Limón: Cantón de Limón: Batán, 15 m) for fuller synonymy see DUELLMAN and TRUEB (26).

DIAGNOSIS: A large species (males to 68 mm, females to 72 mm) with a smooth dorsum, enlarged warts along outer margin of forearm, paired external lateral vocal expansions in males and a broad dark brown lateral band from tympanum to level of axilla. *S. baudinii* lacks the trenchant structural features (fringe-limbs, oblique tympanum, protuberant prepollex, and curved vomerine tooth patches) and coloration (barred posterior or lower thigh surfaces, dorsolateral or lateral light stripes, dorsolateral dark stripe, or spotted posterior thigh surfaces) that diagnose other tree-frog species.

S. baudinii may occasionally be mistaken for individuals of *P. venulosa* which have similar coloration and/or paired vocal sac expansions. The former has a smooth dorsum, a series of warts along the forearm and colorless bones in life *(P. venulosa* has a warty dorsum, no warts along outer margin of forearm and green bones in life).

Examples of *H. pseudopuma* may also superficially resemble *S. baudinii* but the two forms are distinguished by vomerine tooth patch position (at level of middle of choanae in *S. baudinii,* at posterior margin of choanae in *H. pseudopuma)* and a series of warts along posterior margin of lower arm (present in *S. baudinii,* absent in *H. pseudopuma).*

Within the genus *Smilisca, S. baudinii* is most readily distinguished from the other forms as follows: series of well-developed warts along outer margin of forearm (absent in *S. phaeota* and *S. puma);* dorsum smooth (strongly tuberculate in *S. sila);* distinct dark lateral band from tympanum to axilla (absent in *S. puma, S. sordida* and *S. sila)* and toes with one or two phalanges free of web on toes III-IV-V (webbed to base of disks on one or two toes in this series in *S. sordida).*

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout rounded to nearly semicircular; snout round in profile; canthus rostralis sharp; tympanum distinct, horizontal diameter 1/2 to 2/3 eye diameter; male vocal sac external, single, inflates to form two lateral expansions, distinct chin and chest portions; male vocal slits not entirely hidden by tongue, oblique to jaw; vomerine teeth between choanae, transverse; outer finger disks (III, IV) about 2/3 tympanum; finger webbing formula I trace II 2^{--}-3 III 2^{+} -2^{+} IV; subarticular tubercles single to double under outer finger (IV), always single under thumb (I); white nuptial asperities on thumb of male; lower arm with series of light warts; tip

of prepollex not protruding externally; dorsal texture smooth to almost granular; chin, chest, under surface of arm smooth-granular to granular, belly and underside of thigh granular; rest of lower leg surface smooth; toe disk size from inner to outer I<II<III=IV=V; outer toe disks (IV, V) just smaller than outer finger disks; toe webbing formula I 1+-2 II 0-2 III 1+-2+ IV 2-1 V; large oblong inner metatarsal tubercle; outer metatarsal tubercle small, round, or absent; distinct inner tarsal fold, no apparent outer tarsal fold; heel surface smooth or very slightly warty; males to 68 mm, females to 72 mm; tibia 50; dorsum uniform or spotted, brown and tan or green with dark brown spots in life, tan, brown, or gray in preservative; dark interorbital bar usually present; eye mask from nostril to 1/4 body present or absent; sides of body with or without spotting or mottling; venter cream or yellow in life; upper limbs barred; toes yellow in life; posterior surface of thigh suffused with melanophores; sole of foot suffused with melanophores.

DISTRIBUTION: Tropical lowlands of México and Central América to Central (Pacific) and southern (Atlantic) Costa Rica.

LOCALITIES: PROV. DE ALAJUELA: Los Chiles; Orotina; PROV. DE GUANACASTE: 1.6 km W Bagaces, Río Piedra, 45 m; 2 km NE Cañas; 50 km S Cañas, 180 m; 4.3 km NE La Cruz; 18.4, 23.6 km S La Cruz; Las Huacas; 0.5, 2.6, 6.2, 11.6, 13, 22.4 km N Liberia; Nicoya; 8.6 km ESE Playa del Coco; Río Bebedero, 5 km S Bebedero; Finca San Bosco de Tilarán, 640-750 m; Santa Cruz, airport; 3.2 km W Santa Cruz on Playa del Tamarindo road; PROV. DE HEREDIA: 13 km SW Puerto Viejo; PROV. DE LIMON: Batán, 15 m; Guácimo, 103 m; Pandora, 100 m; Suretka; Tortuguero, 16 km W Tortuguero, Río Suerte; PROV. DE PUNTARENAS: 15, 18 km WNW Barranca; mouth of Río Barranca, 5 m; Mata Limón, 7 m (Fig. 45).

REMARKS: Externally *S. phaeota* and this form appear to have paired lateral vocal sacs in males. However, the sacs are continuous internally across the midline of the throat.

Smilisca phaeota (Cope)

1862 *Hyla phaeota* Cope: 1862: 358 (Holotype: US 39899, Colombia: Departamento de Antioquía: Turbo, 10 m.); 1952, Taylor: 837, Fig. 50 (redescription).

1863 *Hyla labialis* Peters: 463 (Holotype: Ber. M 4913, Colombia: vicinity of Bogotá, probably in error).

1923 *Hyla baudinii dolomedes* Barbour: 11 (Holotype: MCZ 8539, Panamá: Provincia de Darién: Valle de Río Sambu: Río Esnape).

1906b *Smilisca phaeota,* Starrett: 302 (redefines genus). For additional synonymy see DUELLMAN and TRUEB (26).

DIAGNOSIS: A large (males to 71 mm, females to 81 mm) species with a smooth dorsum, no series of enlarged warts along outer margin of forearm,

a dark eye-mask from snout, continuing as a lateral band to axilla, usually a well-marked white stripe from heel to foot and a reticulum of narrow dark lines in groin and along flank. In life the dorsal ground color is usually pale green.

S. phaeota lacks limb-fringes, protuberant prepollex, curved vomerine tooth patches, knob-like cephalic projections and the oblique tympanum found in several forms which might be confused with it. The species also lacks a lateral stripe, a mid-dorsal dark stripe, dorsolateral dark stripes, and dark barred or light spotted posterior thigh surfaces, diagnostic features for several other species.

Adult and juvenile *S. phaeota* may be confused with *S. baudinii, S. sordida* or *Phrynohyas venulosa.* From *S. baudinii, S. phaeota* differs in lacking a series of prominent lower arm warts, having a light stripe from heel to foot and a large tympanum usually more than 2/3 diameter of eye (warts present, no light stripe and tympanum usually less than 2/3 diameter of eye in *S. baudinii). S. sordida* also has a series of arm warts, lacks the white heel to foot stripe and lateral dark band, and has one to several toes webbed to base of disks (no arm wart series, a white heel to foot stripe and lateral dark band and all toes with one or two phalanges free of webbing in *S. phaeota).*

P. venulosa is an extremely warty frog with green bones in life. It differs from *S. phaeota* which has a smooth dorsum and colorless bones, by the following additional features: vomerine tooth patches extend posterior to choanae, several toes webbed to base of disks, and groin and flank covered by extension of dorsal coloration (versus vomerine tooth patches between middle of choanae, one or two phalanges of all toes free of web, groin and flank covered by a narrow dark reticulum in sharp contrast to dorsal pattern for *S. phaeota).*

Juvenile *S. phaeota* resemble the medium-sized species of *Smilisca, S. puma* and *S. sila,* to some extent but differ from them as follows: in having a dark ground color (in preservative) uniform or with dark blotches and spots but without paired elongate blotches that anastomose at one to several points across the mid-line, a definite dark eye mask or canthal line that continues onto the side as a lateral band to axilla and a very obvious flank reticulum (Fig. 11) (in *S. puma* the dorsum is light tan with a pair of elongate blotches that anastomose at one to several points across the midline to form an H or A shaped figure (Fig. 16)., no definite eye mask or broad lateral band although a narrow dark canthal stripe and a similar stripe from eye above tympanum onto side may be present and groin and flank reticulum weak, frequently restricted to very small area and not formed by narrow dark lines) and the dorsum smooth and no lower arm wart series (dorsum tuberculate and prominent warts along lower arm in *S. sila).*

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout nearly sub-elliptical to nearly semicircular; snout rounded in profile; canthus rostralis sharp; tympanum distinct, large, horizontal diameter 2/3 to 4/5 eye diameter; male vocal sac external, single, inflates to form two lateral expansions, distinct chin and chest portions; male vocal slits not entirely hidden by tongue, almost parallel to jaw; vomerine teeth between choanae, transverse; outer finger disks

(III, IV) large, 1/2 to 1 times tympanum; finger webbing formula I trace II 2^{-}-3^{-} III 2 1/2-2 IV; subarticular tubercles single to bifid under outer finger (IV), always single under thumb; light tan nuptial asperities on thumb of male; no ulnar fold; tip of prepollex not protruding; dorsal texture smooth to slightly glandular; chin, chest, under surface of arm smooth-granular; belly, under surface of femur granular; rest of under leg surface smooth; toe disk size from inner to outer I<II<III=IV=V; outer toe disks (IV, V) equal to or slightly smaller than outer finger disks; toe webbing formula I 1-2 II 1-2 III 1^{+}-2^{+} IV 2-1/2 V; large oblong inner metatarsal tubercle; outer metatarsal tubercle small, round, present or absent; distinct inner tarsal fold, outer tarsal fold not apparent; heel smooth; males to 71 mm, females to 81 mm; tibia 57; dorsum uniform or blotched, green-brown mottle in life, light brown, chocolate, gray, or almost black in preservative; eye mask from tip of snout through eye and tympanum to above elbow when arm laid posteriorly along side of body, brown in life; upper lip light, cream in life; dark interorbital bar present or absent; edges of granules on side of body black lined, sides tan in life, chin tan-brown in life; venter cream in life; upper limbs barred, or only obscurely so; contrasting stripe along outer arm, heel, and tarsus; posterior surface of thigh suffused with melanophores; sole of foot suffused with melanophores.

DISTRIBUTION: Atlantic lowlands of Nicaragua and Pacific lowands of southwestern Costa Rica, south through Panamá and Colombia to northwestern Ecuador.

LOCALITIES: PROV. DE ALAJUELA: 0.5 km S Cariblanco, 820 m: 4.8 km S Ciudad Quesada; Las Playuelas, 75 m; PROV. DE CARTAGO: Moravia de Chirripó, 1116 m; Peralta; Turrialba, 625 m; Turrialba, IICA, 604 m; PROV. DE GUANACASTE: Arenal, 520 m; Finca San Bosco de Tilarán, 640 m; Tilarán, 560 m; 5 km NE Tilarán, 600 m; PROV. DE HEREDIA: Cariblanco; 4.2, 7.5 km W Puerto Viejo; 1 km S Puerto Viejo; PROV. DE LIMON: Bambú, 60 m; Coen, 60 m; 1.6 km E Los Diamantes, 260 m; Guácimo, 103 m; La Lola, 36 m; Pandora, 50-100 m; Puerto Limón; El Tigre, 680 m; PROV. DE PUNTARENAS: Agua Buena; 1.6 km E Buenos Aires; 3 km NW Buenos Aires; 3.7 km E of Esparta, 280 m; 2.4 km. SE, 7.4 km NE Golfito; Gromaco; Palmar; 4 km ESE Palmar Sur; 7 km ESE Palmar Sur; Parrita, La Julieta, Finca La Ligia, 5-10 m; 8.5 km SE Piedras Blancas; Quebrada Boruca, 22 km E Palmar Norte; Rincón de Osa, 30 m; nr. Rincón, Quebrada Agua Buena, 20 m; Rincón, Camp Seattle, 50 m; 19.2 km E San Isidro de El General on Inter-American Highway, 610 m; 1.6 km NW Villa Neily, 70 m; 8 km NE Villa Neily, 685 m; PROV. DE SAN JOSE: 9.7 km N San Isidro de El General; 3.2 km SSE San Isidro de El General, 690 m; 14.5 km SW San Isidro de El General on Dominical road, 970 m; 16 km SW of San Isidro de El General on Dominical road, 884 m; 17.6 km WSW San Isidro de El General on Dominical road, 825 m (Fig. 46).

Smilisca sila Duellman and Trueb

1924 *Hyla gabbi* Noble: 66 (misidentification).

1937 *Hyla sordida* Dunn: 166 (misidentification).

1946 *Hyla phaeota* Breder: pl. 55 (misidentification).

1966 *Smilisca sila* Duellman and Trueb: 318, pls. 4, 5, 7 (Holotype: KU 91852, Panamá: Provincia de Chiriqui: El Volcán, 1280 m.).

DIAGNOSIS: One of four species in Costa Rica lacking solid dark bars on posterior thigh surfaces, fringes along lower limbs and having dorsum strongly tuberculate (the others are *H. staufferi, H. tica* and *P. venulosa). S. sila* has a prominent series of warts along the lower arm (absent in *H. staufferi* and *P. venulosa)* and the subarticular tubercles under thumb single (double in *H. tica).*

Some *S. sila* may be mistaken for *S. sordida,* but the latter is not strongly tuberculate and has a smooth tympanum (dorsum and tympanum tuberculate in *S. sila).* Occasional examples of *H. pseudopuma* may be difficult to separate from *S. sila,* but none of the latter have a strongly tuberculate dorsum or tympanum or a reticulum of dark lines and light spots along the flanks, although yellow spots may be present in life.

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout round to nearly semicircular; snout rounded in profile; canthus rostralis sharp; tympanum distinct, horizontal diameter about 1/2 eye diameter; male vocal sac external, single, chin and chest portions distinct; male vocal slits not entirely hidden by tongue, oblique to jaw; vomerine teeth between choanae, transverse; outer finger disks (III, IV) 3/4 - 1 times tympanum; finger webbing formula I 3-3 II 1 2/3-2 1/2 III 2-2^{-} IV; subarticular tubercles single to double under outer finger (IV), single under thumb; light brown nuptial asperities on thumb of male; warty ridge along ulnus; tip of prepollex not protruding; dorsal texture tuberculate; chin, chest, under surfaces of arm smooth-granular, belly, under surfaces of thigh granular, rest of underside of leg smooth; toe disk size from inner to outer I<II<III=IV=V; outer toe disks (IV, V) slightly smaller than outer finger disks; toe webbing formula I 1-2^{-} II 0-2^{-} III 1-2^{-} IV 2^{-}-1 V; large oblong inner metatarsal tubercle, outer metatarsal tubercle small, round, indistinct or absent; distinct inner tarsal fold; outer tarsus with or without row of warts; heel tuberculate, as rest of dorsum; males to 41 mm, females 63mm; tibia 54; dorsum indistinctly blotched, brown with dark brown markings with green flecks present or absent in life, dark brown with black markings in preservative; lower lip line white in life; sides of body and groin mottled, brown in life; dorsal limbs barred; thumb pads gray in life; yellow wash on anteroventral thigh, lower surface of tibia and inner foot in life; posterior thigh suffused with melanophores, brown with blue spots in life; sole of foot suffused with melanophores; iris tan.

DISTRIBUTION: Southwestern Costa Rica to northern Colombia.

LOCALITIES: PROV. DE PUNTARENAS: 6 km E Golfito; Quebrada Boruca, 22 km E Palmar Norte; Río Zapote, 7.2 km E of Palmar Norte, 60 m; PROV. DE SAN JOSE: San Isidro de El General, 710 m; 14.5 km SW San Isidro de El General on Dominical road, 970 m; 16 km SW San Isidro de El General on Dominical road, 884 m (Fig. 47).

Smilisca sordida (Peters)

1863 *Hyla sordida* Peters: (Syntypes: Ber. M 3141,2 examples, Panamá: Provincia de Veraguas).

1875 *Hyla gabii* Cope: 103 (Syntypes: US 30658-9, Costa Rica: Provincia de Limón: Cantón de Limón: near Sipurio); 1952, Taylor: 840, Fig. 51.

Hyla nigripes Cope: 104, pl. 23, Fig. 7 (Syntypes: US 30685-6, Costa Rica: Provincia de Limón: Cantón de Limón: Cerro Utyum, erroneously cited as Pico Blanco, 1500 2100 m); 1952, Taylor: 853 (redescription of types).

1882 *Hyla salvinii* Boulenger: 372 (Syntypes: BM 1947. 2. 24. 12-13, Costa Rica).

1958 *Hyla monticola,* Taylor: 26, Fig. 10 (misidentification).

1960b *Smilisca gabbi,* Starrett: 302 (generic allocation).

1966 *Smilisca sordida,* Duellman & Trueb: 323, pl. 4, 5, 7 (redescription).

DIAGNOSIS: A rather variable species of medium (males to 44 mm) to large size (females to 65 mm) without fringed limbs, a protuberant prepollex, curved vomerine tooth patches, oblique tympanum or strongly tuberculate dorsum or tympanum. In addition, this tree frog lacks lateral or dorsolateral dark or light stripes, a suborbital light area, dark bars on posterior surface of thigh, mid-dorsal dark line, or light outlined dark dorsal spots or blotches. The feet of this form have one to several toes webbed to the base of the disks and prominent warts along the lower arm.

The species is most easily confused with *H. pseudopuma* and *S. sila. H. pseudopuma* has one or two phalanges on every toe free of webbing and vomerine tooth patches at posterior margin of choanae (at level of middle of choanae in *S. sordida).* From *S. sila, S. sordida* differs in lacking a tuberculate dorsum and tympanum (present in the former). No other species of *Smilisca* has extensive foot webbing and *S. phaeota* and *S. puma* lack the prominent lower arm warts.

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout rounded, subovoid to subelliptical; snout rounded in profile; canthus rostralis sharp to rounded; tympanum distinct, horizontal diameter 2/5 to 1/2 eye diameter; male vocal sac internal to external, single; male vocal slits not entirely hidden by tongue, oblique

to jaw; vomerine teeth between choanae; outer finger disks (III, IV) 1 to 1/3 times tympanum; finger webbing formula I 3-3+ II 1+-2+ III 2−-1+ IV; subarticular tubercles bifid to double under outer finger (IV), single under thumb; dark brown nuptial asperities on thumb of male; warty ulnar fold; tip of prepollex not free and protruding; dorsal texture usually smooth to very slightly warty; chin, chest, lower surface of arm smooth granular to granular, belly and ventral surface of thigh granular, rest of ventral leg surface smooth; toe disk size from inner to outer I<II<III=IV=V; outer toe disks (IV, V) slightly smaller than outer finger disks; toe webbing formula I 0-1+ II 0-1+ III 0-1 1/2 IV 1 1/2-0 V; large oblong inner metatarsal tubercle, outer metatarsal tubercle small, round, or not apparent; distinct inner tarsal fold, outer tarsal fold not apparent; entire heel region warty; males to 44 mm, females to 65 mm; tibia 56; dorsum uniform to blotched, yellow, tan, red-brown, gray-brown, green-brown, or dark brown with or without dark green markings in life, tan, coffee, chocolate, brown-black, or silver in preservative; groin mottled; venter white in life; some yellow at angle of jaw in life; dorsal limbs barred; ulnar fold usually light; thumb pads black in life; posterior surface of thigh suffused with melanophores, black mottled with light blue, yellow or white in life; sole of foot suffused with melanophores; iris pale gold or brassy gray.

DISTRIBUTION: Lowlands and mountain slopes on the Atlantic versant from southern Nicaragua and on the Pacific versant from northern Costa Rica to extreme western Panamá.

LOCALITIES: PROV. DE ALAJUELA: rd. from Atenas to San Mateo, 547 m; 8 km N Ciudad Quesada, Río Ron Ron, 250 m; La Fortuna, 199 m; 3.2 km E La Fortuna, 150 m; Sarchí; PROV. DE CARTAGO: Headwaters of Río Pacuare, nr. San Vicente, 1100 m; 4.8 km SW Río Revertazón bridge on Paraíso-Orosi road, 1040 m; Turrialba, 625 m; PROV. DE GUANACASTE: 4.8 km E Cañas; Río Cañas at Cañas, 88 m; Río Javillos on Inter-American Highway, 37 km S Cañas, 90 m; Río Lagarto on Inter-American Highway, 100 m; Santa Cecilia; Tilarán, 560 m; 1.3 km SW Tilarán, 500 m; PROV. DE HEREDIA: Puerto Viejo, 100 m; PROV. DE LIMON: Bambú, 60 m; La Lola, 36-40 m; Río Lari, 14.5 km SW Amubri, 300 m; Río Lari, 16 km SW Amubri, 400 m; Pandora, 50 m; Sipurio, 71 m; Suretka; PROV. DE PUNTARENAS: 4.8 km SW Buenos Aires, Río Ceibo, 320 m; 9.7 km W Buenos Aires, Río Volcán, 400 m; Esparta, 208 m; 4 km W Esparta, Río Barranca, 50 m; 16 km NW Esparta, Río Ciruelitas, 45 m; 6.4 km SE Golfito, Río Purruja, 5 m; 3-5 km W Palmar Norte on road to Puerto Cortés, 10 m; 7.2 km E Palmar Norte, Río Zapote, 60 m; Pozo Azul de Pirrís, 100 m; Quebrada Boruca, 22 km E Palmar Norte; Rincón de Osa, Camp Seattle, 50 m; 2.8 km SW Rincón, Quebrada Buena; 7.2 km S Rincón, Río Ferruviosa; Río La Vieja, 110 m; 9.7 km SSE San Isidro del General, 600 m; 3.2 km NW Villa Neily, 50 m; 4.8 km NW Villa Neily, 60 m; 5.1 km NW Villa Neily, 60 m; 14.5 km NW Villa Neily. Río Claro, 60 m; PROV. DE SAN JOSE: Escazú, 1090 m; Desamparados, Río

Jorco, 1030 m; Río Tiribí; Salitral de Santa Ana, 1100 m; San Ignacio, 1095 m; San Isidro del General, 710 m; 17.1 km WSW San Isidro del General on Dominical road, 880 m; San José, 1160 m; Santa Rosa, Río Virilla, 1289 m; 0.4-0.8 km N Santa Rosa on Moravia-La Hondura road, 1525 m (Fig. 48).

REMARKS: Although DUNN (30), originally used the name *gabbi* for this species, he subsequently applied the name *sordida* to this form in his notes and identifications. His notes on the species leave no doubt that he regarded *gabbi* as a strict synonym of *sordida* based upon his examination of the types of the latter. Unfortunately he did not distinguish between *sordida* and the recently described *S. sila* so that the former name was applied to both species (BREDER, 10; ZETEK and WETMORE, 67). The two species are now known to have overlapping ranges in southwestern Costa Rica and extreme western Panamá. *S. sila* occurs over most of Panamá but *S. sordida,* not *sila,* is found in northeastern Costa Rica and along the Atlantic coast. *S. sordida* probably occurs in extreme southern Nicaragua and the Bocas del Toro area of northwestern Panamá.

Smilisca puma (Cope)

1885 *Hyla puma* Cope; 183 (Holotype: US 13735, Nicaragua).

1952 *Hyla wellmanorum* Taylor: 843, Fig. 52 (Holotype: KU 30302, Costa Rica: Provincia de Limón; Cantón de Limón: Batán, 15 m).

1960b *Smilisca wellmanorum,* Starrett: 302 (redefines genus).

1966 *Smilisca puma,* Duellman and Trueb: 314 (redescription).

DIAGNOSIS: A medium-size (males to 36 mm, females to 46 mm) species of *Smilisca* most closely resembling *S. phaeota* in structure and *S. phaeota* and some *S. sordida* in coloration. Distinct from *S. sila* in lacking a prominent series of warts along outer edge of lower arm, in having the dorsum smooth rather than strongly tuberculate, being light tan in dorsal ground color versus dark brown and lacking a thick dark reticulum inclosing obvious light spots along the flank. From *S. baudinii, S. puma* differs in size, webbing and dorsal pattern but most obviously in lacking the prominent series of lower arm warts typical of the former.

S. puma differs from *S. sordida* in dorsal pattern, presence of a light heel to foot stripe and hand webbing (practically no webbing between fingers III-IV, more than two phalanges free of web on finger IV). In *S. sordida* the characteristic *S. puma* dorsal pattern of two elongate blotches connected at one to several points across midline is lacking, no light stripe from heel to foot is present and there is considerable webbing between fingers III-IV, with no more than 1 1/2 phalanges of finger IV free of web. The foot of *S. sordida* also has one to several toes webbed to base of disk while in *S. puma* no toes are webbed past the distal subarticular tubercle.

The differences between *S. puma* and *S. phaeota* are summarized in the following comparison:

S. puma	*S. phaeota*
1. Canthal dark line - postorbital dark stripe above tympanum onto back.	1. A canthal stripe or broad eye mask; broad postorbital band continuing as distinct lateral band from tympanum to axilla.
2. Dorsal ground color tan in life, light brown in preservative.	2. Dorsal ground color dull green in life, very dark brown in preservative.
3. Groin and flank with weak reticulum and scattered dark marks in preservative.	3. Groin and flank with a strong reticulum of thin dark lines (Fig. 11) and large light areas in preservative.
4. A pair of elongate dorsal blotches that anastomose at one to several points across midline to form enclosed light ground color areas (Fig. 16).	4. Dorsum uniform or with solid dark blotches or spots.
5. Tympanum 1/2-2/3 eye.	5. Tympanum 2/3-4/5 eye.

Some *S. puma* resemble examples of *H. pseudopuma, H. tica, H. rivularis* or *H. ebraccata* in coloration but may be distinguished from them as follows: posterior surface of thigh suffused with dark pigment and no light suborbital spot (thigh without dark pigment and a light suborbital spot in *H. ebraccata);* dorsum smooth (tuberculate in *H. tica);* no series of prominent lower arm warts (present in *H. rivularis);* and vomerine teeth at level of middle of choanae (projecting posterior to choanae in *H. pseudopuma).*

SUMMARY OF CHARACTERISTICS: Dorsal outline of snout rounded to almost subelliptical; snout rounded in profile; canthus rostralis sharp; tympanum distinct, horizontal diameter 1/2-2/3 eye diameter; male vocal sac external, single; chest and chin portions distinct; male vocal slits not hidden by tongue, parallel to jaw; vomerine teeth between choanae; outer finger disks 2/3 to equal tympanum; finger webbing formula I none II 2^{+}-3^{+} III 3^{-}-2 1/2 IV; subarticular tubercles single to bifid under outer finger (IV), single under thumb (I); light brown nuptial asperities on thumb of male; ulnar ridge usually not evident; tip of prepollex not protuberant; dorsal texture smooth, some with glandular appearance; chin, chest, lower surface of arm smooth-granular to granular; belly, under surface of femur granular; rest of lower leg surface smooth; toe size from inner to outer I<II<III = IV = V; outer toe disks (IV, V) slightly smaller than outer finger disks; toe webbing formula I 2^{-} -2 1/2 II 1^{+}-2 1/2 III 1 1/3-2 1/3 IV 2 1/3-1^{+} V; large oblong inner metatarsal tubercle; outer metatarsal tubercle small, round, or absent; inner and outer tarsal folds weakly developed or not apparent; heel smooth, or slightly warty along heel stripe; males to 36 mm, females to 46 mm; tibia 52; dorsum with dark interorbital stripe and two stripes from eye down back fusing or not, broken up into spots posteriorly or not, golden tan with dark brown or dark green markings in life, tan, tan-cream, light brown, coffee, chocolate, or almost brown-black in preservative;

dark eye stripe or mask; light line above anus bordered below by dark; upper limbs faintly barred; light stripe along arm, heel, and tarsus; posterior surface of thigh suffused with melanophores; sole of foot suffused with melanophores.

DISTRIBUTION: Caribbean lowlands from Nicaragua through Costa Rica to northwestern Panamá.

LOCALITIES: PROV. DE ALAJUELA: Río La Fortuna at La Fortuna, 200 m; 3 km W La Fortuna; Jabillos, 4.8 km N Santa Clara, 128 m; PROV. DE GUANACASTE: Arenal, 520 m; PROV. DE HEREDIA: Puerto Viejo, 100 m; 5.9 km W Puerto Viejo; PROV. DE LIMON: Batán; La Castilla, 15 m; Los Diamantes, 300 m; 2.4 km E Los Diamantes, 260 m; La Lola, 36 m; Monteverde, 40 m; Tunnel Camp nr. Peralta (Fig. 47).

REMARKS: This species was first called to the attention of modern workers by TAYLOR (62) who described it as a new form, *Hyla wellmanorum.* The species had apparently been described previously, from Nicaragua by COPE (17) as *Hyla puma.* One of us (S) has examined the holotype of *H. puma,* an adult female. The specimen is in excellent condition and exhibits all the diagnostic characteristics of the species. Although originally described as being a uniform brown above, when the type is submerged in liquid the typical dorsal pattern is apparent. The pattern, reduced finger and toe webbing and general habitus of the frog leave no questions as to its identity.

DUELLMAN and TRUEB (26) call attention to the use of the name *Hyla molitor* O. Schmidt, 1857, for specimens of this species in some United States collections. The use of this name for a Central American form is based upon identifications by E. R. Dunn, who examined the types of the following taxa in 1928 at Cracow and Vienna:

1857 *Hyla molitor* O. Schmidt: 11 (Syntypes: KM 1010/1341, and W 16494, Panamá: Bocas del Toro: Río Chiriquí: near Bocas del Toro); 1858, O. Schmidt: 245, pl. 1, Figs. 8-9 (extended description).

Hyla molitor marmoratus O. Schmidt: 12, (Holotype: KM 1010/1342 Panamá: Bocas del Toro: Río Chiriquí: near Bocas del Toro); 1858, O. Schmidt: 246 (description); preoccupied by *Bufo marmoratus* Laurenti 1768:29.

Hyla splendens O. Schmidt: 11 (Holotype: KM 1008/1340, Panamá: Provincia de Bocas del Toro: Río Chiriquí, near Bocas del Toro); 1858, O. Schmidt: 244, pl. 1, Fig. 7 (extended description).

All were collected by the Polish botanist Josef Warszewicz during his work in tropical America from 1848-1851.

Recently, we have been able to examine the Cracow and Vienna type

material of the three nominal forms. The Cracow syntypes of *molitor* and *molitor marmoratus* are in extremely poor condition. The Vienna syntype of the former is in fair condition and is herewith selected as the lectotype of *Hyla molitor* O. Schmidt, 1857. The lectotype, a female, (W 16494), has also been examined by us. It is 36 mm in standard length and the tympanum is 1/2 the diameter of eye, vomerine tooth patches linear and between choanae, finger webbing I trace II 2^{+}-3 III 3^{-}-2 1/2 IV, toe webbing I 1 2/3-2 II 1^{+}-2 1/4 III 1 1/2-3^{-} IV 3^{-}-1 1/2 V and lacks an ulnar ridge or warts. The most striking feature of this individual is the tiny finger and toe disks that are barely enlarged. The specimen is a faded almost uniform brown above, although suggestions of dark and light blotches are evident under magnification. We know of no Central American hylid that agrees with the characteristics of this specimen. The Cracow syntypes of *H. molitor* and *H. molitor marmoratus* are indistinguishable from one another, but are in such poor condition that comparison or identification is difficult. They seem to represent the same species as the Vienna lectotype.

The holotype and only known specimen of *Hyla splendens* has also been examined by us. It is an adult male, 51 mm in standard length and has the following salient features: 1) tympanum distinct, 1/2 diameter of eye; 2) single external vocal sac; 3) vomerine teeth in two short transverse series between the choanae; 4) finger webbing formula I trace II 2^{+}-3^{+} III 3-3^{-} IV; 5) toe webbing formula I 2-2 II 2^{-}-3 III 2^{-}-3 IV 3^{-}-1 3/4 V; 6) light labial stripe; 7) no eye mask; 8) roof of skull rugose, completely covered over; and, 9) upper limb surfaces with a series of transverse bars. We know of no Central American hylid that shares the characteristics of this specimen.

The three nominal forms, *H. molitor, H. molitor marmoratus, H. splendens,* probably were collected elsewhere than in Panamá by Warszewicz, who visited Colombia, Perú, and Bolivia on the same expedition.

DISTRIBUTIONAL PATTERNS

GEOGRAPHIC: The Republic of Costa Rica has an exceedingly complicated topography and corresponding complex of climates, soils and habitats. The country is physiographically transected along a northwest-southeast axis by a more or less continuous montane backbone. As a result five major geographic regions may be recognized:

A. Atlantic Lowlands - entire Caribbean coastal plain.
B. Northwest Pacific Lowlands - region from level of mouth of Golfo de Nicoya northwestward.
C. Southwest Pacific Lowlands - region southeast of the Golfo de Nicoya.
D. Cordilleras Central-Tilarán - mountains of the Cordillera Central and its northwestern extension.
E. Cordillera de Talamanca - mountains of southern Costa Rica.

TABLE 1

Geographic Distribution of Costa Rican Tree Frogs

	A	B	C	D	E
A. coronata				X	X
H. angustilineata				X	
H. boulengeri	X	X	X		
H. colymba					X
H. debilis				X	X
H. ebraccata	X		X		
H. elaeochroa	X		X		
H. fimbrimembra			X		
H. immensa	X				
H. lancasteri				X	X
H. legleri					X
H. loquax	X				
H. lythrodes					X
H. microcephala		X	X		
H. phlebodes	X				
H. picadoi				X	X
H. pictipes				X	X
H. pseudopuma				X	X
H. richardtaylori				X	
H. rivularis				X	X
H. rosenbergi			X		
H. rufioculis				X	X
H. rufitela	X				
H. staufferi	●	X			
H. tica				X	X
H. uranochroa				X	X
H. zeteki				X	X
P. venulosa	●	X	X		
P. annae				X	X
P. calcarifer	X				
P. callidryas	X		X		
P. lemur				X	X
P. saltator	X				
P. spurrelli			X		
S. baudinii	X	X			
S. phaeota	X		X		
S. sila			X		
S. sordida	X	X	X		
S. puma	X				
Totals	14	6	11	16	16

● Single record.

The geographic distribution of Costa Rican species of tree-frogs is summarized (Table 1). The Costa Rican species may be grouped according to geographic range as follows:

1. Wide-ranging forms - found on both Atlantic and Pacific lowlands and sometimes onto mountain slopes (7)

   a. Absent from Pacific northwest (4)

   H. ebraccata
   H. elaeochroa
   P. callidryas
   S. phaeota

   b. Absent from Pacific southwest (1)

   S. baudinii

   c. Ubiquitous (2)

   H. boulengeri
   S. sordida

2. Atlantic lowland forms, frequently ranging onto slopes (6)

   H loquax
   H. phlebodes
   H. rufitela (probably occurs in Pacific southwest)
   P. calcarifer
   P. saltator
   S. puma

3. Pacific lowland forms, frequently ranging onto slopes (6)

   a. Wide-ranging through the Pacific lowlands (2)

   H. microcephala
   P. venulosa (also extreme northern Caribbean lowlands)

   b. Pacific northwest (1)

   H. staufferi (one record for Atlantic versant Costa Rica)

   c. Pacific southwest (3)

   H. rosenbergi
   P. spurrelli
   S. sila

4. Cordilleran forms (20)

   a. Wide-ranging (14)

      i) lower slopes (11)

A. coronata
H. debilis
H. immensa
H. lancasteri
H. pseudopuma
H. rufioculis
H. tica
H. uranochroa
H. zeteki
P. annae
P. lemur

ii) montane (3)

H. picadoi
H. pictipes
H. vivularis

b. Cordillera Central - Tilarán (3)

i) foothills and slopes (2)

H. fimbrimembra
H. richardtaylori

ii) montane (1)

H. angustilineata

c. Cordillera de Talamanca (3)

H. colymba
H. legleri
H. lythrodes

ECOLOGIC: The altitudinal distribution of Costa Rican hylids is summarized (Fig. 49). Distribution appears to correlate rather well with the temperature related life zones of HOLDRIDGE (41). According to this system the most rapid changes in climatic effects and vegetation occur at particular biotemperature isosphenes. The life zones, biotemperature and approximate altitudes in Costa Rica are:

Tropical Lowland - BT°>24°C; sea level to 500-700 m.
Subtropical - BT°=18°—24°C; 500 (700)—1500 (1700) m.
Lower Montane - BT°=12°—18°C; 1500 (1700)—2500 (2700) m.
Montane - BT°=6°—12°C; 2500 (2700)—3500 (3700) m.
Subandean - BT°=3°—6°C; 3500 (3700) m.

The approximate limits of the life zones are indicated on the distributional chart (Fig. 49). From these data it is seen that the number of species for each life zone is:

Tropical Lowland — 21
Subtropical — 19
Lower Montane — 5
Montane — 2

The following patterns are indicated:

I. Species restricted to one life zone (25)

A. Tropical (12)

H. boulengeri
H. elaeochroa
H. microcephala
H. phlebodes
H. rosenbergi
H. rufitela
H. staufferi
P. venulosa
P calcarifer
P. saltator
S. baudinii
S. puma

B. Subtropical (13)

H. colymba
H. debilis
H. fimbrimembra
H. immensa
H. legleri
H. lythrodes
H. richardsaylori
H. rufioculis
H. tica
H. uranochroa
H. zeteki
P. annae
P. lemur

C. Lower Montane (1)

H. angustilineata

II. Species found in two zones (15)

A. Tropical - Subtropical (10)

A. coronata
H. ebraccata
H. lancasteri
H. loquax
P. callidryas
P. saltator
P. spurrelli
S. phaeota
S. sila
S. sordida

B. Subtropical - Lower Montane (2)

H. pseudopuma
H. rivularis

C. Lower Montane - Montane (2)

H. picadoi
H. pictipes

Within the life zones a variety of vegetational formations are present that differ principally in response to differences in precipitation. Only along the Pacific lowlands are these differences so pronounced as to produce striking major vegetational changes. In northwest Costa Rica the vegetation is deciduous in response to an extended dry season December - March. To the south the vegetation is evergreen. Of the 13 tree-frog species in the region 4 are

found in both vegetation types, 2 are found only in the northwest dry forest, 7 are restricted to the southwest evergreen forest. All montane situations in Costa Rica support evergreen associations.

Relatively little is known regarding the habitat requirements of tropical tree-frogs, especially in the non-breeding season. Field observations provide some information on ecological differences during the breeding period in Costa Rica (Fig. 50). Males of each species tend to congregate near bodies of water at this time. The chart indicates the kind of site where the eggs are deposited using the following notations (figures in parentheses indicate number of species).

PM = ponds or marshes (15)
S = streams (12)
T = in trees or bushes out of water (6)
B = in the water trapped in bromeliads (3)

The breeding habits of the fringe-limbed species remain unknown.

Most of the species breed during the wet season from March to December, but *Smilisca sordida* and *S. sila* are dry season breeders. Mating and egg-laying in these forms reaches its peak toward the end of the dry season when the streams are down. In some lowland wet localities, however, male *S. sordida* call at all times of the year.

In addition to broad differences in temporal relations and site of egg deposition, where a number of species breed in the same locality ecologic segregation within a major habitat is also significant. These differences are most noticeably effective in terms of the calling site of the males and where the eggs may be deposited within the habitat. For example in the lowlands of the Caribbean versant *H. boulengeri, H. loquax, H. phlebodes* and *S. phaeota* may all call and breed around the same pond.

The males of *H. phlebodes* call from the stems of grasses or reeds around the margins of the pond; *H. boulengeri* calls from trees or bushes overhanging the pond from 1 to several meters above the water; *H. loquax* calls from low vegetation near the water surface out from shore in the deepest portion of the pond; *S. phaeota* usually calls from low bushes around the edge of the pond.

The accompanying chart indicates the sympatric occurrence of adult breeding tree-frogs in Costa Rica. Sympatry is used in the sense that the individuals were observed at the same general locality at the same time of the year. Where the species are isolated by different breeding season or sites of egg deposition, a major ecologic barrier (E) operates to keep them genetically segregated. Even when they breed at the same time, in the same place and utilize the same general breeding site, minor ecologic barriers (e) may effectively isolate the species. Where there is no evidence of ecologic isolation (X) the species tend to be isolated by other factors the most important of which are call characteristics and size of breeding adults.

The number of species that actually occur together at any one locality is less than suggested by the chart. For example *H. phlebodes* has been taken

in sympatry with 13 other species, but the maximum number of these forms taken at the same time and place with *H. phlebodes* is 6. The maximum number of species taken at the same time and place in our fieldwork is 6, collected at Rincón de Osa on June 17, 1964 *(H. ebraccata, H. rosenbergi, P. spurrelli, P. callidryas, S. sila* and *S. sordida)* and 7 at Finca Jenkins de Tilarán, near Finca San Bosco on August 8, 1964 *(H. ebraccata, H. microcephala, H. phlebodes, H. loquax, H. elaeochroa, P. callidryas* and *P. saltator).*

SUMMARY OF DIAGNOSTIC CHARACTERISTICS

The following list groups the species of Costa Rican hylids by particularly obvious or distinctive diagnostic characteristics. The utilized features are all aspects that may be determined in the field on living or freshly preserved animals. Many of the color characters are lost after a few days or weeks in preservative. All species exhibiting a certain characteristic are listed under it in the list. Species in which the character is not present in all juvenile and adult specimens are denoted by an asterisk (*).

Iris of Eye Bright Red

H. legleri
H. lythrodes
H. rufioculis
H. uranochroa
P. callidryas
P. saltator
P. spurrelli

Posterior Surface of Head Covered by a Series of Bony Projections from Skull

*A. coronata**

Tympanum Oblique, Directed Dorsolaterally (Figs. 8-9).

H. zeteki

Dorsal Ground Color Deep to Bright Green

H. angustilineata
*H. debilis**
*H. pictipes**
H. rufitela
H. uranochroa
P. annae
P. calcarifer
P. callidryas
*P. lemur**
*P. saltator**
P. spurrelli
*S. baudinii**
*S. phaeota**

Bones Green, Visible Through Skin

H. elaeochroa
H. rufitela
P. venulosa

Fleshy Fringe along Arm and Leg

H. fimbrimembra
H. immensa
H. richardtaylori

No Finger Webbing (Fig. 6)

A. coronata
H. angustilineata
H. boulengeri
H. elaeochroa
H. staufferi
P. lemur

Dorsolateral Light Stripe (Fig. 10)

H. angustilineata
H. colymba
*H. ebraccata**
*H. microcephala**
*H. rufitela**
*P. callidryas**
*S. phaeota**

Lateral Light Stripe (Fig. 13)

*H. ebraccata**
H. legleri
H. lythrodes
H. rufioculis
H. uranochroa

Prominent Suborbital Light Spot (Figs. 12-13)

H. debilis
H. ebraccata
H. lythrodes
H. rufioculis
H. uranochroa
*S. baudinii**
*S. phaeota**

Digital Webs Bright Red

*H. loquax**
H. rufitela
*P. callidryas**

Mid-dorsal Dark Stripe

H. rosenbergi

Light-outlined Dark Rings or Bands Nearly Encircling Limbs

A. coronata

Flank Barred with Dark and Light

H. rosenbergi
P. calcarifer
P. callidryas

Paired Odontoids at Tip of Lower Jaw

H. picadoi

Projecting Prepollex, with Spine on Free Tip in Males

H. fimbrimembra
H. immensa
H. richardtaylori
H. rosenbergi
H. rufitela

Dorsum Strongly Tuberculate or Warty

H. boulengeri
H. fimbrimembra
H. immensa
H. lancasteri
H. richardtaylori
H. staufferi
H. tica
P. venulosa
S. sila

No Toe Webs

P. lemur

Posterior Surface of Thigh Uniform:

Red

H. loquax
*H. rufitela**
*P. callidryas**

Yellow to Yellow-Orange

H. angustilineata
H. colymba
H. debilis
H. ebraccata
H. elaeochroa
*H. legleri**
H. lythrodes
H. microcephala
H. phlebodes
*H. pseudopuma**
*H. rivularis**
H. rufioculis
H. tica
H. uranochroa
P. lemur

Blue to Purple

*H. rufitela**
P. annae
*P. callidryas**
P. saltator
*S. phaeota**
*S. sila**
*S. sordida**

Posterior Surface of Thigh:

Dark with Solid Bars

A. coronata
H. boulengeri
H. lancasteri

Spotted

H. pictipes

Reticulated

*S. baudinii**
*S. puma**
*S. sila**
*S. sordida**

Groin:

Reticulated with Blue-Purple or Brown

*S. baudinii**
S. phaeota
S. puma
S. sila
S. sordida

Discrete Light Spots

H. pictipes
H. pseudopuma
*S. baudinii**
*S. sila**
*S. sordida**

Dorsum with Bold Contrasting Dark Blotches and Spots (Figs. 12, 16)

*H. ebraccata**
*H. elaeochroa**
H. lancasteri
*H. phlebodes**
*H. microcephala**
H. pseudopuma
*H. rivularis**
*H. rufioculis**
*S. staufferi**
*H. tica**
*P. venulosa**
*S. baudinii**
*S. phaeota**
S. puma
*S. sordida**

Paired Lateral Vocal Expansions in Males

P. venulosa
S. baudinii
S. phaeota

Dark Nuptial Thumb Asperities in Males (Fig. 18)

A coronata
H. angustilineata
H. debilis
H. lancasteri
H. legleri
H. lythrodes
H. pictipes
H. pseudopuma
H. rivularis
H. rufioculis
H. tica
H. uranochroa
P. venulosa
P. annae
P. calcarifer
P. callidryas
P. lemur
P. spurrelli
P. saltator
S. phaeota
S. puma
S. sila
S. sordida

Size (maximum standard length of adults):

Small Frogs, 20-30 mm.

H. angustilineata (males)
H. debilis
H. ebraccata (males)
H. lythrodes (males)
H. microcephala
H. phlebodes
H. rufioculis (males)
H. staufferi
H. zeteki

Medium Frogs, 31-50 mm.

H. angustilineata (females)
H. boulengeri
H. colymba
H. ebraccata (females)
H. elaeochroa
H. lancasteri
H. legleri
H. loquax
H. lythrodes (females)
H. picadoi
H. pictipes
H. pseudopuma (males)
H. rivularis
H. rufioculis (females)
H. rufitela
H. tica
H. uranochroa
P. lemur
P. saltator (males)
S. puma
S. sila
S. sordida (males)

Large Frogs, 51-80 mm.

A. coronata
H. fimbrimembra
H. pseudopuma (females)
H. richardtaylori
H. rosenbergi
P. annae
P. calcarifer
P. callidryas
P. saltator
P. spurrelli
S. baudinii
S. phaeota
S. sila (females)
S. sordida (females)

Very Large Frogs, 81+ mm.

H. immensa
P. venulosa

A KEY TO THE HYLIDAE OF COSTA RICA

1a. Pupil of eye vertical in bright light or preservative 2
1b. Pupil of eye horizontal in bright light or preservative 7
2a. Considerable webbing on fingers and toes 3
2b. No webbing on fingers (Fig. 6) or toes ..... *Phyllomedusa lemur*
3a. Flanks uniform, no series of contrasting dark and light areas 4
3a. Flanks with a contrasting pattern of light and dark areas 6
4a. Web between second and third fingers originates distal to penultimate subarticular tubercle of third finger; web between third and fourth toes originates distal to penultimate subarticular tubercle of fourth toe; flanks orange in life, light in preservative ..... *Phyllomedusa spurrelli*
4b. Web between second and third fingers originates proximal to penultimate subarticular tubercle of third finger; web between third and fourth toes originates proximal to penultimate subarticular tubercle of fourth toe; flank blue to purple in life, dark in preservative 5
5a. Web between fourth and fifth toes originates distal to proximal subarticular tubercle (3rd from disk) of fourth toe; iris yellow to yellow orange in life; standard length of adult males 58-68 mm, females 67-84 mm ..... *Phyllomedusa annae*

5b. Web between fourth and fifth toes originates at or proximal to proximal subarticular tubercle (3rd from disk) of fourth toe; iris red in life; standard length of adult males 38-53 mm, females 52-62 mm ..... *Phyllomedusa saltator*

6a. Flanks with a series of light vertical bars on a dark field; no transverse dark bars on upper surface of thigh; lower eyelid reticulate; iris red in life ..... *Phyllomedusa callidryas*

6b. 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; iris gray in life ..... *Phyllomedusa calcarifer*

7a. Lower surfaces of limbs without large light-outlined dark markings; no large knob-like cranial projections 8

7b. Lower surfaces of limbs with sharply contrasting large, light outlined dark rings, bars or spots; occipital, temporal and supraorbital surface of head with numerous large knob-like cranial projections in adults ..... *Anotheca coronata*

8a. A circular whitish mental gland; a dorsolateral light stripe from canthus to level of axilla; dorsum greenish-yellow (yellowish white in preservative) ..... *Hyla colymba*

8b. No circular whitish mental gland; no dorsolateral light stripe extending only to axilla; dorsum not uniform yellowish-green nor yellowish white in preservative 9

9a. Vomerine teeth in curved series and/or border the inner margin of the choanae (Fig. 3); protuberant prepollex with a terminal spine in males, usually indicated in females 10

9b. Vomerine teeth in linear series, never bordering the margin of the choanae (Figs. 1-2); no protuberant prepollex 14

10a. An extensive fleshy fringe along posteroventral margin of lower arm and leg 11

10b. No arm or leg fringes 13

11a. Web of hand extending to disk on at least one digit; venter with horny tubercles ..... *Hyla immensa*

11b. Web of hand not extending distal to penultimate subarticular tubercle on any digit; venter granular, without horny tubercles 12

12a. Upper and lower lips with blackish border; digital disks black above; skin finely shagreened above, some tubercles and granules with minute horny tips ..... *Hyla richardtaylori*

12b. No black on lips or tips of digits; skin with scattered tubercles above, none with a horny tip ..... *Hyla fimbrimembra*

13a. Mid dorsal dark stripe from tip of snout at least to level of axilla; dorsal ground color light brown in life and preservative; diameter of tympanum 2/3 to 3/4 diameter of eye; webs brown; bones colorless; adult males 65-75 mm, females 70-75 mm ..... *Hyla rosenbergi*

13b. No mid-dorsal dark stripe; diameter of tympanum 1/2 diameter of orbit; dorsal ground color green in life, pale yellowish-white in preservative; webs bright red in life; bones green in life; adult males 39-44 mm. females 46-53 mm ... *Hyla rufitela*

14a. Finger webs absent (Fig. 6) 15

14b. Webbing between fingers II-III-IV (Fig. 7) 18

15a. Dorsum uniform; a dorsolateral light stripe from eye to level of groin bordered below by a dark line (Fig. 10), flank dark; venter peppered with brown flecks; snout short (distance from eye to nostril 2/3 diameter of orbit); vocal sacs in males internal, paired, lateral ..... *Hyla angustilineata*

15b. Dorsum not uniform, no dorsolateral light stripe from eye onto back; venter usually immaculate; snout long (distance from eye to nostril equal to or greater than diameter of orbit); vocal sacs in males external, single, median 16

16a. Posterior surface of thigh uniform, dusky or dull yellowish-green in life;

no dark spots in groin; adult males 24-35 mm, females 24-40 mm 17

16b. Posterior surface of thigh with dark bars that alternate with light areas (bright yellow in life, white in preservative); a dark spot or spots in groin; adult males 37-48 mm, females 48-50 mm ..... *Hyla boulengeri*

17a. Dorsum tuberculate; finger disks equal to or slightly smaller than tympanum; snout pointed in dorsal outline; vocal slits in males hidden by tongue; bones colorless; adult males 24-27 mm, females 24-28 mm ..... *Hyla staufferi*

17b. Dorsum smooth to granular, never tuberculate; finger disks about 1 1/4 times as large as tympanum; snout rounded in dorsal outline; vocal slits in males not hidden by tongue; bones green in life; adult males 30-35 mm, females 37-40 mm ..... *Hyla elaeochroa*

18a. Posterior surface of thigh without dark bars; no dark blotches in groin although small punctations may be present 19

18b. Posterior surface of thigh with solid dark bars; alternating light areas bright yellow in life, white in preservative; a dark blotch or blotches in groin ..... *Hyla lancasteri*

19a. A pair of odontoids at tip of lower jaw ..... *Hyla picadoi*

19b. No odontoids on lower jaw 20

20a. Dorsum strongly tuberculate or warty 21

20b. Dorsum smooth or weakly granular 23

21a. A series of discrete prominent warts along posteroventral margin of lower arm; vocal sac single in males; bones colorless; adult males 30-40 mm, females 34 41 mm 22

21b. No series of prominent warts along lower arm; paired vocal sacs in males; bones green in life; adult males 70-90 mm, females 65-96 mm ..... *Phrynohyas venulosa*

22a. Subarticular tubercles under thumb double; posterior surface of thigh yellow usually suffused with dark pigment ..... *Hyla tica*

22b. Subarticular tubercles under thumb single; posterior surface of thigh mottled with light and brown to purple ..... *Smilisca sila*

23a. Tympanum vertical, directed laterally (Figs. 4-5); dorsum frequently with pattern of lines or blotches 24

23b. Tympanum oblique, directed dorsolaterally (Figs. 8-9); dorsum nearly uniform with a few dark punctations ..... *Hyla zeteki*

24a. A distinct dark lateral band from tympanum to level of axilla or extending further posterior (Figs. 11-12) 25

24b. No distinct dark lateral band, although entire flank may be darker than dorsum or a narrow dark dorsolateral stripe may be present (Fig. 14) 27

25a. Posterior surface of thigh suffused with dark pigment; groin usually mottled with dark and light pigment that may form a retiform pattern; adult males 45-71 mm, females 57-81 mm 26

25b. Posterior surface of thigh yellow-orange in life, without dark pigment; groin uniform, light; adult males 23-27 mm; females 30-35 mm ..... *Hyla ebraccata*

26a. A narrow white stripe from heel along tarsal segment to foot; no series of prominent warts along the posteroventral margin of lower arm ..... *Smilisca phaeota*

26b. No white stripe from heel to foot; a series of large prominent warts along lower arm ..... *Smilisca baudinii*

27a. A white lateral stripe from below tympanum or axilla to groin and/or expanded white spot under eye (Fig. 13); lateral stripe rarely broken into linear series of white spots 28

27b. No white lateral stripe or suborbital spot, although a dorsolateral stripe from above tympanum posteriorly onto back may be present (Fig. 10) 32

28a. Vomerine tooth patches between choanae (Fig. 1); a continuous white lateral line from head or axilla to groin; iris red in life 29

28b. Vomerine tooth patches extend posterior to choanae (Fig. 2); no continuous white lateral stripe from head to groin although a light lateral stripe or elongate spot between groin and mid-body; iris dull orange in life ..... *Hyla debilis*

29a. Sole of foot heavily suffused with dark pigment; dorsal ground color brown to greenish-brown in life and preservative; snout moderate to short (distance from eye to nostril less than diameter of orbit) 30

29b. Sole of foot not suffused with dark pigment; dorsal ground color uniform leaf green in life, bluish to purplish in preservative; snout moderately long (distance from eye to nostril equals diameter of orbit) ..... *Hyla uranochroa*

30a. Posterior surface of thigh suffused with dark pigment 31

30b. Posterior surface of thigh not suffused with dark pigment ..... *Hyla lythrodes*

31a. White lip stripe not expanded under orbit; throat heavily suffused with dark pigment to form a fine mottling; tympanum moderate, vertical diameter 1/2 diameter of orbit ..... *Hyla legleri*

31b. White lip stripe greatly expanded under orbit (Fig. 13); throat immaculate or with a few large dark blotches; tympanum small, vertical diameter 1/3 diameter of orbit ..... *Hyla rufioculis*

32a. Posterior surface of thigh uniform or with light and dark mottling; never with a series of discrete light spots on thigh or dark venter 33

32b. Posterior surface of thigh with discrete light spots (yellow in life, white in preservative, Fig. 17-18), venter sometimes marked with extensive dark pigment ..... *Hyla pictipes*

33a. Venter immaculate or with a few scattered dark spots laterally; if ventral spots present diameter of tympanum at least 1/2 diameter of eye, and snout rounded in profile (Fig. 5) 34

33b. Venter peppered with dark spots; diameter of tympanum no more than 1/3 diameter of eye; snout acute in profile (Fig. 4) ..... *Hyla rivularis*

34a. Posterior surface of thigh much lighter in color than dorsal surface of tibia; usually no suffusion of dark pigment on posterior surface of thigh; no mottling in groin or along flank 35

34b. Posterior surface of thigh same color or darker than dorsal surface, never lighter than dorsal surface of tibia; usually a considerable amount of dark pigment on posterior surface of thigh; usually dark and light mottling in groin and along flank 37

35a. Usually a dark line from nostril along canthus to eye; usually a series of narrow dark markings on dorsum; posterior surface of thighs and venter yellow-orange in life; adult males 22-28 mm, females 24-30 mm 36

35b. No dark stripe from nostril to eye; dorsum usually without well-developed dark markings, if present not narrow lines but large blotches; posterior surface of thigh bright red, venter bright lemon-yellow in life; adult males 38-46 mm, females 38 47 mm ..... *Hyla loquax*

36a. A dark dorsolateral stripe from eye posteriorly at least to mid-body, almost always reaching to sacrum or to level of groin (Fig. 14); bordered above by narrow white stripe in life (sometimes faded in preservative); usually no interorbital stripe; upper surface of tibia usually without distinct dark bars ..... *Hyla microcephala*

36b. Dark dorsolateral stripe, if present, extends no further posteriorly than point level with elbow when arm folded along side; not bordered by white above (Fig. 15); interorbital stripe usually present, weakly to strongly developed; upper surfaces of tibia usually marked with dark bars ..... *Hyla phlebodes*

37a. Vomerine tooth patches between choanae (Fig. 1) 38

37b. Vomerine tooth patches extend posterior to choanae (Fig. 2) ..... *Hyla pseudopuma*

38a. Practically no webbing between fingers III-IV, more than two phalanges

free of web on finger IV; no distinct series of warts along posteroventral margin of lower arm; a distinct light stripe, bordered below by a dark line, from heel to foot; dorsum with two elongate dark blotches running from head to sacrum that anastomose at one to several points, across midline (Fig. 16); a distinct interorbital dark bar or spot ..... *Smilisca puma*

38b. Considerable webbing between fingers III-IV, no more than 1 1/2 phalanges free of web on finger IV; a distinct series of warts along lower arm; no light stripe from heel to foot; dorsum uniform or with irregular dark blotches, bands or spots, never with a pair of elongate dark blotches from head to sacrum; usually no interorbital dark bar or spot, if present obscure ..... *Smilisca sordida*

CLAVE PARA LAS ESPECIES COSTARRICENSES DE HYLIDAE

1a. Pupila vertical en luz fuerte o en preservativo 2

1b. Pupila horizontal en luz fuerte o en preservativo 7

2a. Manos y pies con membranas interdigitales bien desarrolladas 3

2b. Manos y pies sin membranas interdigitales ..... *Phyllomedusa lemur*

3a. Costados uniformes, sin áreas contrastantes claras y oscuras 4

3b. Costados con áreas contrastantes claras y oscuras 6

4a. La membrana entre los dedos II y III de la mano llega hasta más afuera del penúltimo tubérculo subarticular del tercer dedo; la membrana entre los dedos III y IV del pie llega hasta más afuera del penúltimo tubérculo subarticular del cuarto dedo; costados anaranjados en vida, claros en preservativo ..... *Phyllomedusa spurrelli*

4b. La membrana entre los dedos II y III de la mano no llega hasta el penúltimo tubérculo subarticular del tercer dedo; la membrana entre los dedos III y IV del pie no llega hasta el penúltimo tubérculo subarticular del cuarto dedo, costados azules o púrpura en vida, oscuros en presertavivo 5

5a. La membrana entre los dedos IV y V del pie llega hasta más afuera del tubérculo proximal subarticular (tercero desde el disco) del cuarto dedo; iris amarillo o amarillo naranja en vida; tamaño de los adultos, machos, 58-68 mm, hembras 67 84 mm ..... *Phyllomedusa annae*

5b. La membrana entre los dedos IV y V del pie llega hasta el tubérculo proximal subarticular (tercero desde el disco) del cuarto dedo, o aún más adentro; iris rojo en vida; tamaño de los machos 38-53 mm, hembras 52-62 ..... *Phyllomedusa saltator*

6a. Costados con serie de bandas verticales claras en fondo oscuro; superficie superior del muslo sin bandas transversales oscuras; párpados inferiores reticulados; iris rojo en vida ..... *Phyllomedusa callidryas*

6b. Costados con serie de bandas oscuras transversales; superficie superior del muslo con serie de bandas transversales oscuras; párpados inferiores no reticulados; iris gris en vida ..... *Phyllomedusa calcarifer*

7a. Superficies inferiores de las extremidades sin manchas oscuras grandes bordeadas de claro; cabeza sin protuberancias craneales 8

7b. Superficies inferiores de las extremidades con manchas, barras o anillos oscuros bordeados de claro, muy definidas; superficies occipital, temporal y supraorbital de la cabeza de los adultos con numerosas protuberancias grandes ..... *Anotheca coronata*

8a. Glándula submaxilar circular blanquecina presente; banda clara dorsolateral desde el ángulo del ojo hasta la axila; dorso verde amarillento en vida, blanco amarillento en preservativo ..... *Hyla colymba*

8b. Glándula submaxilar blanquecina ausente; sin banda clara dorsolateral hasta la axila; dorso ni verde amarillento en vida ni blanco amarillento en preservativo 9

9a. Dientes vomerianos en series curvadas y/o bordeando el margen interior de las coanas (Fig. 3); el "prepollex" protuberante, con una espina terminal en los machos, por lo general vestigial en las hembras 10

9b. Dientes vomerianos en series lineares, nunca bordeando el margen de las coanas (Figs. 1-2); el "prepollex" sin protuberancia 14

10a. Antebrazos y piernas con un reborde cutáneo extenso a lo largo del margen posteroventral 11

10b. Antebrazos y piernas sin reborde cutáneo 13

11a. Membrana de la mano alcanza hasta el disco en uno de los dedos por lo menos; vientre con tubérculos córneos ..... *Hyla immensa*

11b. Membrana de la mano no se extiende más allá del penúltimo tubérculo subarticular en ninguno de los dedos; abdomen granular, sin tubérculos córneos 12

12a. Labios superior e inferior con borde negrusco; discos digitales negros por encima; piel finamente granulada por encima, con algunos tubérculos y gránulos con puntitas córneas ..... *Hyla richardtaylori*

12b. Labios y puntas de los dedos sin color negro; piel con tubérculos esparcidos por encima, ninguno con puntas córneas ..... *Hyla fimbrimembra*

13a. Raya oscura medio-dorsal desde la punta del hocico hasta el nivel de la axila; dorso pardo claro (cárneo) en vida y en preservativo; diámetro del tímpano de 2/3 a 3/4 del diámetro del ojo; membranas pardas; huesos incoloros, adultos machos de 65-75 mm, hembras de 70-55 mm ..... *Hyla rosenbergi*

13b. Sin raya oscura medio-dorsal; diámetro del tímpano 1/2 del diámetro del ojo; dorso verde en vida, blanco amarillento pálido en preservativo; membranas rojo subido y huesos verdes en vida; adultos, machos, 39-44 mm de largo, hembras de 46-53 mm ..... *Hyla rufitela*

14a. Membrana interdigital ausente de las manos (Fig. 6) 15

14b. Membrana presente entre los dedos II-III-IV de las manos (Fig. 7) 18

15a. Dorso uniforme; raya dorsolateral clara desde el ojo hacia atrás, bordeada hacia abajo por una línea oscura (Fig. 10); costados oscuros; abdomen perdigonado de manchas pardas; hocico corto (distancia del ojo a la fosa nasal 2/3 del diámetro de la órbita del ojo; sacos vocales de los machos internos, en pares y laterales ..... *Hyla angustilineata*

15b. Dorso no uniforme; sin raya clara dorsolateral desde el ojo hacia atrás; abdomen por lo general sin manchas; hocico largo (distancio desde el ojo a la fosa nasal igual al diámetro de la órbita del ojo, o más grande); sacos vocales de los machos externos, sencillos y medios 16

16a. Superficie posterior del muslo uniforme, pardusca o amarillo verdoso mortecino en vida; sin puntos oscuros en la ingle: adultos, machos, de 24-35 mm, hembras de 24-40 mm 17

16b. Superficie posterior del muslo con bandas oscuras que alternan con áreas claras (amarillo claro en vida, blancas en preservativo); uno o más puntos oscuros en la ingle; machos adultos de 37-48 mm, hembras de 48-50 mm ..... *Hyla boulengeri*

17a. Dorso tuberculado; discos digitales de las manos iguales o algo más pequeños que el tímpano; hocico puntiagudo en aspecto dorsal; ranuras vocales ocultas por la lengua en los machos; huesos incoloros; adultos, machos de 24-27 mm, hembras de 24-28 mm. ..... *Hyla staufferi*

17b. Dorso liso a granular, nunca tuberculado; discos digitales de las manos aproximadamente 1 1/4 veces el tamaño del tímpano; hocico redondeado en aspecto dorsal; ranuras vocales no ocultas por la lengua en los machos; huesos verdes en vida; adultos, machos de 30-35 mm, hembras de 37-40 mm ..... *Hyla elaeochroa*

18a. Superficie posterior del muslo sin barras oscuras; ingle sin manchas oscuras, aunque puede tener puntos pequeños 19

18b. Superficie posterior del muslo con barras alternas oscuras y claras (amarillas

31a. Banda blanca del labio no se ensencha bajo la órbita del ojo; garganta con abundante pigmento oscuro formando un fino moteado; tímpano mediano (diámetro vertical 1/2 del diámetro de la órbita del ojo) ..... *Hyla legleri*

31b. Banda blanca del labio grandemente expandida debajo de la órbita (Fig. 13)); garganta sin manchas o con unas pocas manchas oscuras; tímpano pequeño (diámetro vertical 1/3 del diámetro de la órbita del ojo) ..... *Hyla rufioculis*

32b. Superficie posterior del muslo con puntos claros discretos (amarillos en vida, blancos en preservativo, Figs. 17-18); vientre a veces con extensa pigmentación oscura ..... *Hyla pictipes*

33a. Vientre sin manchas, o con unas pocas manchas oscuras laterales; si hay puntos ventrales el diámetro del tímpano es por lo menos 1/2 del diámetro del ojo y el hocico es romo de perfil (Fig. 5) 34

33b. Vientre aperdigonado con puntos oscuros; diámetro del tímpano no más grande que 1/3 del diámetro del ojo; hocico aguzado de perfil (Fig. 4) ..... *Hyla rivularis*

34a. Superficie posterior del muslo de color mucho más claro que la superficie dorsal de la tibia, y generalmente sin lavado de pigmento oscuro; costados e ingle sin moteado 35

34b. Superficie posterior del muslo del mismo color o más oscura que la superficie dorsal, nunca más clara que la superficie dorsal de la tibia; generalmente con bastante pigmento oscuro en la superficie posterior del muslo; costados e ingle corrientemente moteados de claro y oscuro 37

35a. Cabeza por lo general con una línea oscura desde la fosa nasal hasta el ojo; dorso generalmente con una serie de manchas oscuras angostas; superficie posterior del muslo y vientre amarillo naranja en vida; adultos, machos de 22-28 mm, hembras de 24-30 mm 36

35b. Cabeza sin la línea oscura desde la fosa nasal al ojo; dorso generalmente sin manchas oscuras bien definidas, y si las hay, no son líneas sino manchas grandes; superficie posterior del muslo rojo claro y vientre amarillo limón subido en vida; adultos, machos de 38-46 mm, hembras de 38-47 mm ..... *Hyla loquax*

36a. Una línea oscura dorsolateral desde el ojo hacia atrás, por lo menos hasta el nivel del codo cuando el brazo está replegado contra el costado y casi siempre hasta el sacro o el nivel de la ingle (Fig. 14), bordeada por encima con una línea blanca que a veces se pierde en preservativo; la banda interorbital generalmente falta; superficie superior de la tibia generalmente sin barras oscuras defenidas ..... *Hyla microcephala*

36b. La línea dorsolateral oscura, cuando la hay, no se extiende más allá del codo cuando el brazo está replegado contra el cuerpo, y le falta el borde blanco por encima (Fig. 15); banda interorbital generalmente presente, débil o fuertemente desarrollada; superficie posterior de la tibia generalmente marcada con barras oscuras ..... *Hyla phlebodes*

37a. Dientes vomerianos en grupos, situados entre las coanas (Fig. 1) 38

37b. Dientes vomerianos en grupos que se extienden por detrás de las coanas ..... *Hyla pseudopuma*

38a. Membranas casi nulas entre los dedos III-IV; más de dos falanges sin membranas en el dedo IV; margen posteroventral del antebrazo sin serie de verrugas definidas; línea clara definida bordeada inferiormente por una línea oscura, desde el talón hasta el pie; dorso con dos manchas alargadas oscuras, desde la cabeza hasta el sacro, que se anastomosan en uno o más puntos cruzando la línea media (Fig. 16); una barra o un punto oscuro, definido, interorbital ..... *Smilisca puma*

38b. Membranas bien desarrolladas entre los dedos III IV; no más de 1 1/2 falanges sin membranas en el dedo IV; margen posteroventral del antebrazo con una serie definida de verrugas; falta la línea blanca del talón al pie; dorso uniforme o con manchas, bandas o puntos oscuros irregulares, nunca con

dos manchas alargadas desde la cabeza hasta el sacro; generalmente sin barra o punto oscuro interorbital, que, sí está presente, es poco definido ——— *Smilisca sordida*

SUMMARY

The tree-frog family Hylidae is represented in Costa Rica by 39 species placed in five genera. *Anotheca* and *Phrynohyas* are represented by a single form; *Hyla* by 26 species; *Phyllomedusa* by six species; *and Smilisca* by five species. Within the latter three genera the species may be grouped by similarities as follows: *Hyla* - Miliaria group; *fimbrimembrana, immensa* and *richardtaylori;* Faber group: *rosenbergi;* Albomarginata group: *rufitela;* Leucophyllata group: *ebraccata, loquax, microcephala* and *phlebodes;* Rubra group: *boulengeri, elaeochroa* and *staufferi;* Uranochroa group; *debilis, pictipes, rivularis, tica, legleri, lythrodes, rufioculis* and *uranochroa;* Zeteki group: *picadoi* and *zeteki;* unassigned to group: *angustilineata, colymba, lancasteri* and *pseudopuma; Phyllomedusa* - Callidryas group: *annae, calcarifer, callidryas, saltator* and *spurrelli;* Lemur group: *lemur; Smilisca* - Baudinii group: *baudinii* and *phaeota;* Sordida group: *sila, sordida* and *puma.*

Brief synonymies, diagnoses and a summary of distinguishing characteristics are given for all species except the *Phyllomedusa.* The following names are placed in synonymy: *Hyla cherrei* Cope, *H. microcephala* Boulenger and *H. underwoodi* Boulenger (= *H. microcephala* Cope); *Hyla spilomma Cope* and *Acrodytes modesta* Taylor & H. M. Smith (= *Phrynohyas venulosa* Laurenti).

Twelve of the 39 species are known only from Costa Rica. Within Costa Rica four major geographic distribution patterns are found. Seven species are wide-ranging lowland forms found on both Atlantic and Pacific coasts; six are restricted to the Atlantic lowlands; 20 are found only in the cordilleras.

On an altitudinal basis 21 species occur in the Tropical Lowlands, 19 species in the Subtropical zone, 5 are Lower Montane forms and only 2 are found above 2500 m in the Montane zone. 12 species are restricted to the Tropical Lowlands, 13 to the Subtropical zone and one to the Lower Montane. 10 species occur in both Tropical and Subtropical zones, two in Subtropical and Lower Montane and two in Lower Montane and Montane zones.

The breeding site of each species serves as one measure of its ecologic niche. Fifteen forms breed in ponds or marshes, 12 are stream breeders, six lay eggs out of water on leaves of bushes or trees and three deposit the eggs in water trapped in epiphytic bromeliads. The known sympatric occurrence of Costa Rican hylids is summarized.

A summary of diagnostic characteristics and a key to Costa Rican hylids in English and Spanish is provided to aid in field identification.

RESUMEN

Las ranas arborícolas de la familia Hylidae se encuentran representadas en Costa Rica por 39 especies distribuidas en 5 géneros. *Anotheca* y *Phrynohyas* están representadas por una especie cada uno; *Hyla* por 26 especies; *Phyllomedusa* por 6 especies; y *Smilisca* por 5 especies. En los tres últimos géneros las especies pueden ser agrupadas según sus similitudes como sigue: *Hyla* - grupo Miliaria: *fimbrimembra, immensa y richardtaylori;* grupo Faber: *rosenbergi;* grupo Albomarginata: *rufitela;* grupo Leucophyllata: *ebraccata, loquax, microcephala* y *phlebodes;* grupo Rubra: *boulengeri, elaeochroa* y *staufferi;* grupo Uranochroa: *debilis, pictipes, rivularis, tica, legleri, lythrodes, rufioculis* y *uranochroa;* grupo Zeteki: *picadoi* y *zeteki;* especies no asignadas en un determinado grupo: *angustilineata, colymba, lancasteri,* y *pseudopuma; Phyllomedusa* - grupo Callidryas: *annae, calcarifer, callidryas, saltator* y *spurrelli;* grupo Lemur: *lemur; Smilisca* - grupo Baudinii: *baudinii* y *phaeota;* grupo Sordida: *puma, sila* y *sordida.*

En forma sucinta se dan sinónimos, diagnosis y un resumen de las características que distinguen a todas las especies excepto las de *Phyllomedusa.* Los siguientes nombres han sido puestos en sinonimia: *Hyla cherrei* Cope, *H. microcephala* Boulenger y *H. underwoodi* Boulenger (= *H. microcephala* Cope); *Hyla spilomma* Cope y *Acrodytes modesta* Taylor & H. M. Smith (= *Phrynohyas venulosa* Laurenti).

Doce de las 39 especies son conocidas solamente de Costa Rica. En Costa Rica se pueden distinguir cuatro modelos primarios de distribución geográfica. Siete especies presentan una amplia distribución en tierras bajas, encontrándose en ambas costas, atlántica y pacífica; seis especies aparecen restringidas a las tie- en ambas costas, atlántica y pacífica; seis especies aparecen restringidas a las tierras bajas de la costa atlántica; 20 especies están restringidas a las cordilleras.

Desde el punto de vista altitudinal, en las tierras bajas tropicales aparecen 21 especies, 19 especies en la zona subtropical, 5 son formas de bosque montano bajo y solamente 2 se encuentran en altitudes mayores a 2500 metros en la zona montana. Doce especies están restringidas a las tierras bajas tropicales, 13 a la zona subtropical y una al montano bajo. Diez especies se dan en las zonas tropical y subtropical, dos en subtropical y montana baja y dos en las zonas montana baja y montana.

Los sitios de cría de cada especie sirven de referencia como indicio de sus nichos ecológicos. Quince formas crían en estanques y pantanos, doce especies utilizan riachuelos, seis depositan sus huevos fuera del agua sobre hojas de arbustos o árboles y tres depositan sus huevos en el agua acumulada en bromeliáceas epífitas. Se dan en resumen la presencia simpátrica conocida de las ranas hílidas de Costa Rica, un resumen de las características diagnósticas y una clave para la identificación en el campo de las especies de hílidas de Costa Rica.

ADDENDUM

Two papers that have appeared after the present work was accepted for publication affect the names of several Costa Rican species. Our studies confirm the conclusion of W. E. Duellman (1968), The genera of phyllomedusine frogs (Anura: Hylidae), *Univ. Kansas Publ. Mus. Nat. Hist.,* 18(1):1-10, that the genus *Agalychnis* Cope, 1864, is distinct from *Phyllomedusa* Wagler, 1830. The only representative of the latter genus in Costa Rica is *P. lemur.* All other species referred to *Phyllomedusa* in the present paper should be called *Agalychnis.*

W. E. Duellman (1968), The taxonomic status of some American hylid frogs, *Herpetologica,* 24(3):194-209, presents evidence that *Hyla spinosa* Steindachner, 1864, is a senior synonym of the species called *Anotheca coronata* in the present account. One of us (S) examined the holotype of *spinosa* with Dr. Duellman and verified his identification. The Costa Rica species should stand as *Anotheca spinosa.*

In addition, Duellman (1968), Descriptions of new hylid frogs from Mexico and Central America, *Univ. Kansas Publ. Mus. Nat. Hist.,* 17(13): 559-578, recognizes a new species, *Hyla xanthosticta,* from Costa Rica: Provincia de Heredia: Cantón de San Rafael: Volcán Barba: S fork Río Las Vueltas, near NW base of Cerro Chompipe, 2100 m. Alto del Roble is a general name for the area. The new form is closely allied to *Hyla pictipes* known from the same locality and differs from it in having a bronze canthal stripe, large yellow spots on the posterior surface of thigh and in the groin, small finger disks and a tympanum 1/2 diameter of eye (no canthal stripe, moderate sized yellow spots on thigh and in groin, larger finger disks and tympanum 1/3 diameter of eye in *pictipes).* Other features used by the describer to characterize *xanthosticta:* uniform green dorsum, labial and supranal light stripes and reduced finger webbing all fall within the variation for *pictipes.* If this form proves to represent another reproductively isolated population of the *Uranochroa* group it will bring the total of known species of hylid frogs in Costa Rica to 40. The nominal new species will key to *pictipes* in the present paper.

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Fig. 1-3. Vomerine tooth patch shape and placement. 1. Linear between choanae; 2. Linear, extending posterior to choanae; 3. Curved.

Fig. 4-5. Snout profile shape. 4. Acute. 5. Rounded.

Fig. 6-7. Finger webbing. 6. None, 7. Webbing formula I trace II trace III 2 1/2-2 1/3 IV.

Fig. 8-9. Tympanum oblique, directed dorsally. 8. Dorsal view *Hyla zeteki*. 9. Lateral view *H. zeteki*.

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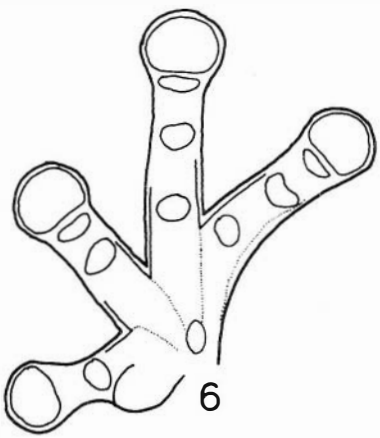

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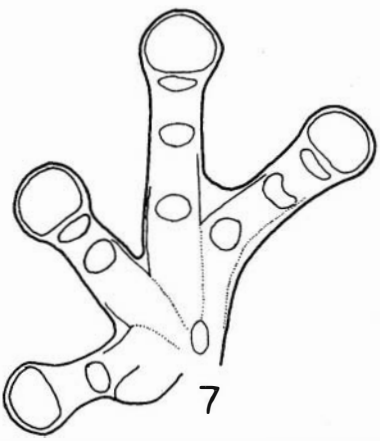

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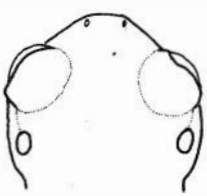

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Fig. 10-16. Diagrammatic representations of color patterns in Costa Rican hylids:

10. Dorsolateral light stripe bordered by dark stripe below.

11. Dark lateral band involving tympanum and fine dark reticulum in groin and along flank

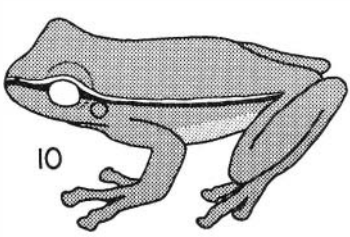
12. Typical pattern of *Hyla ebraccata;* a dorsolateral or lateral light stripe frequently borders the lateral dark band.

13. Lateral light stripe and expanded suborbital light spot.

14. Dorsolateral dark stripe extending to level of groin.

15. Dorsolateral dark stripe extending to level of axilla.

16. Typical pattern of *Smilisca puma.*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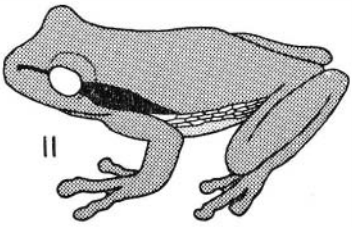
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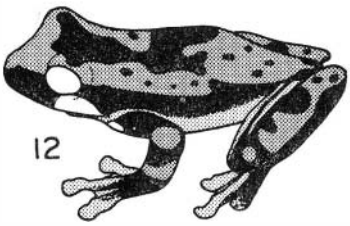
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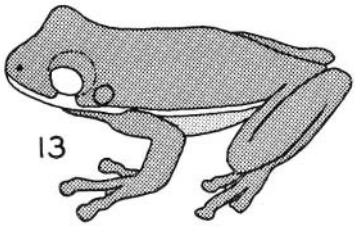
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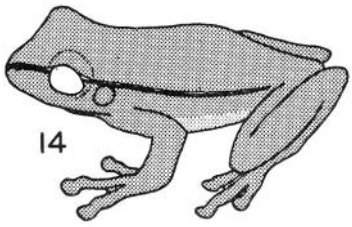
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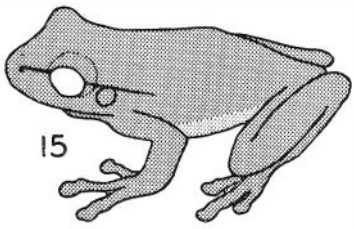
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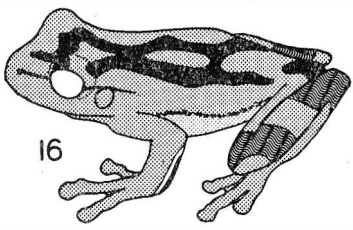
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Fig. 17-18. *Hyla pictipes*. 17. Lateral view. 18. Dorsal view, line equals 10 mm.

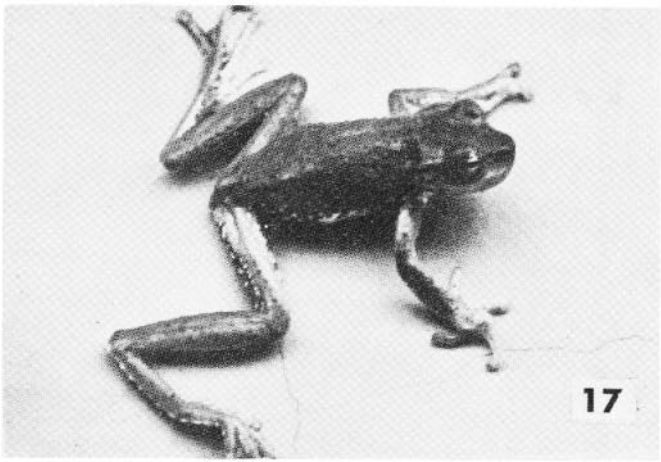

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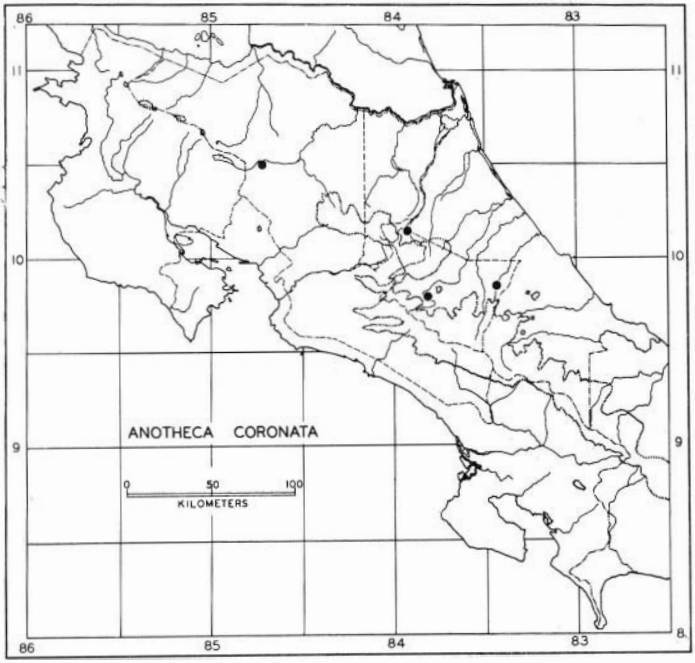
Fig. 19. Distribution in Costa Rica of *Anotheca coronata.*

Fig. 20. Distribution of fringe-limbed tree-frogs *Hyla fimbrimembra, H. immensa* and *H. richardtaylori.*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ANOTHECA CORONATA
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KILOMETERS

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HYLA FIMBRIMEMBRA ▲
H. IMMENSA ●
H. RICHARDTAYLORI ■
0 50 100
KILOMETERS

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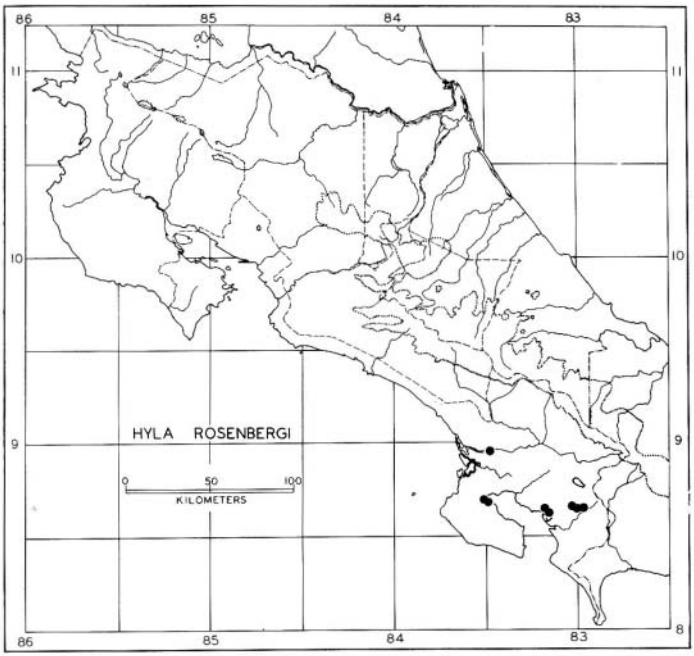
Fig. 21. Distribution in Costa Rica of *Hyla rosenbergi*.

Fig. 22. Distribution of *Hyla rufitela* in Costa Rica.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HYLA ROSENBERGI
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KILOMETERS

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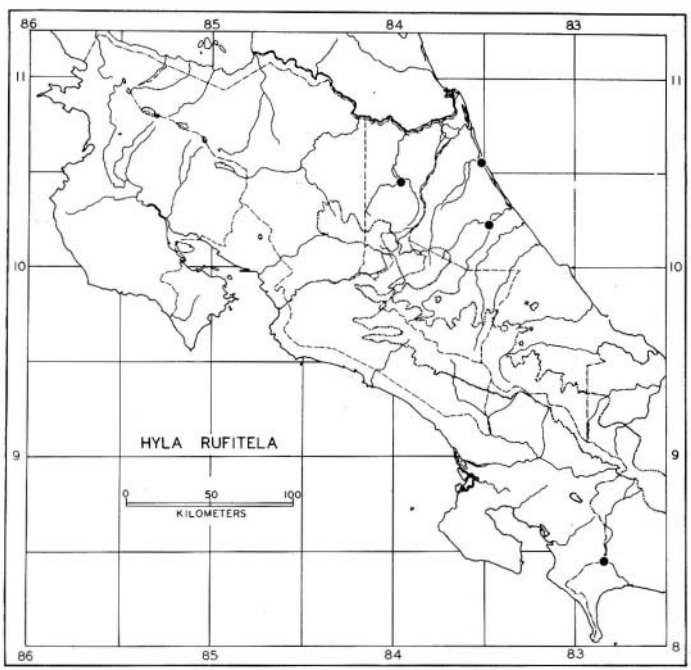
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HYLA RUFITELA
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Fig. 23. Distribution of *Hyla ebraccata* in Costa Rica.

Fig. 24 Costa Rican distribution of *Hyla loquax.*


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HYLA EBRACCATA
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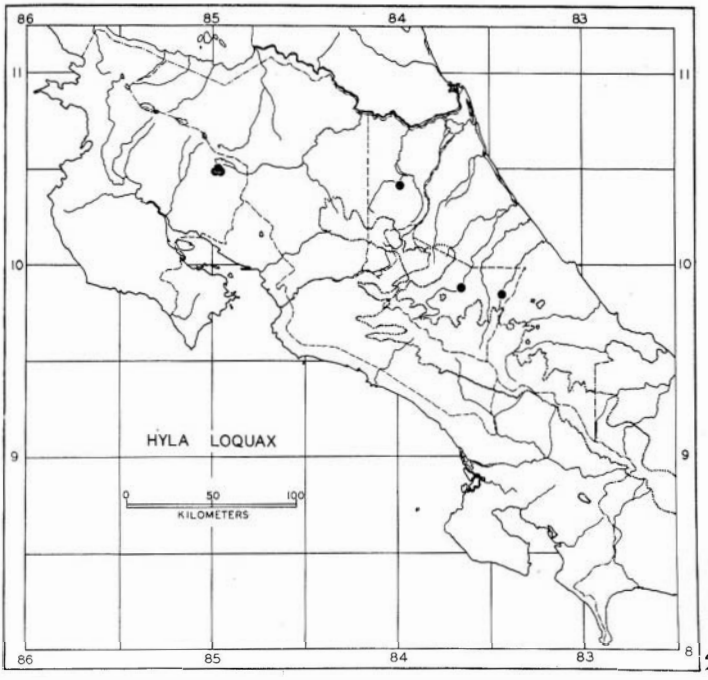
KILOMETERS

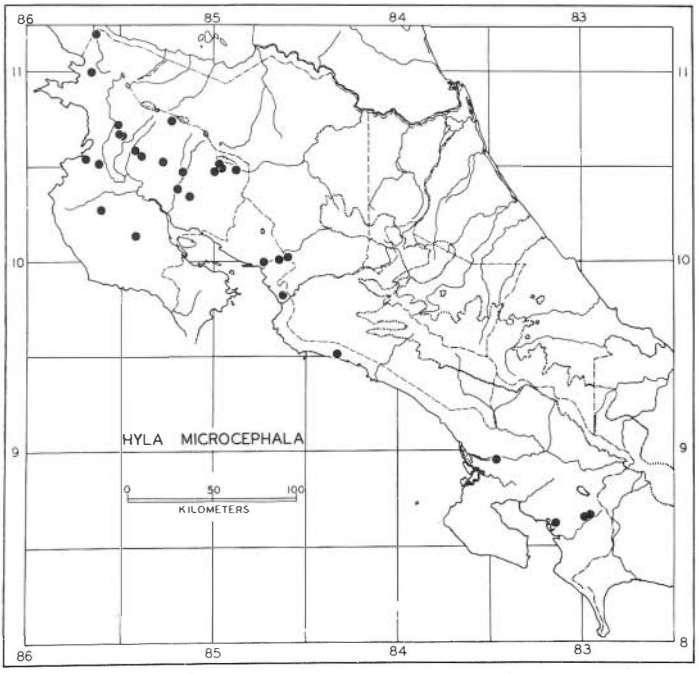
23


86
85
84
83
11
10
9
8
HYLA LOQUAX
0 50 100
KILOMETERS

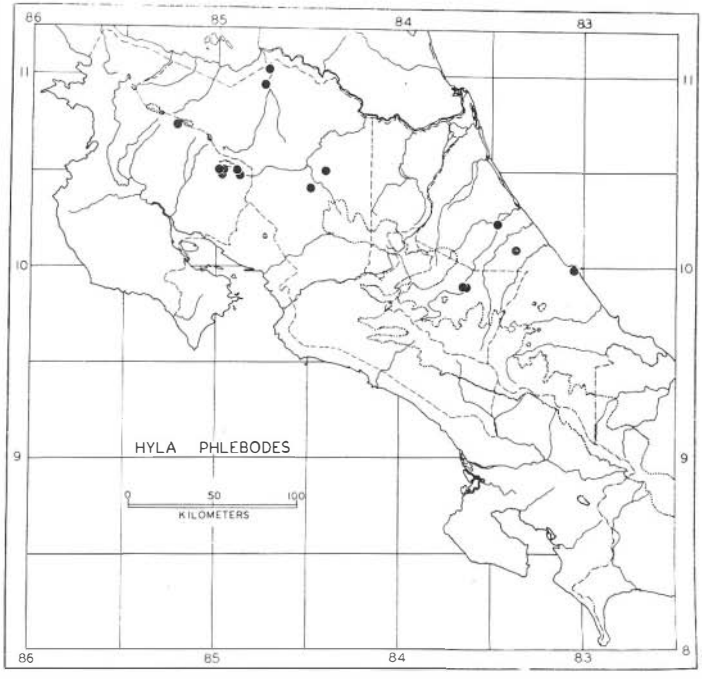
24

Fig. 25. Costa Rican distribution of *Hyla microcephala*.

Fig. 26. Distribution in Costa Rica of *Hyla phlebodes*.


86
85
84
83
11
10
9
8
HYLA MICROCEPHALA
0 50 100
KILOMETERS

25


86
85
84
83
11
10
9
8
HYLA PHLEBODES
0 50 100
KILOMETERS

26

Fig. 27. Distribution of *Hyla boulengeri* in Costa Rica.

Fig. 28. Distribution of *Hyla elaeochroa* in Costa Rica.


86
85
84
83
11
10
9
HYLA BOULENGERI
0 50 100
KILOMETERS

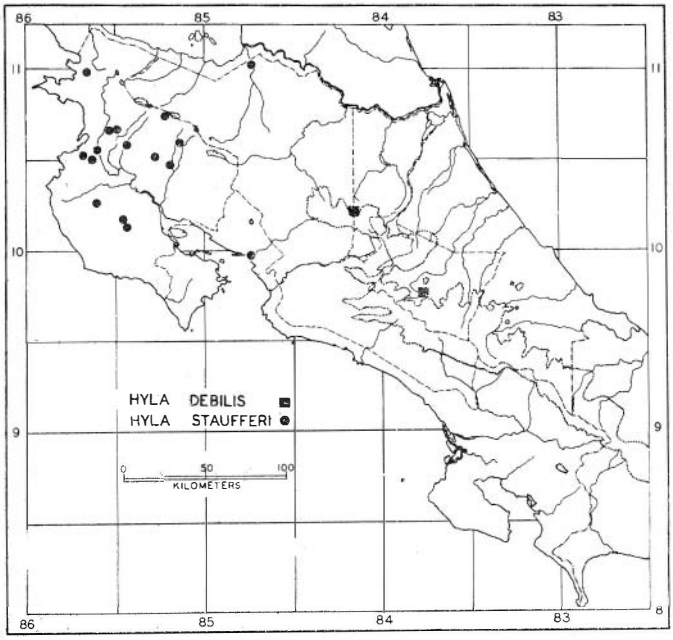
27


86
85
84
83
11
10
9
HYLA ELAEOCHROA
0 50 100
KILOMETERS

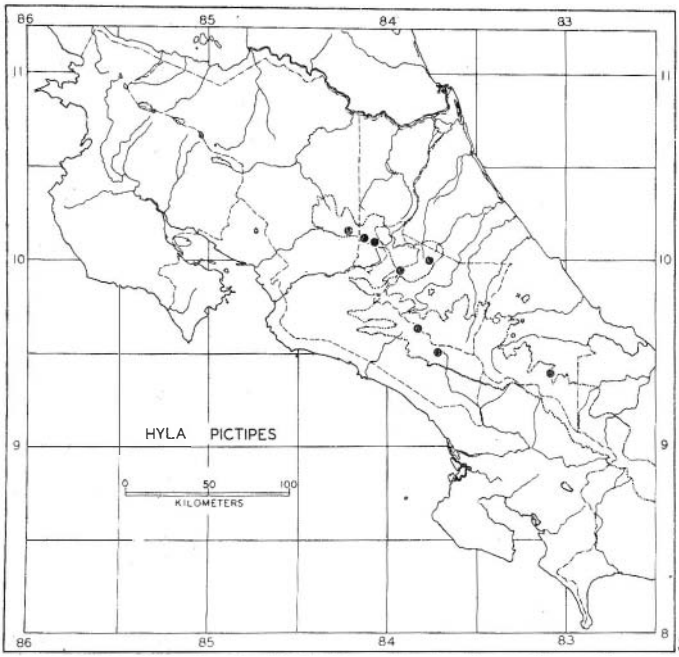
28

Fig. 29. Distribution of *Hyla staufferi* and *Hyla debilis* in Costa Rica.

Fig. 30. Distribution of *Hyla pictipes*.


86
85
84
83
11
10
9
8
HYLA DEBILIS
HYLA STAUFFERI
0 50 100
KILOMETERS

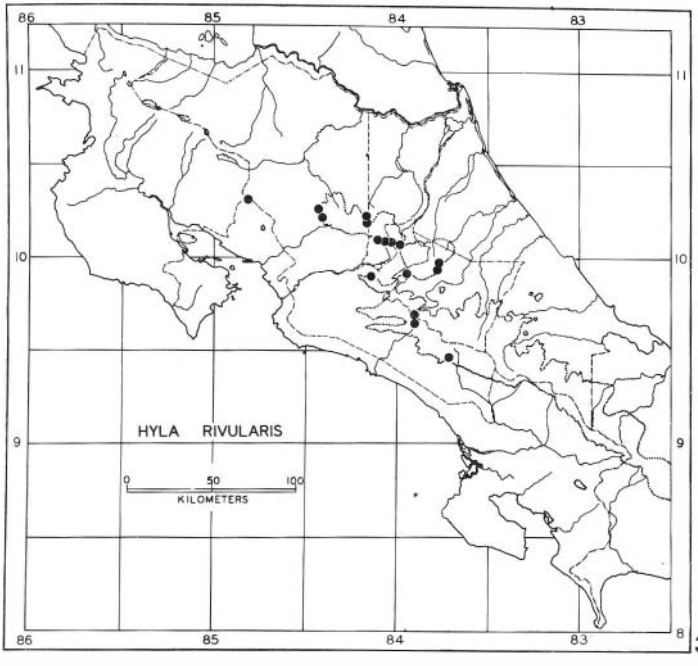
29


86
85
84
83
11
10
9
8
HYLA PICTIPES
0 50 100
KILOMETERS

30

Fig. 31. Distribution of *Hyla rivularis*.

Fig. 32. Distribution of *Hyla tica*.


86
85
84
83
11
10
9
8
HYLA RIVULARIS
0 50 100
KILOMETERS

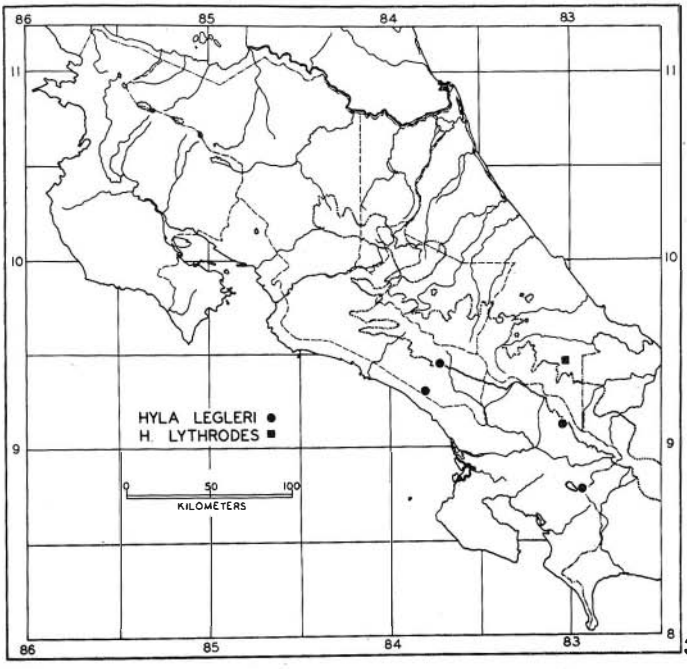
31


86
85
84
83
11
10
9
8
HYLA TICA
0 50 100
KILOMETERS

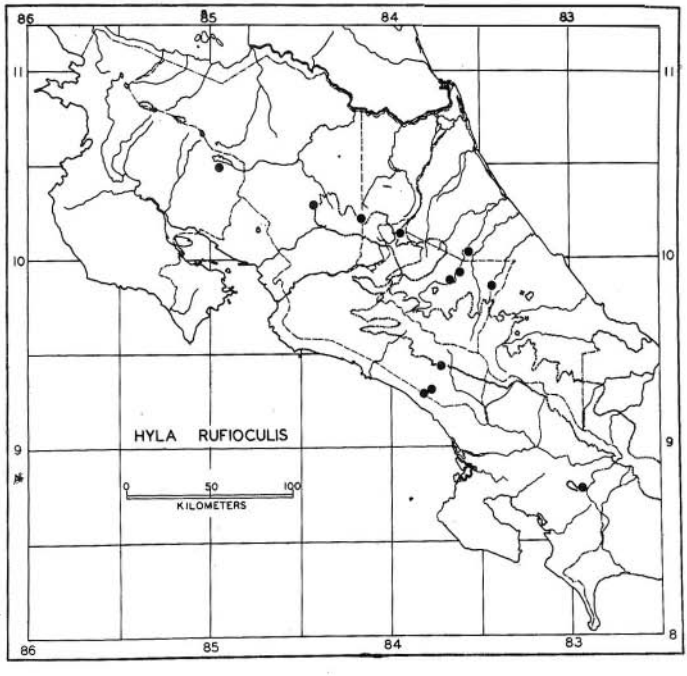
32

Fig. 33. Distribution of *Hyla legleri* and *H. lythrodes*.

Fig. 34. Distribution of *Hyla rufioculis*.


86
85
84
83
11
10
9
8
HYLA LEGLERI ●
H. LYTHRODES ■
0 50 100
KILOMETERS

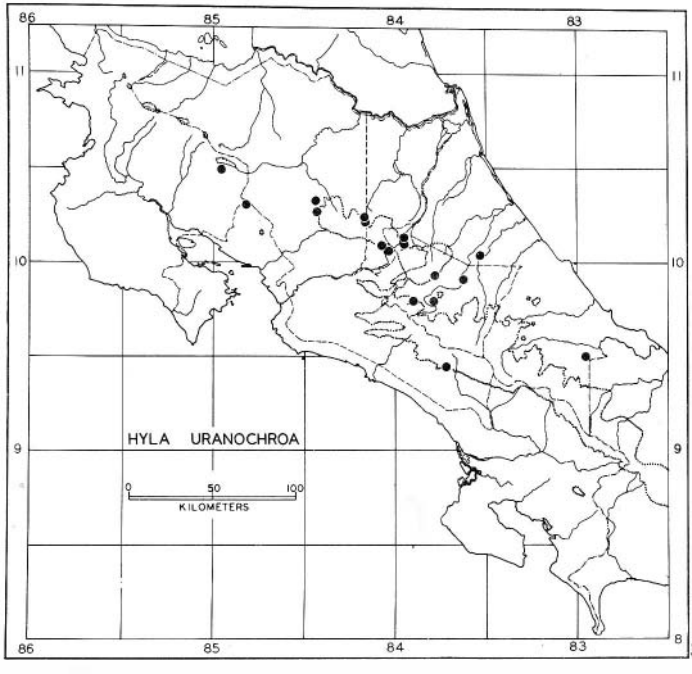
33


86
85
84
83
11
10
9
8
HYLA RUFIOCULIS
0 50 100
KILOMETERS

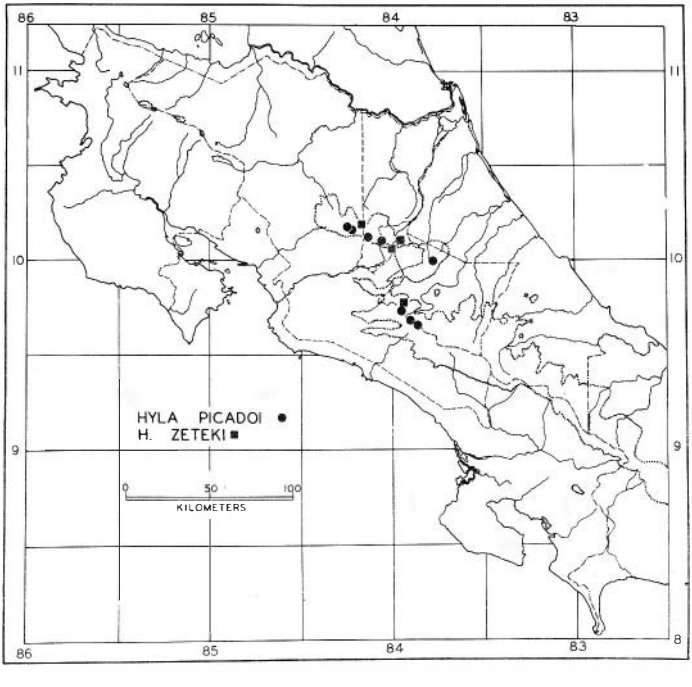
34

Fig. 35. Distribution of *Hyla uranochroa* in Costa Rica.

Fig. 36. Distribution in Costa Rica of *Hyla picadoi* and *H. zeteki.*


86
85
84
83
11
10
9
8
HYLA URANOCHROA
0 50 100
KILOMETERS

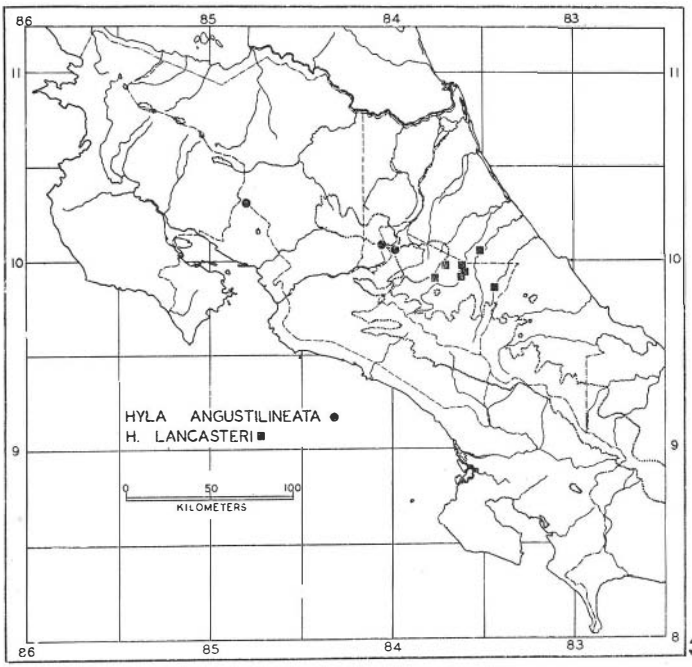
35


86
85
84
83
11
10
9
8
HYLA PICADOI ●
H. ZETEKI ■
0 50 100
KILOMETERS

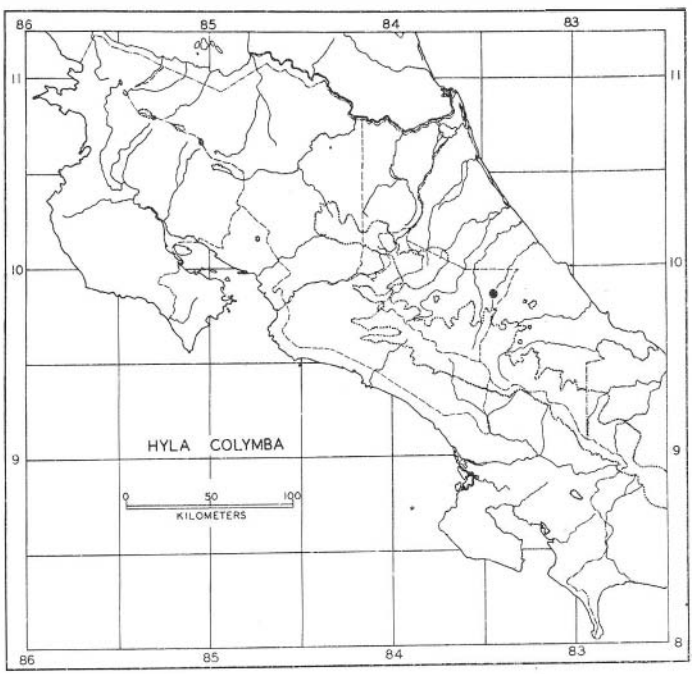
36

Fig. 37 Distribution of *Hyla angustilineata* and *H. lancasteri*.

Fig. 38. Distribution of *Hyla colymba* in Costa Rica.


86
85
84
83
11
10
9
8
HYLA ANGUSTILINEATA ●
H. LANCASTERI ■
0 50 100
KILOMETERS

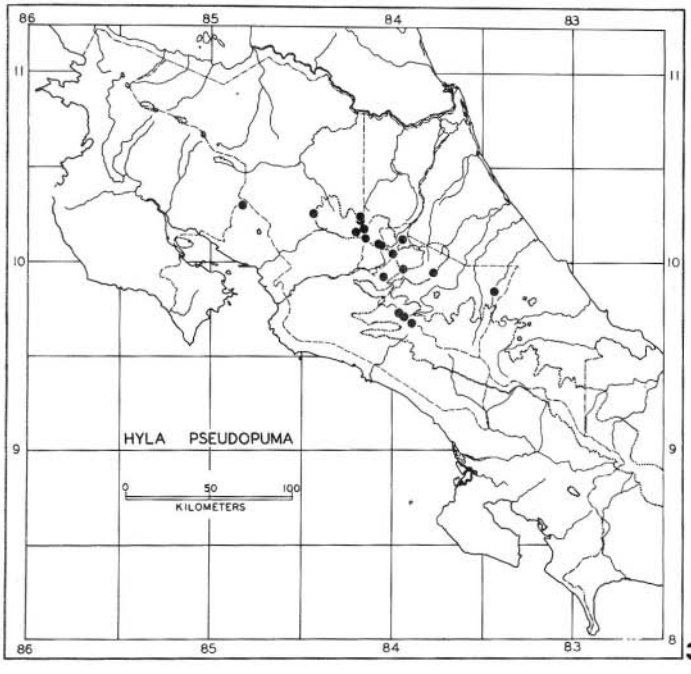
37


86
85
84
83
11
10
9
8
HYLA COLYMBA
0 50 100
KILOMETERS

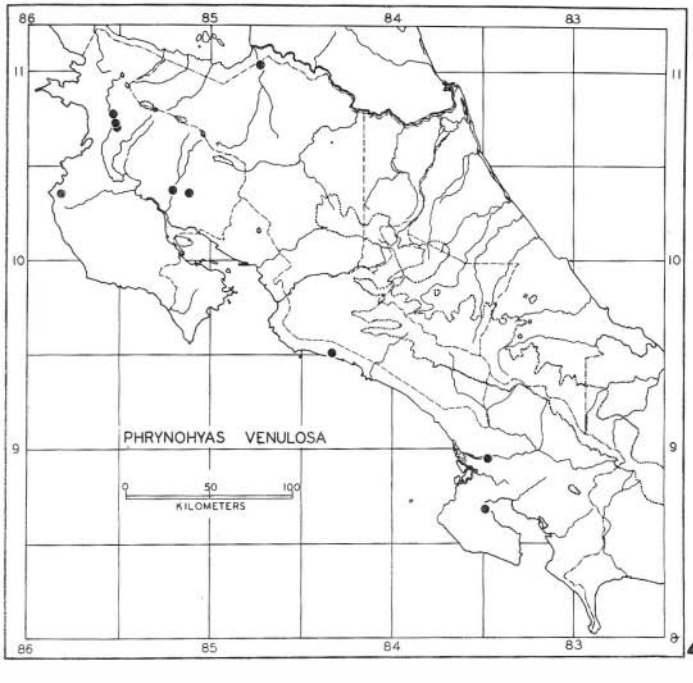
38

Fig. 39 Costa Rican distribution of *Hyla pseudopuma.*

Fig. 40. Costa Rican distribution of *Phrynohyas venulosa.*


86
85
84
83
11
10
9
8
HYLA PSEUDOPUMA
0 50 100
KILOMETERS

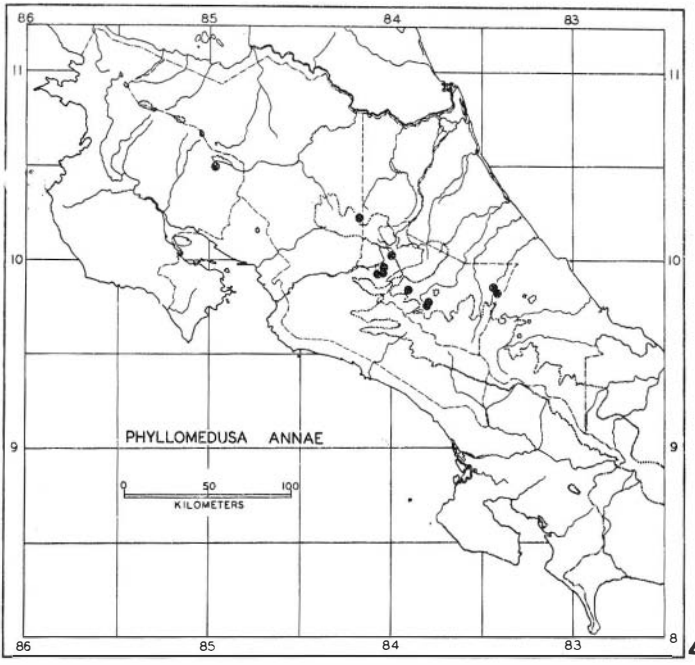
39


86
85
84
83
11
10
9
8
PHRYNOHYAS VENULOSA
0 50 100
KILOMETERS

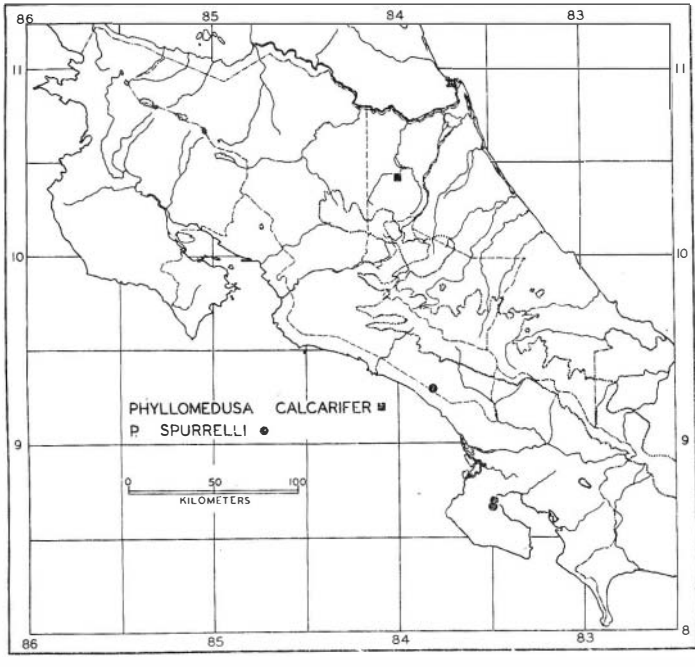
40

Fig. 41. Distribution of *Phyllomedusa annae*.

Fig. 42. Costa Rican distribution of *Phyllomedusa calcarifer* and *P. spurelli*.


86
85
84
83
11
10
9
PHYLLOMEDUSA ANNAE
0 50 100
KILOMETERS

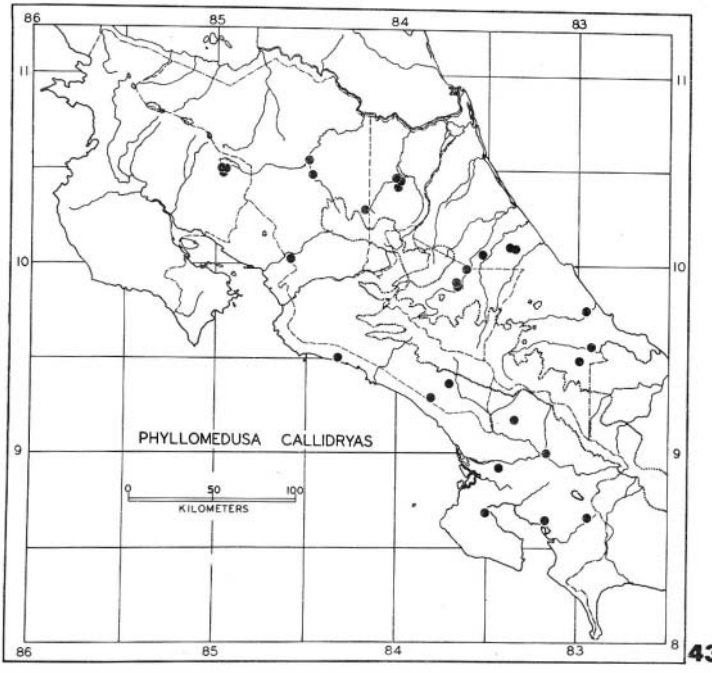
41


86
85
84
83
11
10
9
PHYLLOMEDUSA CALCARIFER
P. SPURRELLI
0 50 100
KILOMETERS

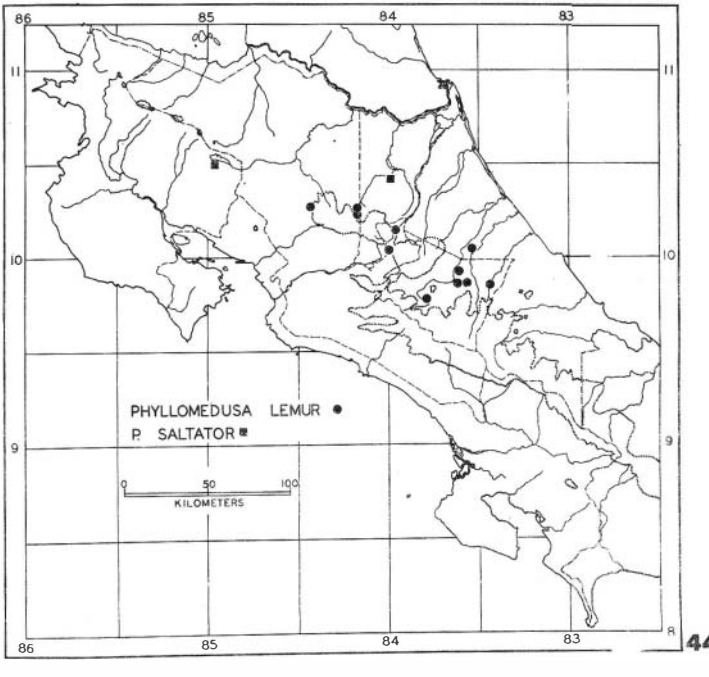
42

Fig. 43. Distribution of *Phyllomedusa callidryas* in Costa Rica.

Fig. 44. Distribution of *Phyllomedusa lemur* and *P. saltator* in Costa Rica.


86
85
84
83
11
10
9
PHYLLOMEDUSA CALLIDRYAS
0 50 100
KILOMETERS

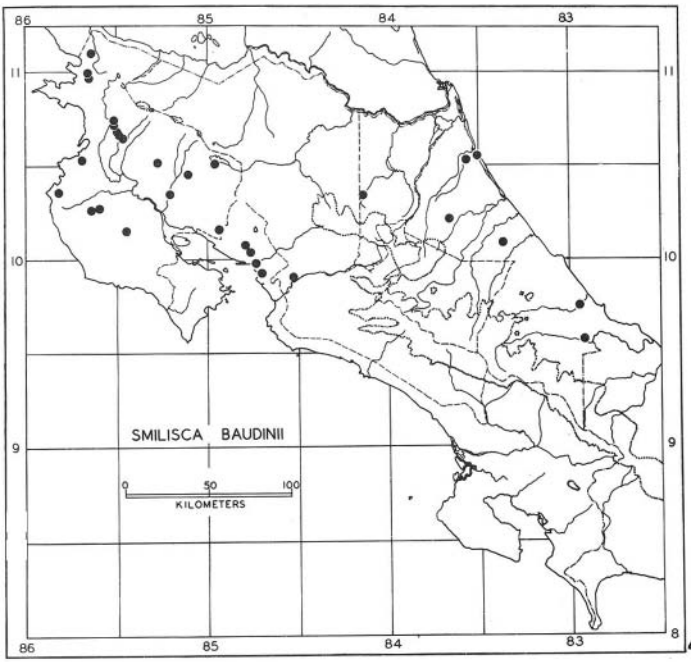
43


86
85
84
83
11
10
9
PHYLLOMEDUSA LEMUR
P. SALTATOR
0 50 100
KILOMETERS

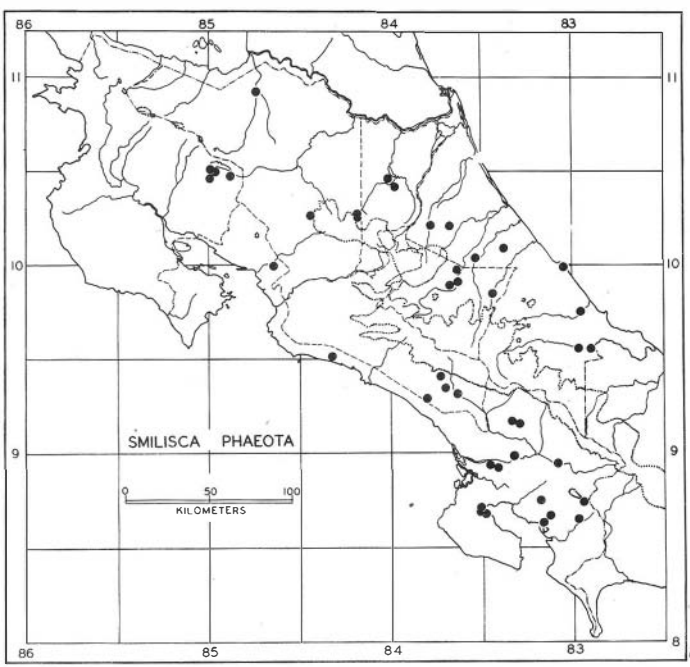
44

Fig. 45. Distribution of *Smilisca baudinii* in Costa Rica.

Fig. 46. Distribution of *Smilisca phaeota* in Costa Rica.


86
85
84
83
11
10
9
SMILISCA BAUDINII
0 50 100
KILOMETERS

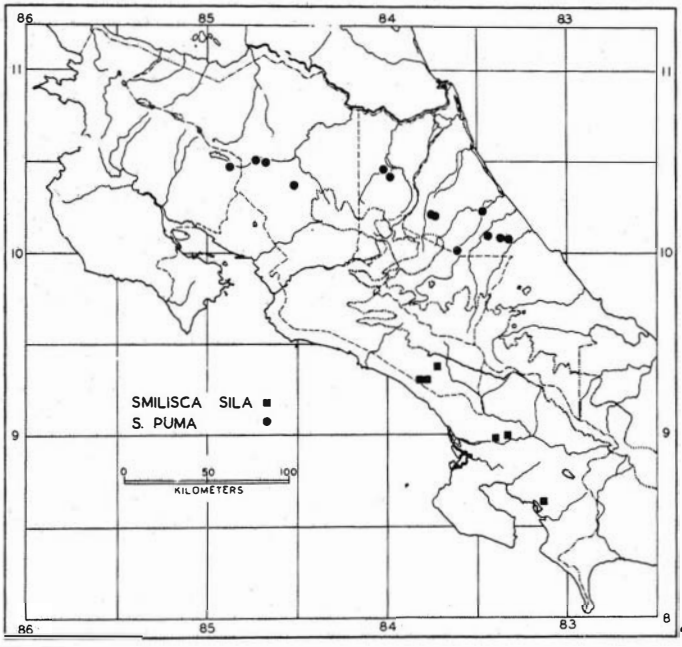
45


86
85
84
83
11
10
9
SMILISCA PHAEOTA
0 50 100
KILOMETERS

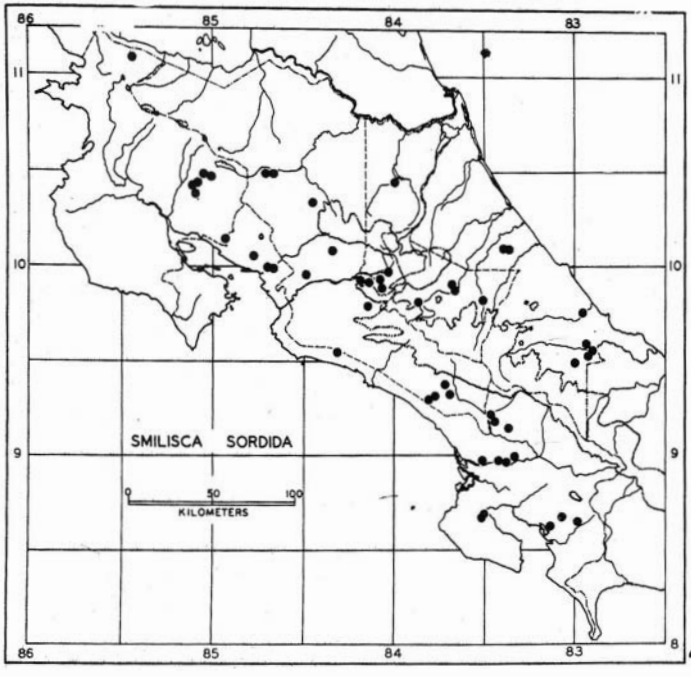
46

Fig. 47. Distribution of *Smilisca sila* and *S. puma* in Costa Rica.

Fig. 48. Distribution of *Smilisca sordida* in Costa Rica.


86
85
84
83
11
10
9
8
SMILISCA SILA
S. PUMA
0 50 100
KILOMETERS

47


86
85
84
83
11
10
9
8
SMILISCA SORDIDA
0 50 100
KILOMETERS

48

Fig. 49. Altitudinal distribution of Costa Rican hylid frogs. See text for explanation.

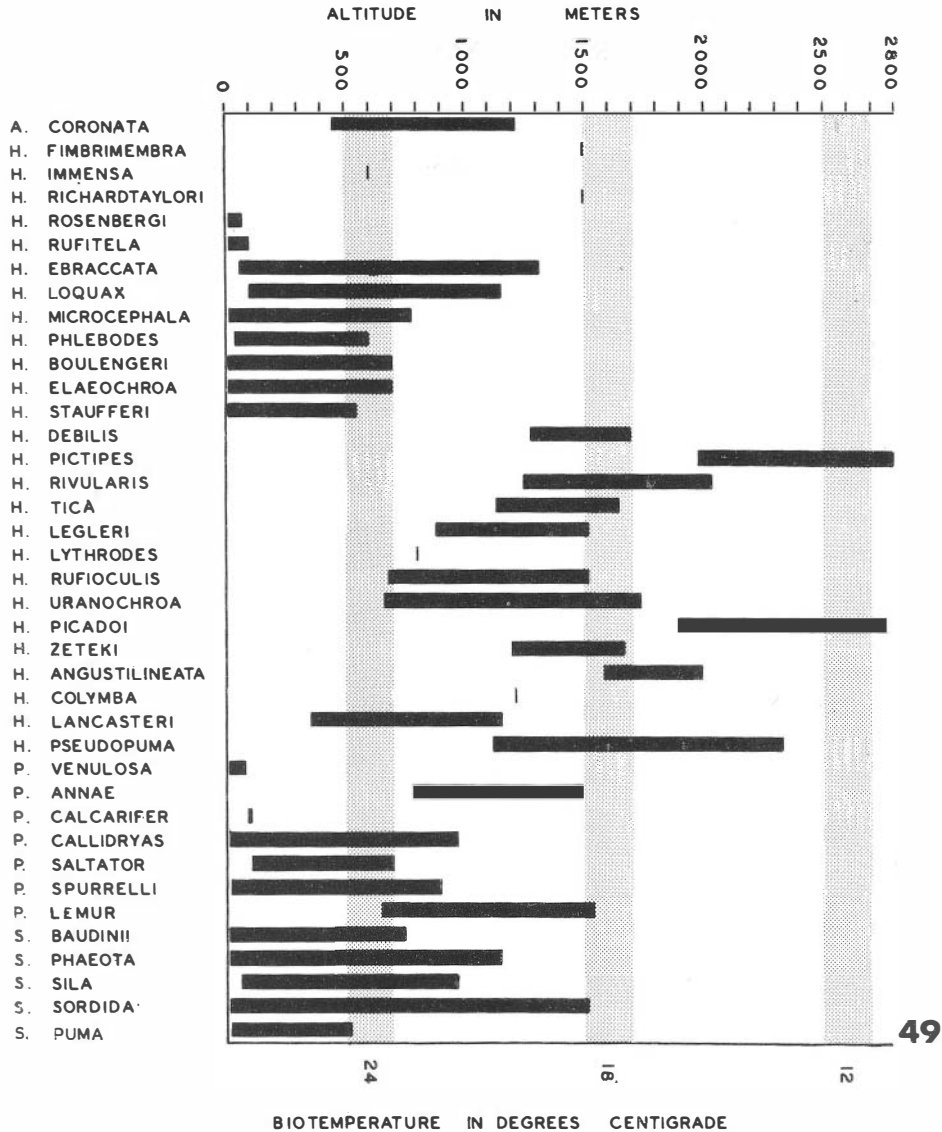
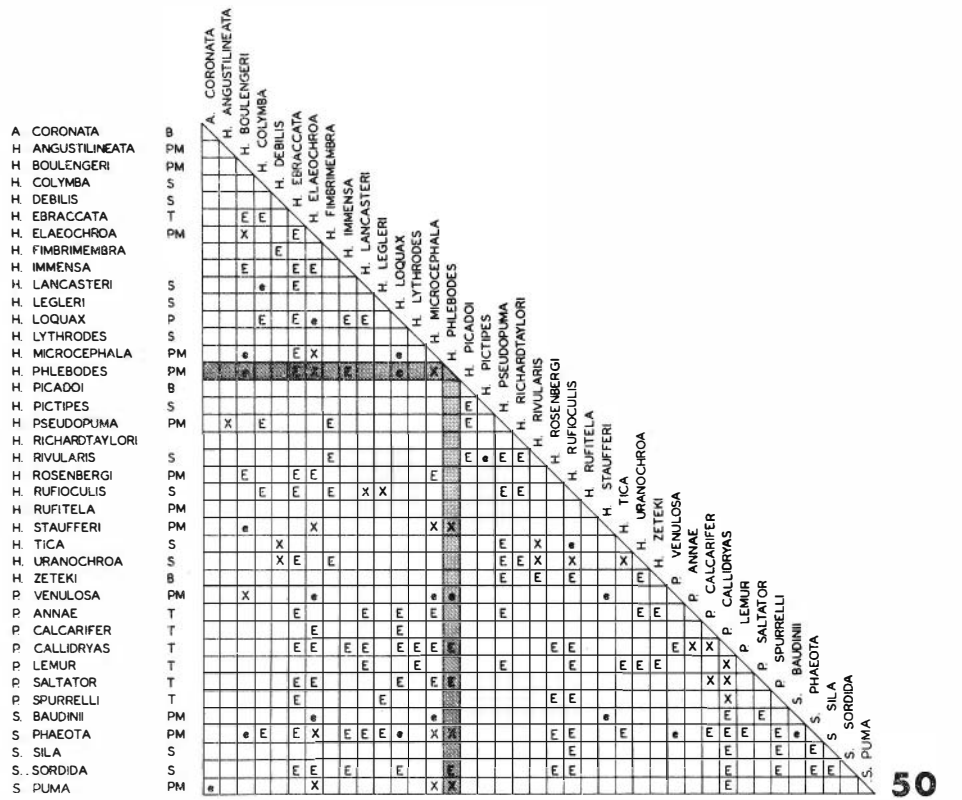

ALTITUDE IN METERS
0
500
1000
1500
2000
2500
2800
A. CORONATA
H. FIMBRIMEMBRA
H. IMMENSA
H. RICHARDTAYLORI
H. ROSENBERGI
H. RUFITELA
H. EBRACCATA
H. LOQUAX
H. MICROCEPHALA
H. PHLEBODES
H. BOULENGERI
H. ELAEOCHROA
H. STAUFFERI
H. DEBILIS
H. PICTIPES
H. RIVULARIS
H. TICA
H. LEGLERI
H. LYTHRODES
H. RUFIOCULIS
H. URANOCHROA
H. PICADOI
H. ZETEKI
H. ANGUSTILINEATA
H. COLYMBA
H. LANCASTERI
H. PSEUDOPUMA
P. VENULOSA
P. ANNAE
P. CALCARIFER
P. CALLIDRYAS
P. SALTATOR
P. SPURRELLI
P. LEMUR
S. BAUDINII
S. PHAEOTA
S. SILA
S. SORDIDA
S. PUMA
49
24
18
12
BIOTEMPERATURE IN DEGREES CENTIGRADE

Fig. 50. Sympatric occurrence of Costa Rican tree-frogs. To determine the forms with which a particular species may be found follow the appropriate column across and down as indicated for *H. phlebodes*. Other details explained in text.


A. CORONATA B
H. ANGUSTILINEATA PM
H. BOULENGERI PM
H. COLYMBA S
H. DEBILIS S
H. EBRACCATA T
H. ELAEOCHROA PM
H. FIMBRIMEMBRA
H. IMMENSA
H. LANCASTERI S
H. LEGLERI S
H. LOQUAX P
H. LYTHRODES S
H. MICROCEPHALA PM
H. PHLEBODES PM
H. PICADOI B
H. PICTIPES S
H. PSEUDOPUMA PM
H. RICHARDTAYLORI
H. RIVULARIS S
H. ROSENBERGI PM
H. RUFIOCULIS S
H. RUFITELA PM
H. STAUFFERI PM
H. TICA S
H. URANOCHROA S
H. ZETEKI B
P. VENULOSA PM
P. ANNAE T
P. CALCARIFER T
P. CALLIDRYAS T
P. LEMUR T
P. SALTATOR T
P. SPURRELLI T
S. BAUDINII PM
S. PHAEOTA PM
S. SILA S
S. SORDIDA S
S. PUMA PM
A. CORONATA
H. ANGUSTILINEATA
H. BOULENGERI
H. COLYMBA
H. DEBILIS
H. EBRACCATA
H. ELAEOCHROA
H. FIMBRIMEMBRA
H. IMMENSA
H. LANCASTERI
H. LEGLERI
H. LOQUAX
H. LYTHRODES
H. MICROCEPHALA
H. PHLEBODES
H. PICADOI
H. PICTIPES
H. PSEUDOPUMA
H. RICHARDTAYLORI
H. RIVULARIS
H. ROSENBERGI
H. RUFIOCULIS
H. RUFITELA
H. STAUFFERI
H. TICA
H. URANOCHROA
H. ZETEKI
P. VENULOSA
P. ANNAE
P. CALCARIFER
P. CALLIDRYAS
P. LEMUR
P. SALTATOR
P. SPURRELLI
S. BAUDINII
S. PHAEOTA
S. SILA
S. SORDIDA
S. PUMA

50