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Frogs of the *Hyla geographica* Group

WILLIAM E. DUELLMAN

Frogs of the *Hyla geographica* species group are widespread in the tropical lowlands of South America east of the Andes. Members of the group share many characteristics with the *Hyla boans* group. Multivariate analysis of 18 morphometric, structural and color pattern characters and analysis of the mating calls reveals the existence of three species in the group—*Hyla calcarata* Troschel, *H. fasciata* Günther, and *H. geographica* Spix. The three species occur sympatrically in the upper Amazon Basin. *Hyla calcarata* and *fasciata* display little geographic variation, but *H. geographica* is highly variable. *Hyla geographica* has the broadest geographic distribution, with populations in Bolivia and southern Perú that differ from other populations in web color. This species also undergoes striking ontogenetic change in coloration. *Hyla leptoscelis* Boulenger is a junior synonym of *H. calcarata*, and the following names are junior synonyms of *H. geographica*: *Hyla geographica* var. *semilineata* Spix, *Hyla punctatissima* Reinhardt and Lütken, *Centrotelma cryptomelan* Cope, *Cophomantis punctillata* Peters, and *Hyla appendiculata* Boulenger.

FIELD work by the author and his associates at the University of Kansas in South America, principally in the Amazon Basin, has produced sufficient material to clarify certain taxonomic problems in the rich anuran fauna of that region. Data on osteology, mating calls, life history and coloration, in addition to conventional morphological characters, have provided a basis for the interpretation of intraspecific variation and interspecific relationships among three species of *Hyla* included here in the *H. geographica* group. Three major problems are involved with the group: 1) confusion of two taxa—*Hyla calcarata* Troschel and *H. fasciata* Günther; 2) ontogenetic change in *Hyla geographica*; and 3) geographic variation in *Hyla geographica*.

Previous workers have been hampered by inadequate material and have been unable

TABLE 1. SAMPLES USED IN STATISTICAL ANALYSES

Locality code no.	Locality	♂♂	♀♀	Total
	Hyla calcarata			
–	Ecuador: Santa Cecilia	20	4	24
	Hyla fasciata			
–	Ecuador: Santa Cecilia	25	9	34
	Hyla geographica			
1	Brasil: Santa Catarina	8	2	10
2	Brasil: Espírito Santo	17	10	27
3	Brasil: Belém	16	2	18
4	Brasil: Manaos	10	4	14
5	Trinidad	5	–	5
6	Ecuador: Santa Cecilia	16	9	25
7	Perú: Río Ucayali	11	5	16
8	Perú: Pilcopata	9	1	10
9	Bolivia: Chipiriri	16	3	19

to determine if *Hyla calcarata* and *H. fasciata* were distinct species. The recent acquisition of large series of both species from the upper Amazon Basin has brought to light evidence that two specifically distinct populations are involved. Examination of large series of *H. geographica* from throughout its range and study of developing individuals have provided the data for an interpretation of the ontogenetic and geographic variation in that species. All statistical analyses were accomplished by use of the numerical taxonomy (NT-SYS) programs on the Honeywell 635 computer at the University of Kansas Computation Center. Museum abbreviations are listed in the Acknowledgments.

THE *HYLA GEOGRAPHICA* GROUP

The following combination of characters distinguishes this group from other *Hyla*: 1) Skull longer than wide, weakly ossified; 2) nasals slender, broadly separated posteriorly by sphenethmoid; 3) frontoparietal fontanelle large, elongate; 4) sphenethmoid broad, depressed medially, broadly separating frontoparietals from nasals; 5) squamosals large with otic plates, and zygomatic processes extending about one-half of distance to maxillaries; 6) prevomers large with angular dentigerous processes, each bearing as many as 20 teeth; 7) palatines slender, in contact with maxillary and sphenethmoid; 8) pterygoids slender, having long medial rami firmly articulating with otic capsules; 9) parasphenoid large with acuminate cultriform process and slender lateral alae; 10) transverse processes of vertebrae long, slender, with those of third vertebra equaling width of sacral diapophyses; 11) sacral diapophyses moderately dilated, posterolaterally inclined; 12) vocal sac single, median, subgular; 13) nuptial excrescences present in breeding males; 14) projecting prepollices absent in both sexes; 15) skin on dorsum smooth in both sexes; 16) calcars present; 17) tympanum large with distinct tympanic ring; 18) inner tarsal fold absent (*H. calcarata* and *fasciata*) or weak (*H. geographica*); 19) inner metatarsal tubercle unmodified; 20) webbing variable, less than two-thirds on hands, more than one-half on feet; 21) palpebrum clear (*H. calcarata* and *fasciata*) or reticulated (*H. geographica*); 22) dorsum brown or tan with irregular or transverse darker brown markings and with or without narrow brown middorsal stripe; 23) flanks bearing black spots, reticulations, or vertical bars; 24) known tadpoles (only *H. geographica*) uniform black with two upper and three lower rows of teeth; 25) mating calls consisting of one or more soft, low-pitched, poorly modulated notes.

Content.—Three species are placed in the group: *Hyla calcarata* Troschel, *H. fasciata* Günther, and *H. geographica* Spix.

Distribution.—The Guianas, Amazon Basin and coastal lowlands of southeastern Brasil.

Remarks.—The *Hyla geographica* group seems to be most closely related to the *Hyla boans* group, which contains six species in South America and Central America (see Duellman, 1970:399). Members of the *H. boans* group are large frogs; males have projecting prepollices. This character alone distinguishes them from members of the *H. geographica* group. All species in both groups have depressed, weakly ossified skulls and angular dentigerous processes on the prevomers.

CHARACTER ANALYSIS

Eighteen characters were employed in the statistical analysis. Seven of these were morphometric characters measured in the manner described by Duellman (1970): snout-vent length, tibia length, foot length, head length, head width, eye diameter and tympanum di-

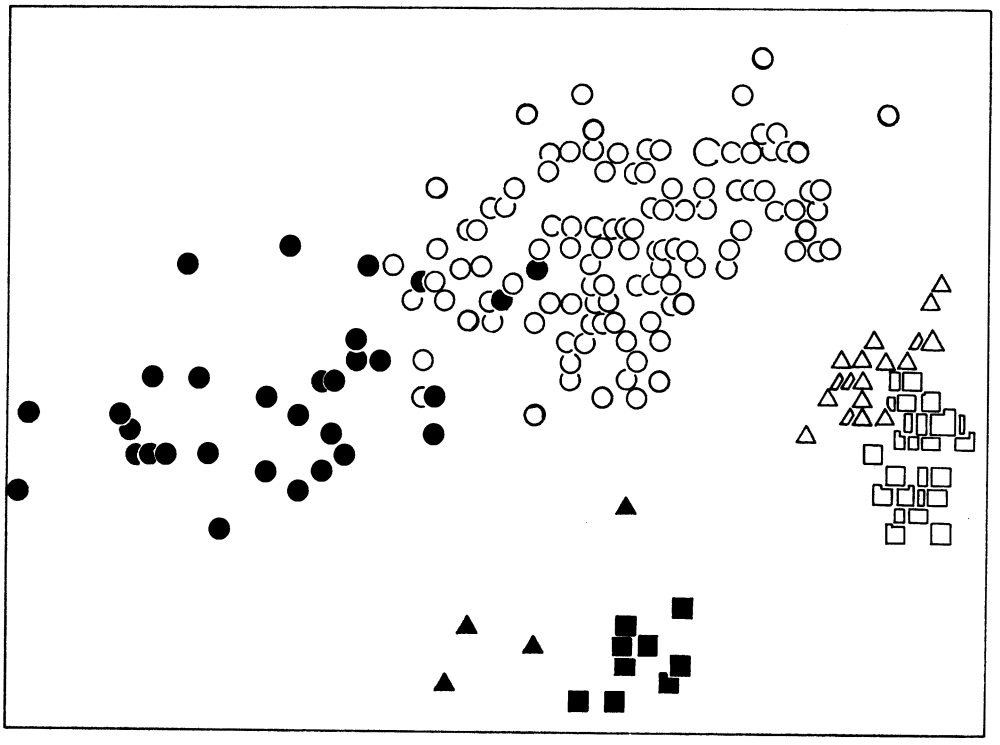

Fig. 1. Plot of 205 OTUs; horizontal axis = Factor I; vertical axis = Factor II. Circles = *Hyla geographica*; triangles = *H. calcarata*; squares = *H. fasciata*; open symbols are males, solid symbols, females. Oversized symbols = two specimens.

ameter. Two structural characters were coded: extent of webbing on the outer edge of the second finger [1) vestigial, 2) base of penultimate phalange, 3) middle of penultimate phalange, 4) base of disk] and size and shape of calcar [1) small, tubercular, 2) large, triangular]. The remaining nine characters involve the color pattern and were coded, as follows: dorsal pattern [1) plain or irregularly marked, 2) X-shaped scapular mark, 3) transverse marks], middorsal stripe [1) absent, 2) present], dorsal light spots [1) absent, 2) present], flank pattern [1) dark with light flecks, 2) single vertical dark bars, 3) paired vertical dark bars, 4) dark spots], belly pattern [1) plain, 2) small dark flecks, 3) dark spots], posterior thigh pattern [1) dark with light spots, 2) single vertical dark bars, 3) paired vertical dark bars, 4) irregular black marks], ventral thigh pattern [1) plain, 2) barred, 3) spotted, 4) flecked], web color [1) brown, 2) red], and palpebral membrane [1) plain, 2) reticulated].

Only samples for which the coloration in life was known were analyzed, except one sample from the Río Ucayali, Perú, in which for some analyses the web color was assumed to be brown. Only adults were used; males were considered to be adult if they possessed nuptial excrescences and/or had distended vocal sacs, whereas females were considered adult if they were gravid or equal in size to gravid females from the same locality. Eleven samples, representing 205 specimens, were analyzed (Table 1).

Recordings of the mating calls of 13 individuals were analyzed for six parameters: notes per call group, note repetition rate, phase, duration, pulse rate and dominant frequency (see Duellman, 1970, for methodology).

Results of the Analyses

Factor analysis of the 205 specimens was carried through 10 reiterations (see Sokal and Sneath, 1963, and Blackith and Reyment, 1971, for discussions of philosophy, methods, and terminology). Factor I had an Eigen-

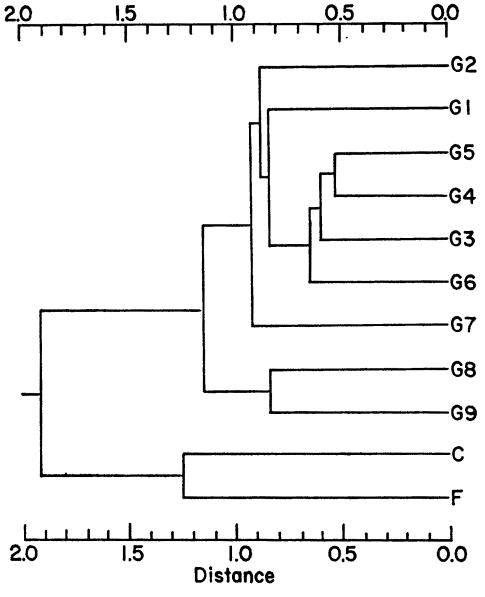

Fig. 2. Distance phenogram for 11 samples. C = *Hyla calcarata*; F = *H. fasciata*; G1–G9 = *H. geographica*; numbers refer to samples given in Table 1.

value of 153.56 and accounted for 96.00% of the variation, whereas Factor II had an Eigenvalue of 2.64 and accounted for 1.65% of the variation. The first five factors included an accumulated 99.95% of the variation. In Factor I the five characters having the heaviest loading (i.e. phenetic significance) are, in descending order: snout-vent length, tibia length, head width, foot length and head width; in Factor II the five characters having the heaviest loading are, in descending order: tibia length, extent of webbing on second fingers, head width, ventral thigh pattern and flank pattern. A plot of OTUs (operational taxonomic units) on the basis of Factors I and II shows distinct intraspecific sexual dimorphism and separates the three species, although there is some overlap between *H. calcarata* and *fasciata* (Fig. 1). Obviously size-related characters are the most important in distinguishing *H. geographica* from the other two species; whereas, tibia length, finger webbing and various color characters help to define *H. calcarata* and *fasciata*.

Cophenetic and distance matrices of unweighted arithmetic character states of the 205 OTUs provided absolute separation of the three species; however, there were varying amounts of overlap among samples of *H. geographica*. Subsequent analysis of the data, using sample means as OTUs, produced a distance phenogram which shows the level of phenetic difference among the samples (Fig. 2).

The mating calls are soft, low-pitched and poorly modulated. The calls of *H. calcarata* and *H. fasciata* have only one note per call group and a faster pulse rate than *H. geographica*. The calls of *H. calcarata* and *H. fasciata* differ in phase and pulse rate (Table 2, Fig. 3).

Geographic Variation in Hyla geographica.— The most striking character variation in *Hyla geographica* is the presence of red, instead of brown, webbing on the hands and feet of individuals from Bolivia and southern Perú. Red webbing was first noted by Gans (1960) in specimens from Roboré, Bolivia. Series obtained at Chipirri, Bolivia, by Thomas H. Fritts and at Pilcopata in southern Perú by Fritts and me also had red

TABLE 2. COMPARISON OF MATING CALLS OF MEMBERS OF *Hyla geographica* GROUP. Means are given in parentheses below observed ranges; see text for explanation of short and long notes.

Species	Individuals per Note	Notes per Call Group	Note Repetition Rate (min)	Phase	Duration	Pulses per sec.	Dominant Frequency
H. calcarata	3/11	1	8	1	0.07–0.12	180–240	1400–2100
					(0.097)	(206)	(1927)
H. fasciata	1/6	1	5	2–3	0.12–0.16	140–180	1700–1800
				(2.2)	(0.145)	(164)	(1766)
H. geographica	7/20	1–12	10–52	1	0.04–0.10	170–200	1400–2000
(short notes)		(3.3)	(29)		(0.060)	(188)	(1750)
H. geographica	5/23	1–6	2–10	1–3	0.13–0.35	80–200	1000–1400
(long notes)		(3.6)	(7)	(1.9)	(0.224)	(139)	(1208)

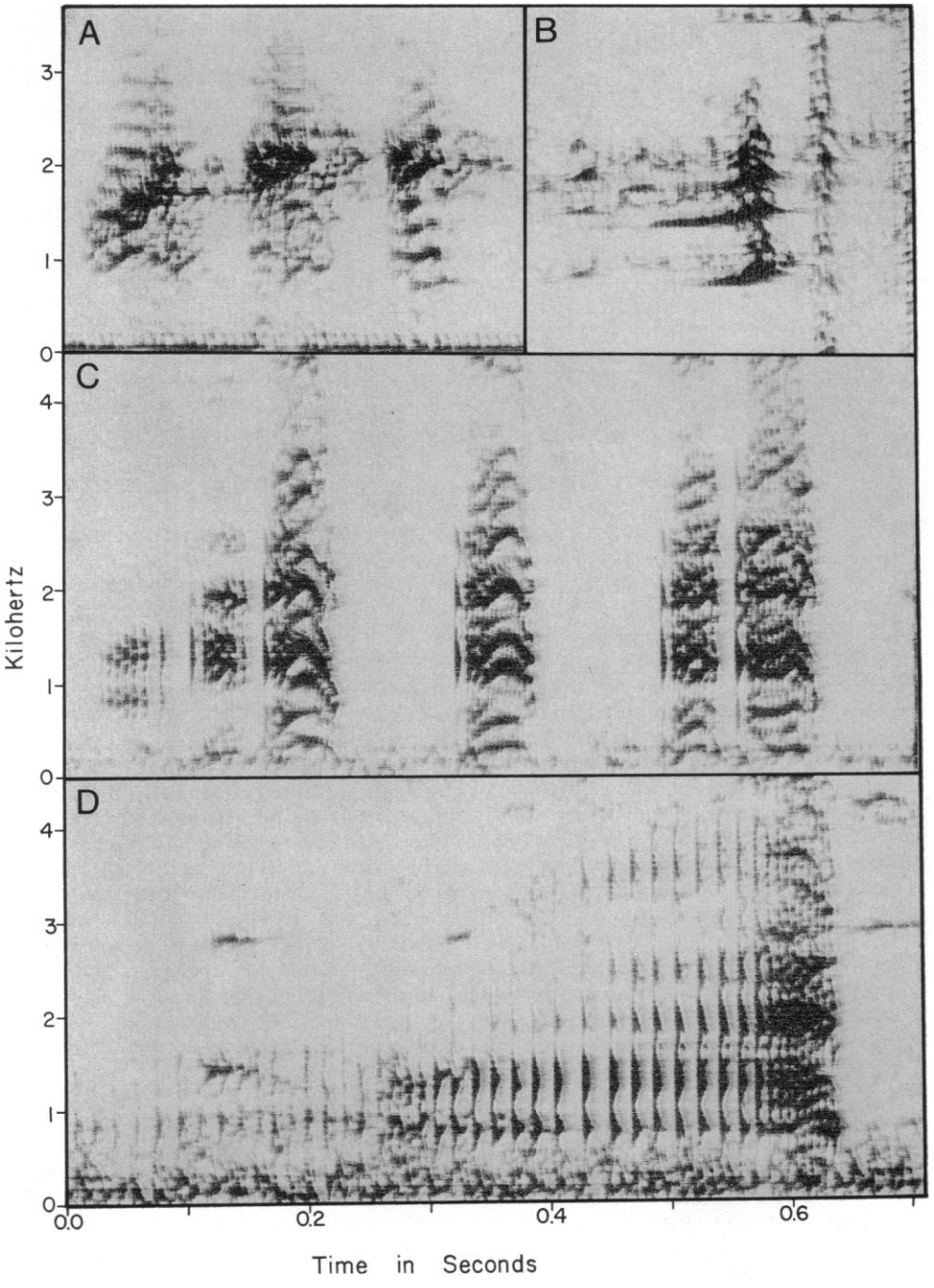

Fig. 3. Audiospectrograms of mating calls. A. *Hyla calcarata*, KU Tape 960, recorded at Belém, Pará, Brasil, 24.5 C. B. *Hyla fasciata*, KU Tape 721, recorded at Santa Cecilia, Napo, Ecuador, 23.0 C. C–D. *Hyla geographica*, KU Tape 1140, recorded at Santa Cecilia, Napo, Ecuador, 23 C. C and D illustrate long and short notes, respectively, of *Hyla geographica*. Band width 40 Hertz.

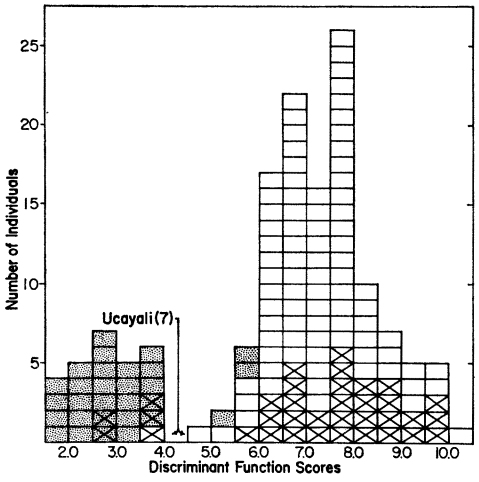

Fig. 4. Histogram depicting discriminant function scores for 147 OTUs of *Hyla geographia*. Each rectangle = one specimen; X's = female; open rectangles = males. Red webbed specimens are stippled.

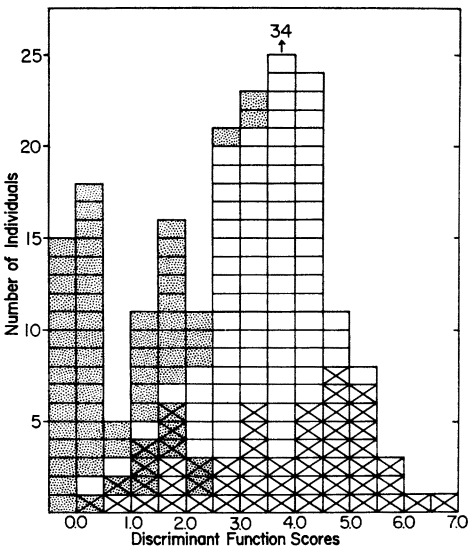

Fig. 5. Histogram depicting discriminant function scores for 191 OTUs of *Hyla geographica*. Symbols same as in Fig. 4, except that all specimens from Bolivia and southern Perú are stippled.

webbing in life. Specimens from southern Perú and Bolivia have black spots on the throat and belly; elsewhere in the range, ventral spotting is common only from Trinidad, where the webs are brown. Ventral spotting is best developed in larger individuals, especially females, whereas web color does not change with age. Variance-covariance correlation between web color and ventral coloration throughout the geographic range is 0.115, and the correlation between snout-vent length and ventral coloration is 2.009.

In treating geographic variation in *H. geographica* the first multivariate analysis was carried out on 18 characters for the 147 specimens in nine samples (see Table 1 for localities and codes). The samples were divided into three groups: localities 1–6 known to have brown webs, 8 and 9 known to have red webs and 7, presumed to have brown webs, from the Río Ucayali; the last sample was treated as an unknown. Arrangement of specimens in a histogram of discriminant function scores shows two separate groups (Fig. 4); three of 29 red-webbed individuals are located in the combined brown-webbed sample and one of the unknowns is located in the red-webbed sample.

Nine characters were used in a second analysis of the same 147 specimens, with an additional 44 specimens from throughout the range of the species. Because web color was unknown for the additional 44 specimens, this character was not used in the analysis. In the first analysis there was a high correlation between different body measurements; therefore, all measurements, except snout-vent length, were excluded from the analysis. Furthermore, in *H. geographica* the size and shape of the calcar and pigmentation of the palpebral membrane are invariable so those characters were also omitted. Discriminant function scores still tended to separate Bolivian and southern Perúvian specimens from those from the rest of the range, but there was still a noticeable overlap (Fig. 5). Thus, on the basis of the characters used and/or on the basis of preserved specimens, it is not possible to separate completely the southwestern samples from the others.

The mating calls of *H. geographica* are highly variable. Some individuals produce long notes; others produce short notes, and at least some produce both long and short notes (Table 2). Other parameters are correlated with the length of the notes: notes per call group, note repetition rate, phase, pulse rate, and dominant frequency (Fig. 3). One individual from Surinam produced only

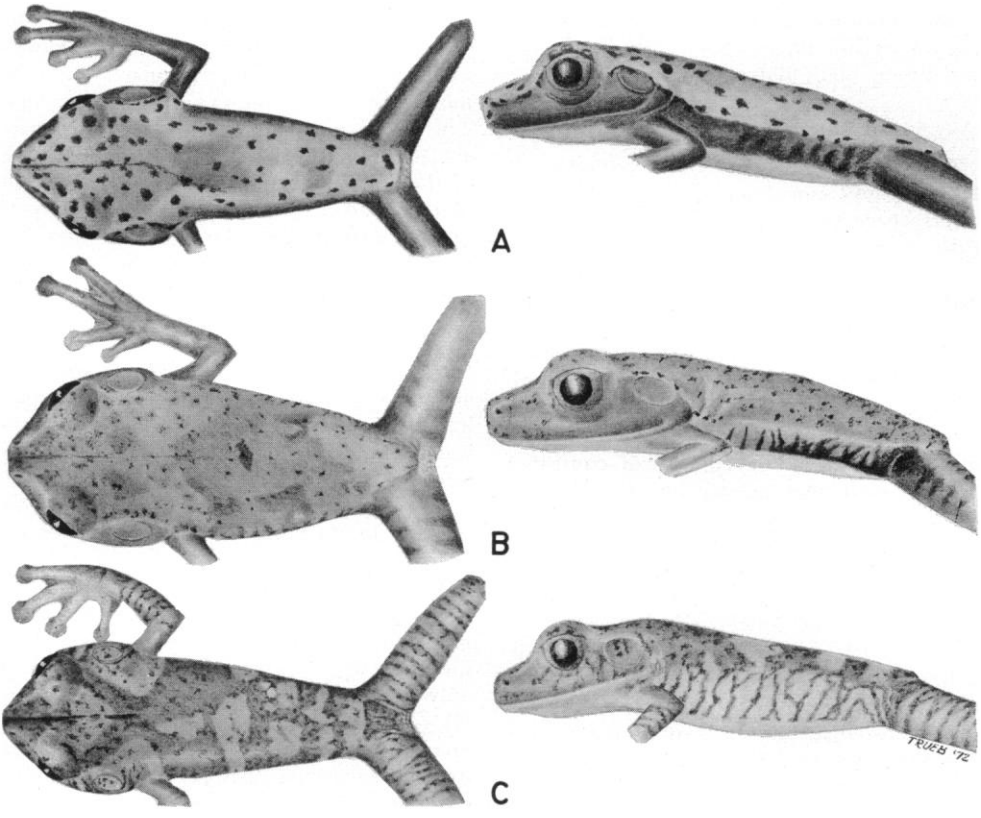

Fig. 6. Ontogenetic change in color pattern in *Hyla geographica*: A. Juvenile, KU 104882, 30.4 mm SVL. B. Subadult male, KU 104879, 36.2 mm SVL. C. Adult female, KU 122728, 47.0 mm SVL.

long notes. Of four individuals from Santa Cecilia, Ecuador, one produced only long notes, one only short notes and two both. An individual from Espírito Santo, Brasil, produced only short notes, and one from São Paulo, Brasil, produced a mixture of 10 short and 14 long notes. Two red-webbed individuals at Pilcopata, Perú, produced only short notes. The complexity of, and variation in, the mating call of *H. geographica* precludes meaningful analysis until many more recordings become available.

Ontogenetic Variation in Hyla geographica.— Ontogenetic change in coloration is striking in *Hyla geographica* (Fig. 6). Changes in color pattern from tadpoles to adults can be summarized, as follows:

Tadpoles are uniform black.

Recently metamorphosed young have a creamy tan dorsum with many black flecks on head, back and dorsal surfaces of limbs. The venter is pale gray; flanks, anterior and posterior surfaces of thighs and inner surfaces of shanks are black.

With an increase in size adult pigmentation replaces juvenile pattern, which is a remnant of larval pigmentation.

Black spots on dorsum disappear.

Black pigment on flanks and thighs concentrates to form of a pattern, either reticulations or vertical bars.

Venter changes to white or creamy orange.

The ontogenetic change in pigmentation is documented in detail by Hennessy (1968), who showed that the melanophores in the larvae are destroyed at, or shortly after, metamorphosis and that the melanophores and lipophores of the adult develop at metamorphosis. The last change to be completed

is the development of the adult pattern on the flanks and thighs. Some breeding males still retain black flanks and thighs.

Taxonomic Conclusions

On the basis of multivariate analysis of 18 structural, morphometric and color characters, three taxa can be distinguished. Distinctive differences in mating calls and the sympatric occurrence of the three taxa in the upper Amazon Basin necessitate the recognition of three species. Considerable geographic variation occurs in *Hyla geographica*; the populations in Bolivia and southern Perú differ from populations throughout the rest of the range by having red, instead of brown webbing. The absence of consistent differences in mating calls between the two color variants suggests that the red-webbed populations represent a geographic variation at an infraspecific level. Taxonomic recognition of these populations is deferred until the limits of the range and areas of intergradation (if any exist) can be determined.

Detailed information on synonymies and their justification, diagnostic characters, variation, and distribution is provided in the following species accounts.

Hyla calcarata Troschel

Hyla calcarata Troschel, 1848:660 [type unknown, from British Guiana; Richard Schomburgk collector].

Hyla leptoscelis Boulenger, 1918:432 [holotype BMNH 1947.2.23.10 from Lago do Tachy, Rio Solimoes, above São Paulo Olivença, Amazonas, Brasil; J. J. Mouncey collector]. New synonymy.

Justification of Synonymy.—No type specimen is known for *Hyla calcarata*, and Troschel's (1848) type description in Schomburgk's book is not readily available. Consequently I provide here a free translation from the original German. The first paragraph is Troschel's description, whereas the second paragraph was identified as being contributed by Schomburgk.

"The body of this very distinctive species is slender and easy to recognize by the color as well as the dermal spur. The latter is evident as a long, sharp extension of skin at the heel joint. The head is rather sharp anteriorly; eyes large protruding, tympanic membrane roundish, slightly longer than broad, its diameter half as large as that of the eyes. The fingers are only basally webbed, the inner finger is entirely free, the toes are webbed to the penultimate phalange. The color in alcohol is reddish-brown with a black longitudinal stripe down the middle of the smooth back. Posteriorly on the side of the head are about seven short, perpendicular dark stripes. On the leg there are dark transverse bars, the number of which is almost doubly as large on the posterior side as on the anterior side.

'I have always found this lowly small tree frog along the banks of streams where it generally sits on the leaves of bushes which have their branches spread directly over the water. Its skin is always very sticky to the touch, a condition, because leaves are their favorite perching spot, that must be of advantage to them in clinging to the leaves.' *Schomb.*"

Many specimens fitting Troschel's description are known from Guyana and the Amazon Basin. Despite the absence of a type specimen, the description seems to point to only two known species of South American *Hyla—calcarata* and *fasciata*. Troschel's emphasis on the large size of the calcar is strongly suggestive that the description cannot apply to *fasciata*, which has a smaller, tubercular calcar. Furthermore, *Hyla fasciata* is not known in Guyana or anywhere else in north-eastern South America.

Boulenger (1882:359) considered *Hyla calcarata* and *H. fasciata* to be conspecific and, without regard to priority, used the name *Hyla fasciata*. Boulenger (1918) based his description of *Hyla leptoscelis* on a juvenile (BMNH 1947.2.23.10) with a S-V length of 26.2 mm. This specimen has a large triangular calcar and rudimentary webbing on the hand. I examined the specimen on 17 June 1969; it was badly discolored—dorsum grayish green with darker dorsal markings. This is in contrast to Boulenger's (1918) description: "Yellowish above, with purplish-brown markings; a large spot on the snout, two V-shaped bands between the eyes, two cross-bars on the back, a V-shaped band on the sacral region, and angular cross-bars on the limbs." In some juveniles of *H. calcarata* the dorsal markings are bold, and some of the markings are more chevron-shaped than transverse. The flanks of juveniles are either pale creamy tan or have small black flecks. The size, proportions, coloration, amount of

webbing, and large calcar of the holotype of *Hyla leptoscelis* are consistent with these characters in juvenile *Hyla calcarata*, here considered to be a senior synonym.

Diagnosis.—Maximum snout-vent length of males 39.9 mm and females, 55.6 mm. 1) Webbing vestigial on the hand; 2) calcar large, triangular; 3) palpebrum clear; 4) dorsum pale yellowish tan with darker tan transverse marks; 5) middorsal dark stripe present; 6) flanks white or blue with bold black spots or single vertical bars; 7) posterior surfaces of thighs white or blue with irregular black spots or single vertical bars; 8) ventral surfaces of thighs uniform white; 9) belly white; 10) webbing on feet tan. *H. calcarata* is most easily confused with *H. fasciata*, which has a smaller, elongate calcar, dark flecks on the venter, and usually irregular black spots (instead of bold vertical bars) on the flanks and thighs. *H. geographica* differs from *H. calcarata* by having extensive webbing on the hand and a reticulated palpebrum. Other species resembling *H. calcarata* and *H. fasciata* are distinguished in the diagnosis of *H. fasciata.*

Variation.—Absence of webbing on the hand and presence of large, triangular calcars is uniform in all specimens examined. The feet are one-half (males and small females) to two-thirds webbed (large females). The dorsum is pinkish brown with darker brown markings, consisting of: 1) five to seven broad transverse marks, sometimes interconnected, 2) narrow brown transverse lines in interspaces between broad marks in some individuals, 3) a narrow dark brown middorsal line beginning on the tip of the snout and terminating at a point between the occiput and sacrum, 4) transverse bars on the limbs (one or two each on upper arm and forearm and three to five each on thigh, shank, and foot). The webbing on the foot is brown. Narrow white stripes are present above the anus and on the outer edge of the foot. The posterior flanks and anterior and posterior surfaces of the thighs are pale cream or gray with black markings. In most specimens these markings are vertical bars about equal in width to the interspaces (Fig. 7A–B). As many as eight bars may be present on the flank and an equal number on the thigh. In about 10% of the specimens examined the dark markings formed irregular spots. The venter is creamy white; in large females there is a tan suffusion along the margin of the chin.

Ontogenetic color change involves the development of transverse dark markings on the dorsum and black bars on the flanks and thighs. Juveniles (S-V length less than 25 mm) lack dark markings on the flanks and thighs; a faint middorsal stripe also is present with five or six dark lateral expansions (incipient transverse marks?). Narrow transverse bars are present on the limbs.

At night, living adults have a pale yellowish tan dorsum with faint darker markings; by day the dorsum is pale reddish brown with brown markings. The posterior flanks and anterior and posterior surfaces of the thighs are bluish white (smaller individuals) or blue (larger individuals) with black markings. The venter is white, and the anal and tarsal stripes are creamy white. The iris is creamy silver.

Natural History.—Eggs and tadpoles are unknown; the smallest juveniles (S-V length 22.5 mm) were obtained at Santa Cecilia, Ecuador, on 25 July 1967. Calling males were found there from March through May and in October, and calling males were found at Belém, Brasil, in April. Males call from branches of low trees and bushes over water in forest. The call is a low-pitched rattling note (Fig. 3A).

Distribution.—The Guianas, northern Amazon Basin, and upper Orinoco Basin in eastern Colombia (Fig. 8). Most records are from localities at elevations of less than 500 m, but the species occurs up to 1240 m in Ecuador. In addition to the 180 specimens examined from 28 localities, Goin (1971:8) recorded the species from the following localities in Surinam: Brokopondo, Coppenameweg, Powakka, and Toekoemoetoekreek.

Hyla fasciata Günther

Hyla fasciata Günther, 1859:100 [holotype BMNH 58.4.25.22 from "Andes of Ecuador"; Mr. Fraser collector].

Diagnosis.—Maximum snout-vent length of males 36.1 mm and females, 50.0 mm. 1) Webbing vestigial on hand; 2) calcar small, elongate, tubercular; 3) palpebrum clear; 4) dorsum pale yellowish tan with faint trans-

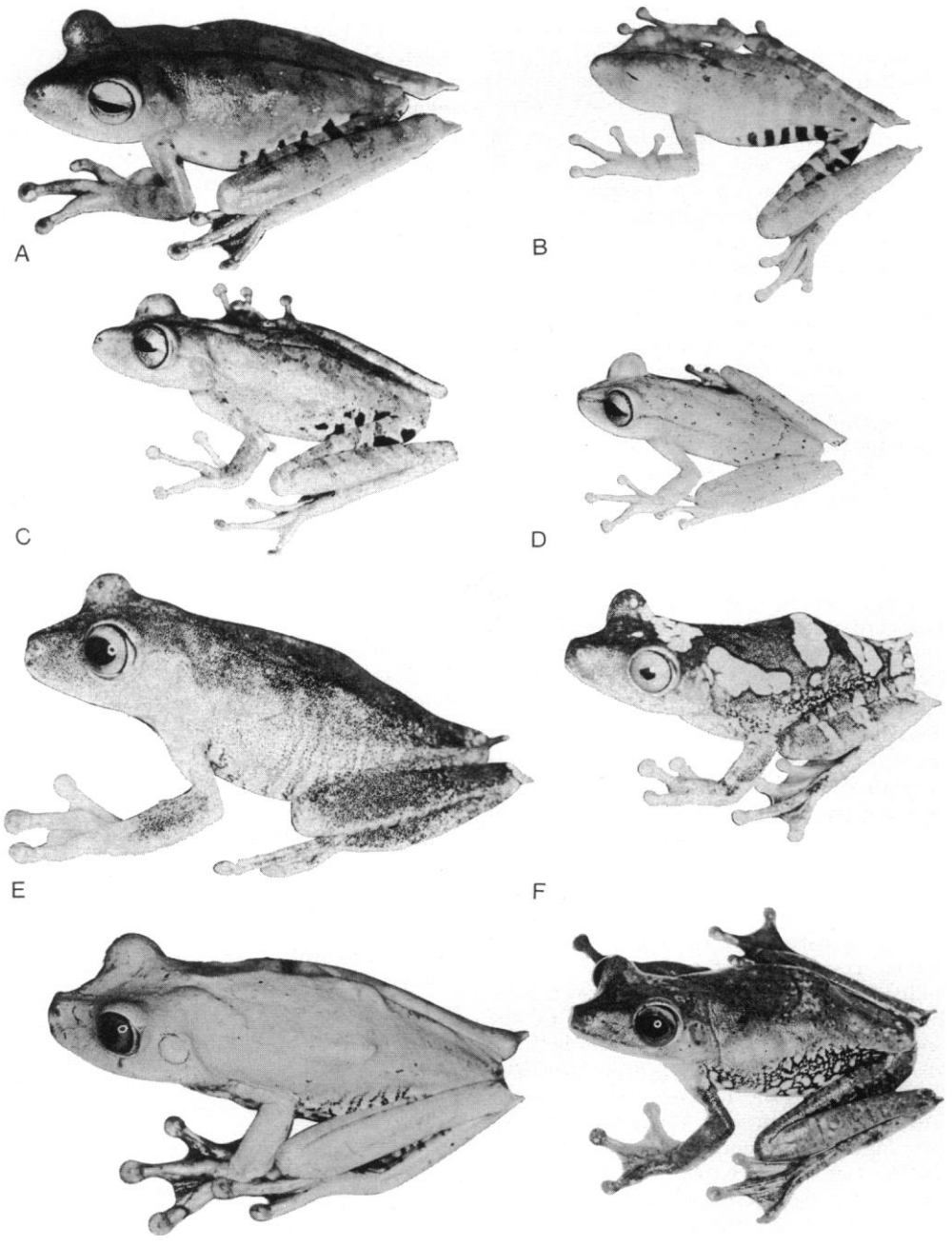

Fig. 7. Frogs of *Hyla geographica* group. A. *Hyla calcarata*, KU 128361, ♀ 50 mm SVL, IPEAN, 3 km E Belém, Pará, Brasil. B. *Hyla calcarata*, KU 111677, ♂ 37 mm SVL, Santa Cecilia, Napo, Ecuador. C. *Hyla fasciata*, KU 122682, ♀ 47 mm SVL, Santa Cecilia, Napo, Ecuador. D. *Hyla fasciata*, KU 139213, ♂ 32 mm SVL, Pilcopata, Cuzco, Perú. E. *Hyla geographica*, KU 111686, ♀ 62 mm SVL, Santa Cecilia, Napo, Ecuador. F. *Hyla geographica*, KU 127640, ♂ 48 mm SVL, IPEAN, 3 km E Belém, Pará, Brasil. G. *Hyla geographica*, KU 139220, ♀ 60 mm SVL, Pilcopata, Cuzco, Perú. H. *Hyla geographica*, KU 128388, ♂ 48 mm SVL, IPEAN, 3 km E Belém, Pará, Brasil.

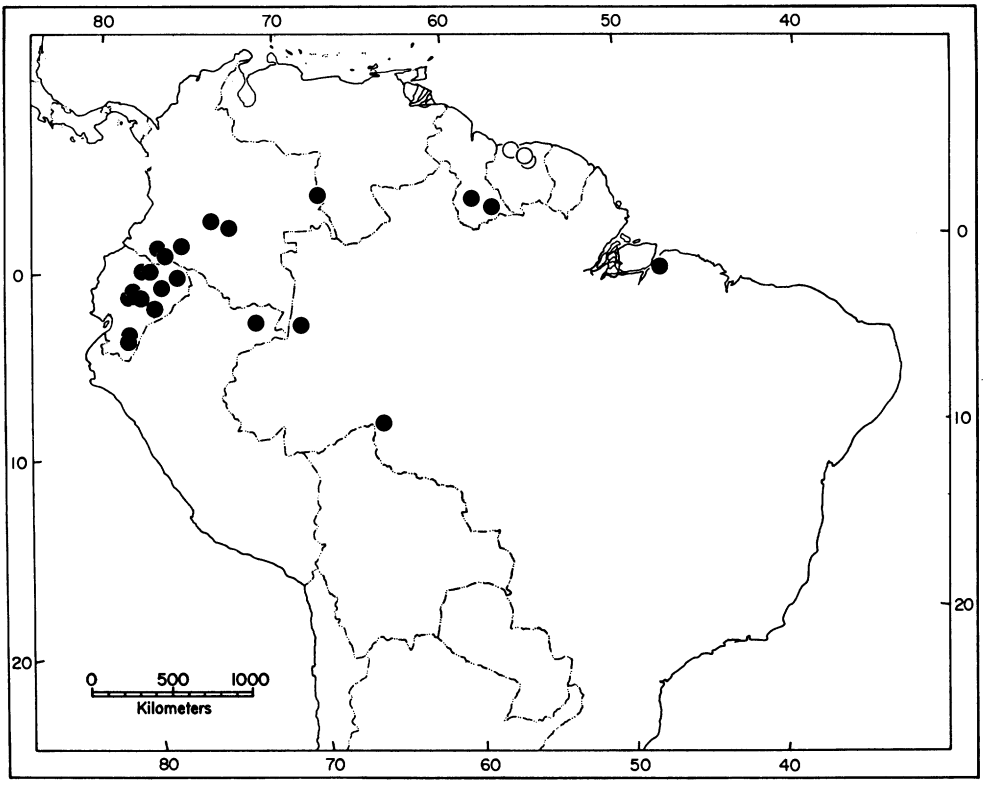

Fig. 8. Locality records for *Hyla calcarata*. Solid symbols = localities from which specimens were examined; open circles = literature records.

verse darker tan markings; 5) dark middorsal stripe present; 6) flanks white or tan with black spots; 7) posterior surfaces of thighs pale tan or gray with black spots or single vertical bars; 8) ventral surfaces of thighs white with or without black flecks; 9) belly white with black flecks; 10) webbing on feet tan. *H. fasciata* is most easily confused with *H. calcarata*, which has a larger, triangular calcar, uniformly white venter, and usually more regular, distinct vertical bars on the flanks and thighs. The markings on the flanks and thighs of *H. fasciata* tend to be irregular spots, which are fragmented into dorsal and ventral components in some individuals. Vestigial webbing on the hand and the absence of a pigmented reticulation on the palpebrum distinguish *H. fasciata* from *H. geographica*, which usually has many narrow, vertical dark bars on the flanks and thighs. Other Amazonian frogs having transverse dark markings on the dorsum include *H. lanciformis, H. multifasciata, H. raniceps* and juvenile *Osteocephalus leprieurii*. All of these lack calcars. The three species of *Hyla* have acuminate snouts. *H. lanciformis* has a gray-brown venter with cream spots on the chest, a pale labial stripe and uniform gray-brown flanks and thighs. *H. multifasciata* is like *H. lanciformis* except that it has a creamy white venter; *H. raniceps* has creamy tan flanks and thighs with dark brown vertical bars. Juveniles of *Osteocephalus leprieurii, Hyla calcarata* and *H. fasciata* have dark transverse marks on the dorsum; these usually are narrower and more distinct in *O. leprieurii*, which has a broad flat head and a creamy tan labial stripe that is expanded below the orbit.

Variation.—The amount of webbing and the size of the calcar are nearly uniform in all specimens examined. Webbing is absent on the hand, and the feet are only about half webbed. The calcar is small and conical. With the exception of the black markings on the flanks and thighs, the color pattern is consistent within size groups. These

markings usually are irregular spots but in some individuals are vertical bars (Fig. 7C). All individuals have a narrow brown mid-dorsal stripe and four or five irregular, broad, transverse brown marks on a tan or pale brown dorsum. Narrower diagonal brown markings are present on the dorsal surfaces of the limbs; there is one on the upper arm, two or three on the forearm, four or five on each thigh and shank, and two or three on each foot.

Ontogenetic color change is slight. Larger frogs tend to be darker and have a comparatively obscure dorsal pattern (Fig. 7C); this is especially noticeable in mature females. In juveniles and males, the ground color is paler and the pattern more distinct. Small specimens have a distinct, narrow, dark brown stripe extending from the nostril through the eye, above the tympanum, to the midflank (Fig. 7D). This stripe is absent posteriorly, and absent or indistinct anteriorly in large adults. Brown flecks are present on the throat and chest in all individuals, but the flecks are more numerous in large females.

In life, the dorsum is yellowish tan with faint darker markings. The flanks and thighs are grayish white (pale blue in large females) with black markings. The venter is yellowish white with brown flecks on the throat and chest. The iris is creamy silver.

Natural History.—Eggs and tadpoles are unknown. At Santa Cecilia, Ecuador, calling males have been found from mid-March to early June. Males call from branches of low trees and bushes over forest pools. The call consists of three or four quickly repeated, short, moderately high-pitched notes (Fig. 3B).

Distribution.—The upper Amazon Basin from Ecuador to Bolivia; all localities are at elevations between 300 and 1000 m near the Andean front (Fig. 9). One hundred and twenty-three specimens have been examined from 13 localities.

Remarks.—Most specimens of *H. fasciata* are from the lowlands just east of the Andes. The majority of these have black spots, instead of vertical bars, on the flanks and thighs. The holotype (BMNH 58.4.25.22 from "Andes of Ecuador") has distinct vertical bars on the flanks and thighs. Three specimens (FMNH 23516, 23513, USNM 104455) closely resemble the holotype in color pattern; these are from "Los Llanganati," a broad eastward protrusion of the Andes northwest of Puyo.

Hyla geographica Spix

Hyla geographica Spix, 1824:39 [type formerly in ZSM, now lost, from Rio Tefé. Amazonas, Brasil; collector unknown].

Hyla geographica var. *semilineata* Spix, 1924: 40 [type formerly in ZSM, now lost, from Rio de Janeiro, Guanabara, Brasil; collector unknown].

Hylella punctatissima Reinhardt and Lütken, 1862:200 [holotype UZM R1436 from Tabuleiro Grande near Lagôa Santa, Minas Gerais, Brasil; Johannes Reinhardt collector].

Centrotelma cryptomelan Cope, 1867:204 [holotype MCZ 1530 from Bahia, Brasil; Antonio de Lacerda collector].

Cophomantis punctillata Peters, 1870:651 [holotype ZMB 6953 from Santa Catarina, Brasil; Carl Burmeister collector].

Hyla appendiculata Boulenger, 1882:349 [Syntypes BMNH 1947.2.13.6 from Bahia, Brasil, BMNH 1947.2.13.2–3 from Santarém, Pará, Brasil, BMNH 1947.2.13.7 from "interior" of Brasil, BMNH 1947.2. 13.8 from Brasil, BMNH 1947.2.13.1, 1947. 2.13.4–5 from Canelos, Pastaza, Ecuador, and BMNH 1947.2.13.9 from Sarayacu, Pastaza, Ecuador; type locality restricted to Canelos by Cochran and Goin (1970:204); BMNH 1947.2.13.1 (80.12.5.168) collected by Mr. Buckley designated as lectotype by Parker (1933:5)].

Justification of Synonymy.—The multiplicity of names assignable to the synonymy of *Hyla geographica* is due to the early misconception that *H. geographica* was a synonym of *H. boans* (Linnaeus, 1758); other names were applied to the juveniles and subadults, which exhibit color patterns different from those of adults. Spix's (1824) descriptions of *H. geographica* and *H. geographica* var. *semilineata* were based on adult specimens from the middle Amazon Basin (Río Tefé) and coastal southeastern Brasil (Rio de Janeiro), respectively. Duméril and Bibron (1841:544) stated that they could not determine the identity of *H. geographica* Spix. Peters (1873) reviewed the Spix Brasilian collection and concluded that *H. geographica* was a

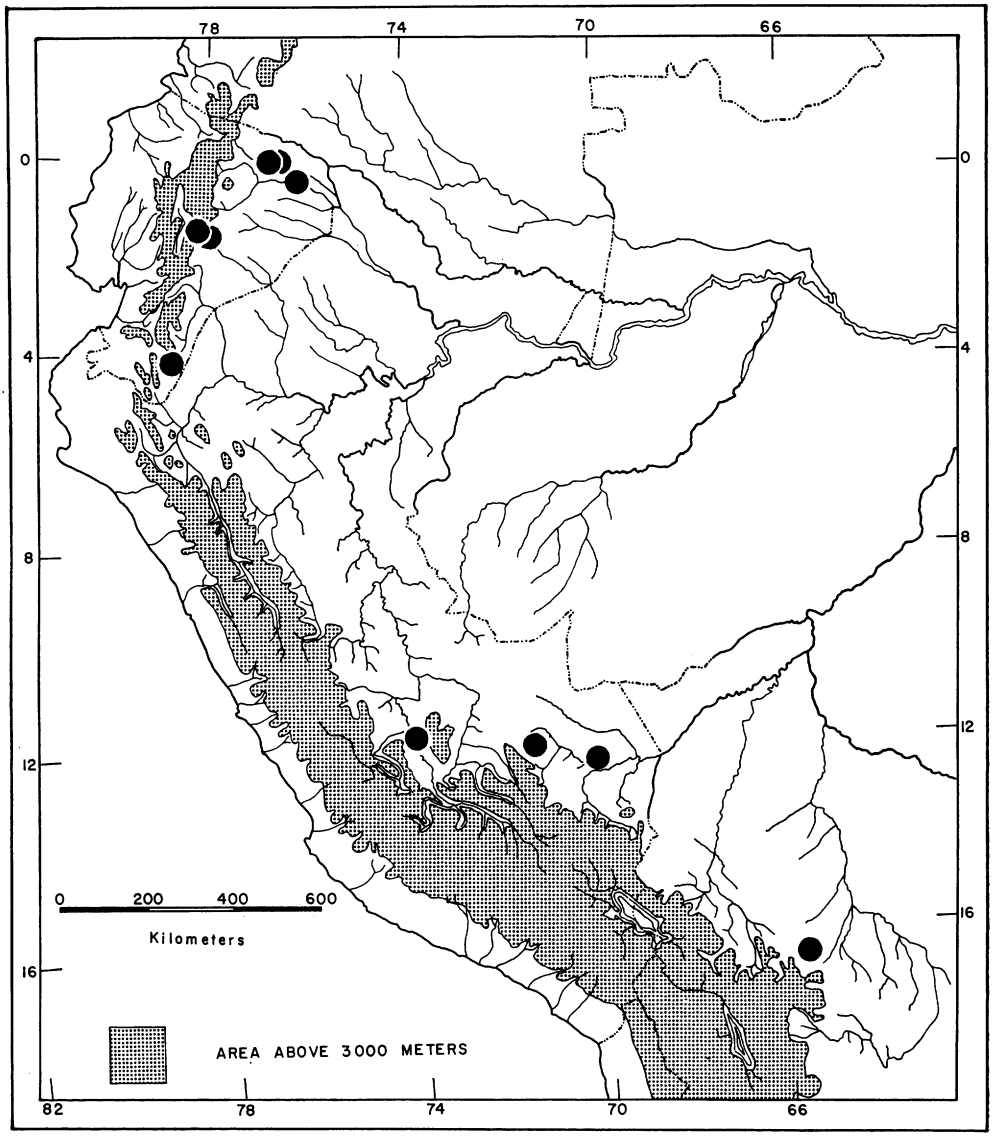

Fig. 9. Locality records for *Hyla fasciata*. Note the proximity of all localities to Andean front.

junior synonym of *Hyla maxima* Laurenti, 1768 (= *Rana boans* Linnaeus, 1758) and that *H. geographica* var. *semilineata* was a junior synonym of *Hyla faber* Wied, 1821.

In the meantime Reinhardt and Lütken (1862) named *Hylella punctatissima* on the basis of a juvenile from Minas Gerais, Brasil. Cope (1867) named *Centrotelma cryptomelan*, also based on a juvenile, from Bahia, Brasil; however, Cope recognized *geographica* as a valid species of *Centrotelma*, a genus made up of species characterized by having a reticulate palpebral membrane, angular dentigerous processes of the prevomers and lacking prepollical spines. Peters (1870) named *Cophomantis* and used the absence of prevomerine teeth, tympanum, and eustachian tubes to characterize the genus; he named *C. punctillata* from Santa Catarina, Brasil, as the sole member of the genus. Peters (1873) considered *Cophomantis* to be indistinguishable from *Hyla* but noted dif-

ferences in coloration between *H. punctillata* and *H. punctatissima.*

Boulenger (1882) followed Peters in assigning *Hyla geographica* to the synonymy of *H. maxima* and *H. geographica* var. *semilineata* to *H. faber.* He recognized *H. cryptomelan, H. punctatissima* and *H. punctillata* as valid and named *H. appendiculata* on the basis of nine adults from Brasil and Ecuador. Müller (1922) showed that *H. geographica* was distinct from *H. maxima* and that *H. punctatissima* was a juvenile of *H. geographica.*

Parker (1933) was unaware of Müller's action and concluded that *H. punctatissima, H. punctillata* and *H. cryptomelan* were synonymous and that *H. appendiculata* was a subspecies of *H. punctatissima.* Parker (1935) agreed with Müller's findings and recognized two populations—*H. geographica geographica* and *H. g. punctatissima.*

Most authors have followed Peters (1872) and Boulenger (1882) in placing *H. geographica* var. *semilineata* in the synonymy of *H. faber,* but Bokermann (1966:51) placed *semilineata* in the synonymy of *H. geographica.* Brokermann (1966:65) raised doubts about the identity of *H. punctatissima* and suggested that it was not the same as *H. geographica.*

Workers familiar with *Hyla geographica* are aware of the striking ontogenetic change in coloration. Recently metamorphosed young are cream above with many small black dots; the flanks and hidden surfaces of the limbs are black. The black coloration diminishes with age resulting in gray or black vertical bars or mottling on the flanks and thighs and a brown or cream dorsum with darker brown markings (Fig. 6). This ontogenetic change and the disposition of the pigment cells has been carefully documented by Hennessy (1968). I have examined the type specimens of the three nominal species based on juveniles and conclude that they all are juveniles of one species, *Hyla geographica.*

The holotype of *Hylella punctatissima* (UZM R1436) is the smallest of the types and has a S-V length of 21.0 mm. When I examined the type on 14 July 1969, it was badly faded. The head was partly mashed; the roof of the mouth was destroyed, and no prevomerine teeth were apparent. No color pattern was visible, but under a microscope a few red-brown dots were evident on the top of the head. The specimen is a recently metamorphosed individual, as evidenced by the cluster of melanophores above the vent.

The holotype of *Cophomantis punctillata* (ZMB 6953) has a S-V length of 28.1 mm. It was in fair condition when I examined it on 23 July 1969. All dorsal surfaces were gray with a dense sprinkling of black dots. The flanks were heavily suffused with black. The dentigerous processes of the prevomers are angulate, but no teeth were apparent.

The holotype of *Centrotelma cryptomelan* (MCZ 1530) has a S-V length of 35.8 mm. It was in fair condition, but soft, when I examined it on 18 March 1971. The dorsum was creamy tan with an even sprinkling of small red-brown dots. The flanks, anterior and posterior surfaces of the thighs, and inner surfaces of the shanks and feet were black. There are 11–12 teeth on angulate dentigerous processes of the prevomers.

The structure of the hands and feet, the amount of webbing, and the shape of the head is essentially the same in all three types. Likewise, each specimen has a weak supratympanic fold. Reticulations are barely evident on the palpebrum in the type of *C. cryptomelan,* but reticulations are not apparent on the other types.

The structural features and coloration of the types can be matched by many specimens in large developmental series from Amazonian Ecuador. Thus, I conclude, as did Parker (1933:5) that *Hylella punctatissima* Reinhardt and Lütken, *Centrotelma cryptomelan* Cope, and *Cophomantis punctillata* Peters, are representatives of one taxon.

The type series of *Hyla appendiculata* consists of nine specimens; BMNH 80.12.5. 168 (= 1947.2.13.1) from Canelos, Ecuador, was designated as the lectotype by Parker (1933). This guadily patterned, adult female, 66.8 mm in S-V length, was illustrated by Boulenger (1882, pl. 23, fig. 2). It is typical of well-marked *H. geographica* from throughout the Amazon Basin.

Lutz (1927) erroneously applied the name *Hyla spectrum* Reinhardt and Lütken, 1862, to specimens of *H. geographica* from Trinidad and Rio de Janeiro. From his description it seems certain that he had juveniles of *H. geographica.* The type of *H. spectrum* (UZM R3432) is a juvenile *H. albopunctata* Spix. Cochran and Goin (1970:204), apparently on the basis of Lutz's statement,

included *H. spectrum* in the synonymy of *H. geographica.*

Diagnosis.—Maximum snout-vent length of males 59.2 and females, 75.5 mm. 1) Fingers about one-half webbed; 2) calcar large, triangular; 3) palpebrum reticulated; 4) dorsum tan or brown usually with irregular dark brown markings frequently including an X-shaped mark in scapular region; 5) dark middorsal stripe present or absent; 6) flanks gray or brown with black spots or vertical black lines (either single or paired), or black with white flecks (uniform black in juveniles); 7) posterior surfaces of thighs colored like flanks; 8) ventral surfaces of thighs white to creamy orange, plain or marked with black spots on transverse lines posteroventrally; 9) belly white to creamy orange, plain or spotted with black; 10) webbing on feet brown or red. The presence of webbing on the hand and a reticulated palpebrum distinguishes *H. geographica* from *H. calcarata* and *H. fasciata,* both of which are smaller species with broader black marks on the flanks and thighs. Members of the *Hyla boans* group are similar to *H. geographica,* but have prepollical spines in the males. Only two members of that group (*H. boans* and *H. pardalis*) have calcars; *H. boans* has a reticulated palpebrum but has the hands nearly fully webbed as opposed to half-webbed in *H. geographica. Hyla pardalis* further differs from *H. geographica* by having a scalloped dermal fringe along the outer edge of the foot and tuberculate dorsal skin.

Variation.—Most aspects of geographic and ontogenetic variation in *H. geographica* have been presented in the foregoing analysis of characters; the taxonomic significance of this variation has been discussed above in the justification of synonymy section.

Considerable color variation is common within series from one locality. Whereas most individuals from a given locality are rather drab in coloration, a few specimens may be boldly marked. Two of 18 adults from Belém, Brasil, have bold dorsal patterns (Fig. 7F). The dorsum is dull brown with faintly darker dorsal markings in most specimens (Fig. 7E, H), but individuals from Chipiriri, Bolivia, and Pilcopata, Perú, were pale tan dorsally (Fig. 7G).

Examples of coloration in life are as follows:

"Dorsum tan with black flecks and middorsal line; flanks and anterior and posterior surfaces of thighs gray with faint darker vertical lines on flanks; venter white, creamy yellow laterally; labial stripe yellow; iris pale gray, reddish above; palpebrum reticulated with gold." (W. E. Duellman; Limón Cocha, Ecuador; 22 November 1966; subadult female.)

"Dorsum dull yellow with or without brown mottling, or mottled light and dark brown, with black spots on dorsum; dorsal surfaces of limbs brown; concealed surfaces of limbs and flanks black; side of head brown; venter chalk white; iris brown with orange wash; palpebrum reticulated." (J. D. Lynch; Mera, Ecuador; 1 July 1968; small calling males.)

"At night pale yellowish tan with slightly darker transverse markings on dorsum and limbs; flanks and posterior surfaces of thighs creamy white with grayish brown vertical lines; venter pale creamy yellow. By day, dorsum dull brown with darker brown markings; flanks cream with dark gray vertical lines; calcars creamy white; webbing dark brown; throat creamy yellow; belly and undersides of limbs pale orange; iris cream; palpebrum reticulated with gold." (W. E. Duellman; Santa Cecilia, Ecuador; 22 March 1967; adult female).

"Dorsal ground color metallic green-gold with dark brown blotches and small black spots in blotches; black middorsal line on head; belly, flanks, anterior and posterior surfaces of thighs, forearms, and hands pale orange, all but belly marked with brown transverse bars; labial stripe pale yellow; throat and pectoral region creamy white; iris pale creamy orange with small amount of brown medially; palpebrum reticulated." (W. E. Duellman; Santa Cecilia, Ecuador; 13 June 1968; adult male).

"Dorsum tan mottled with white; flanks and anterior and posterior surfaces of thighs cream with vertical black bars; venter orange; iris bronze." (M. L. Crump; Belém, Brasil; 11 February 1969; adult female).

"Most with yellowish tan dorsum, occasionally with prominent yellow spots and blotches; flanks yellowish white to white with narrow black bars; anterior and posterior surfaces of thighs white with gray suffusion and black bars; inner toes and fingers and webbing reddish orange; venter white with black spots; iris dull tan-bronze." (T. H. Fritts; Chipiriri, Bolivia; 16 February 1970; adult males and females).

"At night dorsum dull brown; by day changed to pale yellow with little evidence of dorsal markings; venter white with or without black spots; first and second fingers, toes 1–3, and webbing orange-red; trace of orange on ventral surfaces of thighs in some specimens; in larger individuals flanks creamy yellow and posterior surfaces of thighs pale bluish gray with black bars; in smaller individuals flanks and posterior surfaces of thighs black; iris pale creamy bronze; palpebrum finely reticulated with golden yellow." (W. E. Duellman; Pilcopata, Perú; 15 January 1971; adult males and females).

Natural History.—Calling males have been found at Santa Cecilia, Ecuador, from September to March; at Belém, Brasil, in February, March, June, and July; at Pilcopata, Perú, in January; and at Chipiriri, Bolivia, in February. Males call from low vegetation near or over standing water. At Santa Cecilia breeding congregations were found only at the shore of a lake; no breeding was observed at temporary ponds or swamps. However, at Belém males called in varzea forest, and

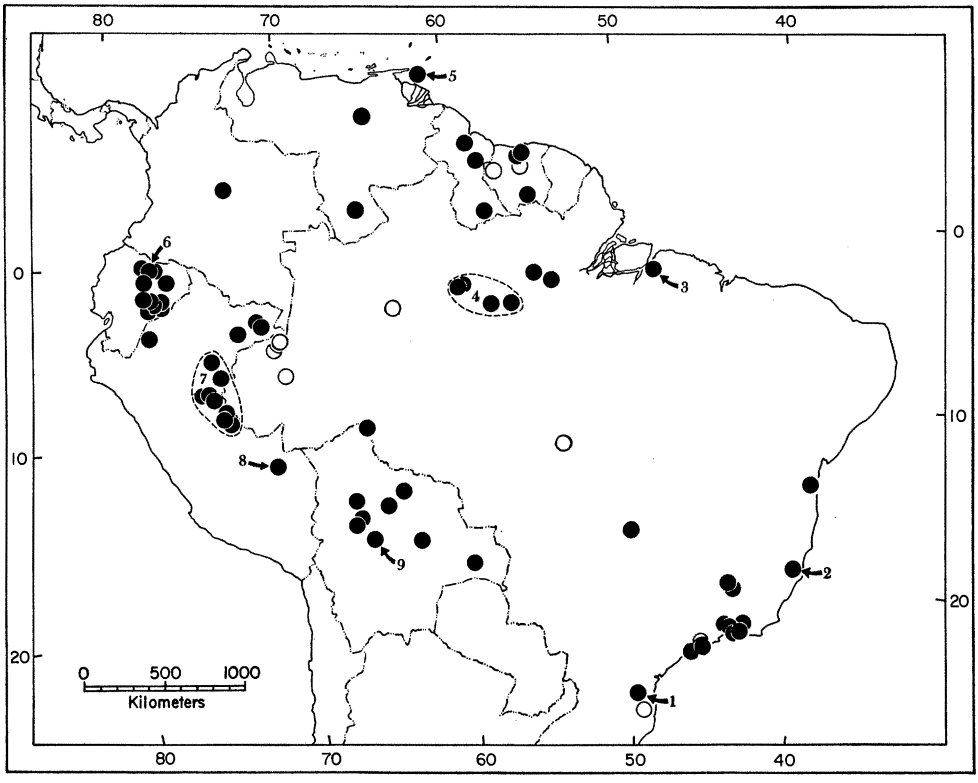

Fig. 10. Locality records for *Hyla geographica*. Solid symbols = localities from which specimens were examined; open symbols = literature records. Numbers refer to samples used in the statistical analyses (see Table 1).

recently metamorphosed young were found there in July. At Santa Cecilia large congregations of tadpoles were found in the lake from March to July.

Distribution.—The Guianas, Amazon Basin southward to eastern Bolivia and Mato Grosso, Brasil, coastal lowlands of Brasil from Bahia to Santa Catarina, upper Rio São Francisco drainage in southern Brasil, Orinoco Basin in Colombia and Venezuela, Trinidad (Fig. 10). Most records of occurrence are at localities at elevations of less than 500 m, but the species ascends the Pastaza Valley in Ecuador to 1410 m. In addition to the 676 specimens examined from 92 localities, the species has been reported from the following localities: BRASIL: *Amazonas*: Benjamin Constant, Eirunepé, Itacoaí (Lutz and Kloss, 1952), Tefé (Spix, 1824); *Mato Grosso*: Jacaré (Bokermann, 1962); *Santa Catarina*: Itapoçó (Cochran, 1955:184); *São Paulo*: São Paulo (Cochran, 1955:184). SURINAM: *Brokopondo*: Brownsweg; *Nickerie*: Kabalebo River (Goin, 1971).

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Academy of Science (CAS) and Stanford University (CAS-SU); Hymen Marx, Field Museum of Natural History (FMNH); Robert H. Mount, Auburn University Museum (AUM); Charles W. Myers, American Museum of Natural History (AMNH); Günther Peters, Zoologisches Museum, Berlin (ZMB); James A. Peters, United States National Museum (USNM); Dorothy M. Smith, University of Illinois Museum of Natural History (UIMNH); Haydee Solano, Universidad Central, Caracas (UCV); Greta Vestergren, Naturhistoriska Riksmuseet, Stockholm (NHRM); Charles F. Walker, University of Michigan Museum of Zoology (UMMZ); Ernest E. Williams, Museum of Comparative Zoology, Harvard (MCZ); and John W. Wright, Los Angeles County Museum (LACM). Tape recordings were generously loaned by Werner C. A. Bokermann and M. S. Hoogmoed. I am especially grateful to Stephen R. Edwards for his assistance with programming and interpretation of computer output.

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Specimens Examined

Hyla calcarata

BRASIL: *Amazonas*: Lago do Tachy, above São Paulo de Olivença, Rio Solimões, BMNH 1947.2.23.10. *Pará*: IPEAN, 3 km E Belém, KU 127561–4, 128361–4, 130029. *Rondônia*: Igarapé Marmelo, KU 91984.

COLOMBIA: *Meta*: Río Guapaya, Serranía de Macarena, FMNH 81333–4. *Putumayo*: Puerto Asís, USNM 152279; Río Mecaya, FMNH 69715; San Antonio, Río Guamués, KU 140388. *Vaupés*: San José del Guaviare, KU 133393. *Vichada*: Amanavén, Río Guaviare, USNM 152317.

ECUADOR: *Morona-Santiago*: Misión Bomboiza, KU 146014–31; Río Zamora, 760 m, KU 146033; San José, KU 146032. *Napo*: Cuyabeno, UIMNH 90110; Limón Cocha, KU 99201, 99204, UIMNH 54188, 54288, 63101, 64681, 90077; Puerto Ore, Río Aguarico, KU 122666–77; Santa Cecilia, AUM 8118, KU 104395–6 (skel.), 104423 (skel.), 104848–66, 105188, 106975, 111656–79, 111973, 122658–65, 125946 (skel.), 126372–82, UMMZ 129298(5). *Pastaza*: Abitagua, CAS-948894, CAS-SU 5075, KU 120825, UMMZ 90426(5), 90427–8; Colonia Mena, Río Conambo, ZSM 34/1962; Mera, KU 120822–4, 120827, UMMZ 90429, 92076; 3 km S Puyo, KU 127088; Veracruz, KU 120826. *Tungurahua*: Río Negro, KU 120828–30; 8 km E. Río Negro, KU 145997–6005. *Zamora-Chinchipe*: 2 km SW Cumbaraza, KU 120810–17; Zamora, KU 120818–21.

GUYANA: *Rupununi*: Matamki River, upper Essequibo River, BMNH 1936.4.2.35; New River, BMNH 1939.1.1.61.

PERÚ: *Loreto*: Pebas, CAS-SU 6320.

Hyla fasciata

BOLIVIA: Cochabamba: 6.5 km N Chipiriri, KU 136225.

ECUADOR: "Andes," BMNH 58.4.25.22. *Napo*: Lago Agrio, KU 126388–9; Limón Cocha, KU 99203, LACM 72593–600, UIMNH 53894, 80728–9, 90095, 90099; Santa Cecilia, BMNH 1969.645, KU 104867, 109377–91, 111911–22, 122678–723, 124141–2 (skel.), 125947 (skel.), 126383–7, 143132, 146006–8, UMMZ 129299–300. *Pastaza*: San Francisco, NHRM 1957. *Tungurahua*: "Los Llanganti," FMNH 23513, 23516, USNM 101455. *Zamora-Chinchipe*: Zamora, BMNH 1933.6.24.67.

PERU: *Ayacucho*: Sivía, La Mar, FMNH 39850. *Cuzco*: Pilcopata, KU 139213–6. *Loreto*: Pebas, CAS-SU 6347; Pucallpa, MJP 141. *Madre de Dios*: Boca Amigo, FMNH 81512–5.

Hyla geographica

BOLIVIA: *Cochabamba*: 6.5 km N Chipiriri, KU 136256–74. *El Beni*: Huachi, UMMZ 76076 (tadpoles), 89413(6); Pena Colorado, upper Río Beni, UMMZ 89412(10); Puerto Almacen, AMNH 72148; "upper Río Beni," UMMZ 64138; Río Iténez, Carasco, AMNH 79241; Río Mamoré, Boca Ibarre, AMNH 79240; Río Mamoré, 3 km E Navidad, AMNH 79242. *La Paz*: "lower Río Beni," UMMZ 64139(3). *Santa Cruz*: Santa Cruz: AMNH 22621–2, 33949, FMNH 16787, 27084–90, MCZ 12866–9, UMMZ 63891(9), 65033–4, 66584–6, USNM 75053–4, 93219–21; Roboré, MCZ 29849–51.

BRASIL: No specific locality, BMNH 1947.2.13.8; "Interior," BMNH 1947.2.13.7. *Acre*: Tarauacá, FMNH 83567, *Amazonas*: Ducke Reserve, 26 km E Manáus, KU 130047–54, 130155 (tadpoles), 130156; Manáus, AMNH 22847, Maués, AMNH 76171–3; *Bahia*: No specific locality, BMNH 1947.2.13.6, MCZ 1530; Itabuna, MCZ 75317–8. *Espírito Santo*: Linhares, Sooretama, KU 92035–9, 92040 (skel.), WCAB 20642–52, 20671, 20684, 20687, 20689–95, 20711, 20715–7, 20721, 20723, 20725, 20728, 20731, 20736. *Goiás*: Rio Doce, USNM 137743. *Guanabara*: Jacarepagua, USNM 96386; Rio de Janeiro, AMNH 23002–4, 25235–6. *Minas Gerais*: Covanca, USNM 123573–4; Lagôa Santa, UZM 1436. *Pará*: IPEAN, 3 km E Belém, KU 127631–45, 128387–90, 130037–45;

"Manjuru," AMNH 73544; Óbidos, KU 130046; Rio Manjuru, AMNH 76169–70; Santarém, BMNH 1947. 2.13.2–3. *Rio de Janeiro*: Ipiabas, USNM 27215–6; Palmerras, USNM 81122–3; Teresópolis, USNM 97719–22, 129366–7. *Santa Catarina*: No specific locality, ZMB 6953; "Rio Humboldt," AMNH 15562–5, 15566 (tadpoles), FMNH 6472, 6519 (tadpole), MCZ 8933, 8936–44 (tadpoles), 11686–90 (tadpoles), 19540–4, USNM 66556–8 (tadpoles). *São Paulo*: Bertioga, FMNH 175879; Fazenda Poço Grande, nr. Juquiá, UMMZ 104190; 8 km N Juquiá, USNM 132950; Piassaguera, KU 74261–2.

COLOMBIA: *Boyacá*: Guairaramo, USNM 152100.

ECUADOR: ? *Esmeraldas*: Carondelet, UIMNH 53583. *Morona-Santiago*: Macuma, UIMNH 63144. *Napo*: Borja, ZSM 52/1957; Dureno, KU 10497 (skel.); Lago Agrio, KU 126398–9; Limon Cocha, KU 99202, 99230–80, 106976, 122733–4, LACM 72261–2, 72280–322, MCZ 56304, 57342–58, 57673–98, UIMNH 63083–6, 63104, 63210, 63241, 63256, 63259–60, 63299, 64680, 64682, 64684–754, 88105, 88590, 88622–3, 90041–52, 90069, 90072, 90795, 90968–79; Puerto Ore, Río Aguarico, KU 122732; Río Cotopino, CAS-SU 10333–4, UMMZ 90430(4), 90431; Santa Cecilia, KU 104868–82, 109392–3, 111685–96, 112327–9 (tadpoles), 122726–31, 124171–3 (tadpoles), 125950 (skel.), 143138–47, 146009–12, MCZ 57871–2. *Pastaza*: Abitagua, UMMZ 92087–90; Alpayaca, BMNH 1912.11.1.65–6; Arajuno, USNM 166076–7; Canelos, BMNH 80.12.5.165, 80.12.5.180, 80.12.5.182, 1947.2.13.1, 1945.2.13.4–5; Chicherota, CAS-SU 10308; Conambo, UIMNH 63134–6; Mera, KU 120861, 120064–9, 121395 (tadpoles), NHRM 1955/3, UMMZ 92086, 92091; 3.5 km W Mera, KU 146013, Puyo, USNM 166061, 166072–4; 3–13 km N Puyo, CAS 85159; Río Alpayacu, KU 120862–3; Río Cabeceras at Río Soris, USNM 166064–9; Río Pastaza, CAS-SU 5040, NHRM 1956; "Río Pastaza watershed," NHRM 1955/1; Río Shilcayacu, USNM 166070–1; Río Villano, USNM 166075; San Francisco, NHRM 1955/2, USNM 166062–3; Sarayacu, BMNH 80.12.5.207, CAS-SU 10311, MCZ 19942–5, ZMB 10171; Shell Mera, KU 99190; Tena, UMMZ 123902.

GUYANA: *Mazaruni-Potaro*: Kartabo, AMNH 70493, *Rupununi*: N Acarahy Mts, W New River, KU 69719, *West Demerara*: Malali, UMMZ 77513.

PERU: *Amazonas*: Río Ayambis, tributary Río Santiago, AMNH 43481. *Cuzco*: Pilcopata (Cozñipata), KU 139217–25, 139271. *Loreto*: Contamana, AMNH 42646, 43271; "Estiron, Río Ampiyacu," CAS 93288, 93296–8; Iquitos, AMNH 43464; Pebas, CAS-SU 6345–6; "100 km SE Pucallpa," TAM 24038; Puerto Oriente, 5 km above Contamana, UMMZ 123917–8; Río Alto Tapiche at Río Contaya, AMNH 43245; Río Pacaya, tributary Río Ucayali, BMNH 1913.7.28.23; Río Tamaya, AMNH 42026–8, 42277; Sobral, Río Tamaya, AMNH 42675, 42677–9, 42683, 43240, 43243. Tipishca, Río Ucayali, AMNH 42937; Utoquinia-Tapiche (Brasilian border), AMNH 43222.

SURINAM: *Marowijne*: Paloemeu, USNM 159023–4: *Suriname*: Moeroekreek, Saramacca River, RMNH 16581–5; Republiek, RMNH 16606.

TRINIDAD AND TOBAGO: *Trinidad*: Arima, USNM 166576; Churchill-Roosevelt Hwy, AMNH 55697–703; Marne Bleu, FMNH, 49694; Milestone, USNM 166574–5.

VENEZUELA: *Amazonas*: Iguapo, SMF 2432. *Bolivar*: Guri, UCV 45.

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A Biogeographical History of *Chirostoma* (Pisces: Atherinidae): A Species Flock from the Mexican Plateau

CLYDE D. BARBOUR

The genus *Chirostoma* is virtually restricted to the Mesa Central, the southern part of the Mexican Plateau. The evolution of the 18 species and six subspecies is examined from the standpoint of the major factors underlying their present distribution: the geological history of central México and their trophic relationships as deduced from morphology. An attempt is also made to find evolutionary patterns common to fish species flocks in general.

The Mesa Central has a long history of geological instability. Tectonic movements associated with the Laramide Orogeny, mid-Tertiary and Plio-Pleistocene vulcanism and mid-Pleistocene uplift and associated vulcanism have resulted in continuously changing drainage patterns. During the Tertiary and early Pleistocene, the ancestral Río Lerma probably flowed westward, perhaps through a series of lakes, to the Pacific Ocean. The exact course and extent of the ancestral system at this time are unknown. Mid-Pleistocene uplift compartmentalized the drainage. At first the river was able to continue a course through the ancestral Chapala basin probably utilizing the present Ríos Tuxpan, Ameca and perhaps the Río Grande de Santiago drainages as exits. Finally, however, uplift blocked the flow and the present outlet to the Río Grande de Santiago was gained. Lakes, playa lakes, and lacustrine deposits which occur across the Mesa Central are evidence of the size of this late Pleistocene system. Changes in lake levels, presumably reflecting late Pleistocene pluvial periods, are indicated by terraces.

Interior basins formerly part of the Lerma system, as indicated by the distribution of *Chirostoma*, are the Llanos de Puebla, Puebla-Tlaxcala; the Llanos de Apan, Hidalgo; the Valley of México, Federal District-State of México; Lakes Zirahuén, Pátzcuaro and Cuitzeo, Michoacán; Lakes Atotonilco and San Marcos, Jalisco; Lakes Santa Maria and San Pedro Lagunillas, Nayarit; Lake Juanacatlán, Jalisco and Laguna de Santiaguillo, Durango.

There appear to have been two centers of evolution for the *jordani* species group: the Chapala basin and the Uruapan-Lakes Pátzcuaro and Zirahuén region of Michoacán. *C. humboldtianum* has a distribution which probably antedates the uplift, whereas the range of *C. jordani* more probably reflects the extent of aquatic connections across the Mesa Central late in the Pleistocene. The species of the *arge* species group have differentiated throughout most of the Lerma basin. The presence of *C. arge*