AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2947, 16 pp., 9 figs. August 8, 1989

A New Frog of the Genus *Ctenophryne* (Microhylidae) from the Pacific Lowlands of Northwestern South America

RICHARD G. ZWEIFEL[1] AND CHARLES W. MYERS[1]

ABSTRACT

A single specimen of narrow-mouth frog (Microhylidae), from lowland rain forest in southwestern Colombia, is assigned to the genus *Ctenophryne* on the basis of radiographic data and external resemblance. It appears to represent a smaller and differently proportioned species than the only other member of this genus, *C. geayi*, which is widespread in Amazonian and northeastern South America. Even with the addition of *Ctenophryne minor*, new species, microhylids remain an insignificant part of the richly endemic anuran fauna on the Pacific versant of northwestern South America, although the family is well represented east of the Andes.

The distribution and variation of *Ctenophryne geayi* are briefly reviewed in order to help determine the status of the trans-Andean *C. minor*. Specimens from northern and western populations of *C. geayi* (including the holotype)—from Guyana to Ecuador and south to central Peru—have pale-flecked venters. Specimens from most of the region south of the east-west axis of the Amazon River, however, have the venter marked with larger spots. A call from a northern population is contrasted with one from a southwestern population (ventral pattern unknown); the latter shows a faster pulse rate at a *lower* temperature.

Although lacking corroboration, these differences suggest a possibility that northern and southern *Ctenophryne geayi* might represent different species. The new trans-Andean species, *C. minor*, is geographically closer to northern *C. geayi* (sensu stricto), but its ventral color pattern is closer to that of southern *geayi*.

RESUMEN

Un ejemplar de la "rana boca angosta" (Microhylidae) de la selva pluvial baja del suroccidente de Colombia ha sido asignado al género *Ctenophryne*, basándose en datos radiográficos y de

[1] Curators, Department of Herpetology and Ichthyology, American Museum of Natural History.

ISSN 0003-0082 / Price $1.90

apariencia externa. El ejemplar parece más pequeño y de proporciones diferentes de las del único miembro de este género, *C. geayi*, ampliamente distribuído en Amazonia y noreste de Suramérica. Aún con la adición de *Ctenophryne minor*, nueva especie, los microhílidos representan una parte insignificante de la rica fauna endémica de los anuros de la vertiente Pacífica al noroeste de Suramérica, aún así, la familia está bien representada al este de los Andes.

Se hace una breve revisión de la distribución y variación de *Ctenophryne geayi* con el fin de ayudar a determinar la posición sistemática de *C. minor* transandina. Ejemplares proveniente del norte y occidente de poblaciones de *C. geayi* (incluyendo el holotipo)—desde Guyana hasta Ecuador y hacia el sur hasta Perú central—poseen vientre de manchas pálidas. Sin embargo, ejemplares de la mayor parte de la región al sur del eje este-oeste del Río Amazonas poseen vientres marcados con manchas más grandes. Se compara el canto de una población septentrional con el de una población más al sudoeste (con la coloración ventral desconocida). Este último muestra la tasa del pulso más acelerada a más baja temperatura.

Aún cuando falta corroboración, estas diferencias sugieren la posibilidad de que *Ctenophryne geayi* septentrional y meridional representen especies diferentes. La nueva especie transandina, *C. minor*, geográficamente está más cercana al *C. geayi* (sensu stricto), pero su patrono de coloración ventral está más cercano al del *geayi* meridional.

INTRODUCTION

The 34 currently recognized species of South American narrow-mouth frogs (Microhylidae) are distributed mostly east of the Andes. Exceptions include species of *Elachistocleis* (and the questionably distinct *Relictovomer*), which occur in northern Colombia and Panama, and *Nelsonophryne*, found in Costa Rica, Panama, Colombia, and Ecuador. *Nelsonophryne aequatorialis* (Peracca) is a high-elevation species of the Ecuadorian Andes. The other species of this genus, *N. aterrima* (Günther), is the only microhylid reported from the rainforested lowlands of western Colombia and northwestern Ecuador (Boulenger, 1913); it occurs also in Costa Rica and Panama (often at elevations above 1000 m). Given this context, the discovery of an undescribed species of microhylid in southwestern Colombia is of both systematic and zoogeographic interest. The purposes of this contribution are to describe the new species found west of the Andes and to summarize the variation and distribution of its probable sister species, *Ctenophryne geayi* Mocquard, which occurs east of the Andes.

ACKNOWLEDGMENTS

We thank Drs. Darrel Frost and John D. Lynch for commenting on the manuscript. We are grateful to Drs. William E. Duellman (KU) and W. Ronald Heyer (USNM) for access to specimens in their care, and to Dr. Janis A. Roze for the Spanish abstract.

The new species was discovered in western Colombia in 1973, during fieldwork conducted under the auspices of the late F. Carlos Lehmann Valencia, then director of the Museo Departamental de Historia Natural, in Cali. For courtesies rendered in support of this program of fieldwork, grateful acknowledgment is due also to authorities in the Sección de Recursos Naturales, CVC (Corporación Autónoma Regional del Cauca).

COLLECTION ABBREVIATIONS

AMNH	American Museum of Natural History, New York
KU	Museum of Natural History, University of Kansas, Lawrence
MNHN	Muséum National d'Histoire Naturelle, Paris
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

GENERIC ASSIGNMENT OF A NEW MICROHYLID

This paper had its genesis when we tried to identify a specimen (fig. 1) of microhylid frog from the Pacific lowlands of western Colombia. South American Microhylidae are placed in 16 genera, 11 of them monotypic (Nelson, 1985; Zweifel, 1986; Frost, 1987). The similarity of the new specimen to *Ctenophryne geayi* in color pattern suggested its

status as a member of this currently monotypic genus.[2] Confirmation of this generic assignment must await availability of additional specimens that can be used for osteological preparation, inasmuch as genera of microhylid frogs are defined largely on characters of the skeleton. However, details that can be observed through radiography (see Osteology) are consonant with assignment to *Ctenophryne*.

Four South American microhylid genera additional to *Ctenophryne* lack the clavicle and procoracoid and so are appropriate to consider with regard to the generic placement of the Colombian specimen: *Adelastes*, *Myersiella*, *Synapturanus*, and *Nelsonophryne*. Among other differences from *Ctenophryne*, the first three genera agree in lacking contact between the quadratojugal and maxilla. This contact is clearly visible in the radiograph of our new specimen. The fourth genus, *Nelsonophryne* (formerly *Glossostoma*, see Frost, 1987) possesses a full complement of palatal bones (Zweifel, 1986: fig. 10A), whereas our specimen resembles *C. geayi* (op. cit.: fig. 10B) in lacking posterior elements of the vomeropalatine complex. Thus, the Pacific lowland specimen is most comfortably accommodated within *Ctenophryne*, but it appears specifically distinct from the widespread *C. geayi* that occurs east of the Andes.

Ctenophryne minor, new species

Figures 1, 2A, B, 4

HOLOTYPE: AMNH 88977 (field no. CWM 11893), a subadult female brought into camp by Emberá Chocó Indians for C. W. Myers and J. W. Daly on February 17, 1973, at Quebrada Guanguí, about 0.5 km above its junction with Río Patia,[3] 100–200 m elev., in upper Río Saija drainage, Department of Cauca, Colombia. The type locality is roughly 2°50′N, 77°25′W.

ETYMOLOGY: The name *minor* is a Latin adjective meaning smaller, in comparison with the apparently larger *C. geayi*.

Fig. 1. *Ctenophryne minor*, new species. The holotype (AMNH 88977) shown about 2.2 times life size.

DIAGNOSIS: *Ctenophryne minor* differs from its only congener, *C. geayi*, in size, certain aspects of color pattern, and in most proportions. The female holotype appears to be near maturity at 30 mm SVL (see Description following), whereas a female *geayi* of 39 mm is immature and the smallest mature female measures 42 mm SVL (Lynch, 1988, mentioned a juvenile female *geayi* of 41.8 mm). A continuous light line from nose to groin in *minor* is nearly straight, passing well above the arm insertion so that the dark area below this line is neither broken nor appreciably narrowed above the arm (fig. 1). The homolog of this line in *geayi* dips down behind the eye, closely approaching or reaching the arm before elevating again behind it. Thus, the dark lateral area of *geayi* is broken or greatly narrowed above the arm (Schlüter, 1980, fig. 9). Black diagonal marks dorsally on the femur, shank, and foot of *minor* are absent or infrequent in *geayi* (cf., figs. 2A, 2C). The pale ventral spots in *minor* are larger than in northern populations of *geayi* and also seem to differ in color in life (pale blue in *minor*, white in *geayi*). Among various proportional differences (fig. 5), the eye is larger in *minor* (Eye/SVL 0.083 vs. maximum of 0.075 in *geayi*), head narrower (HW/SVL 0.353 vs. minimum of 0.360), and legs longer (TL/SVL 0.443 vs. maximum of 0.421).

Nelsonophryne aterrima, the only other

[2] See Zweifel (1989) for the disposition of *Ctenophryne marmorata* Ahl 1935, an African *Phrynomerus* erroneously attributed South American provenance.

[3] This is the same as "Río Patía del Norte," a cartographic invention. Not to be confused with the Río Patía; see Myers et al. (1978: 313) for comments on the orthography of *Patia* vs. *Patía*.

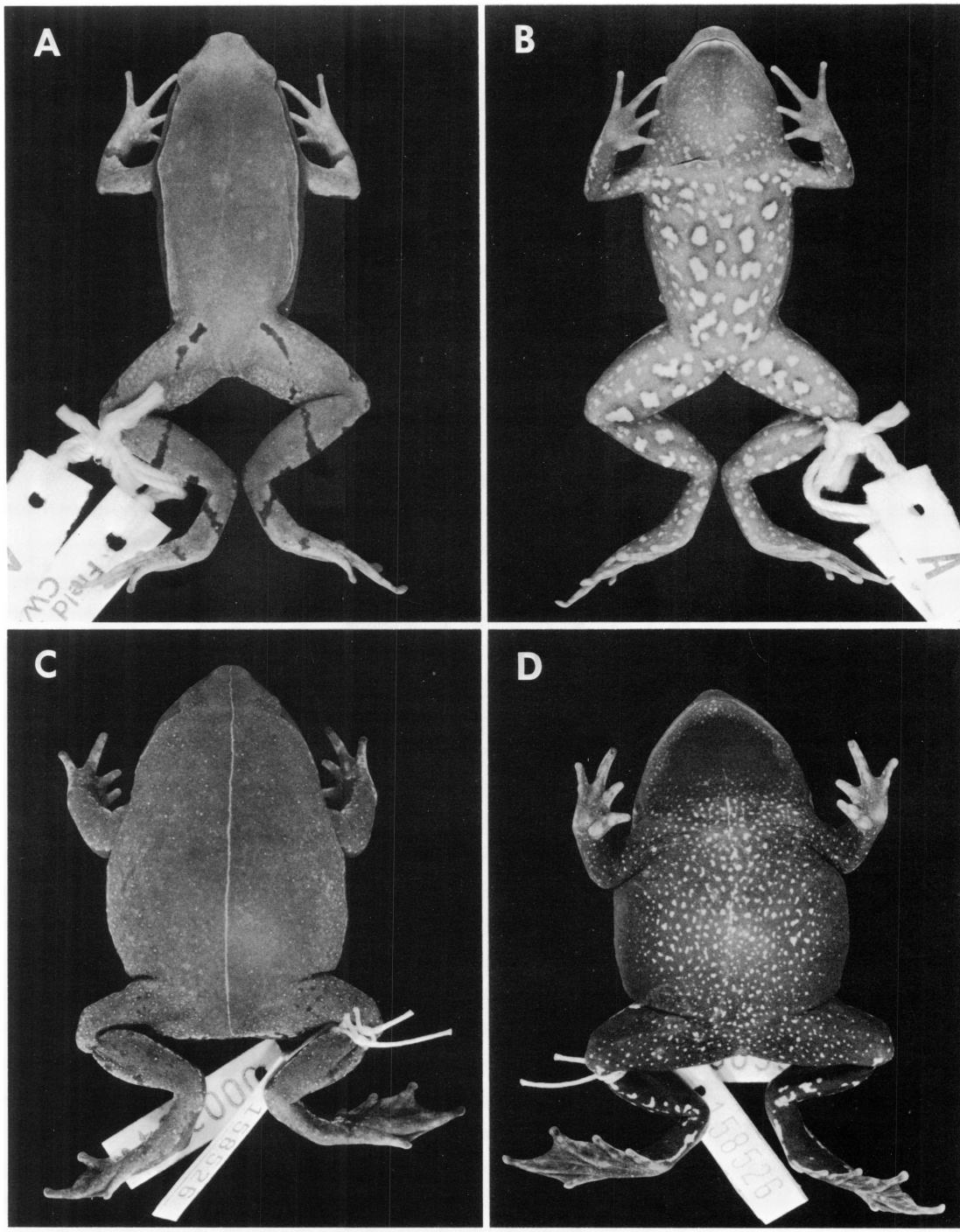


Fig. 2. The species of *Ctenophryne*: **A, B.** *C. minor*, new species; dorsal and ventral view of the holotype (AMNH 88977), ×1.7. **C, D.** *C. geayi* Mocquard (KU 158526), from a population (Sta. Cecilia, Ecuador) geographically close to the Colombian type locality of *C. minor* above; ×1.3.

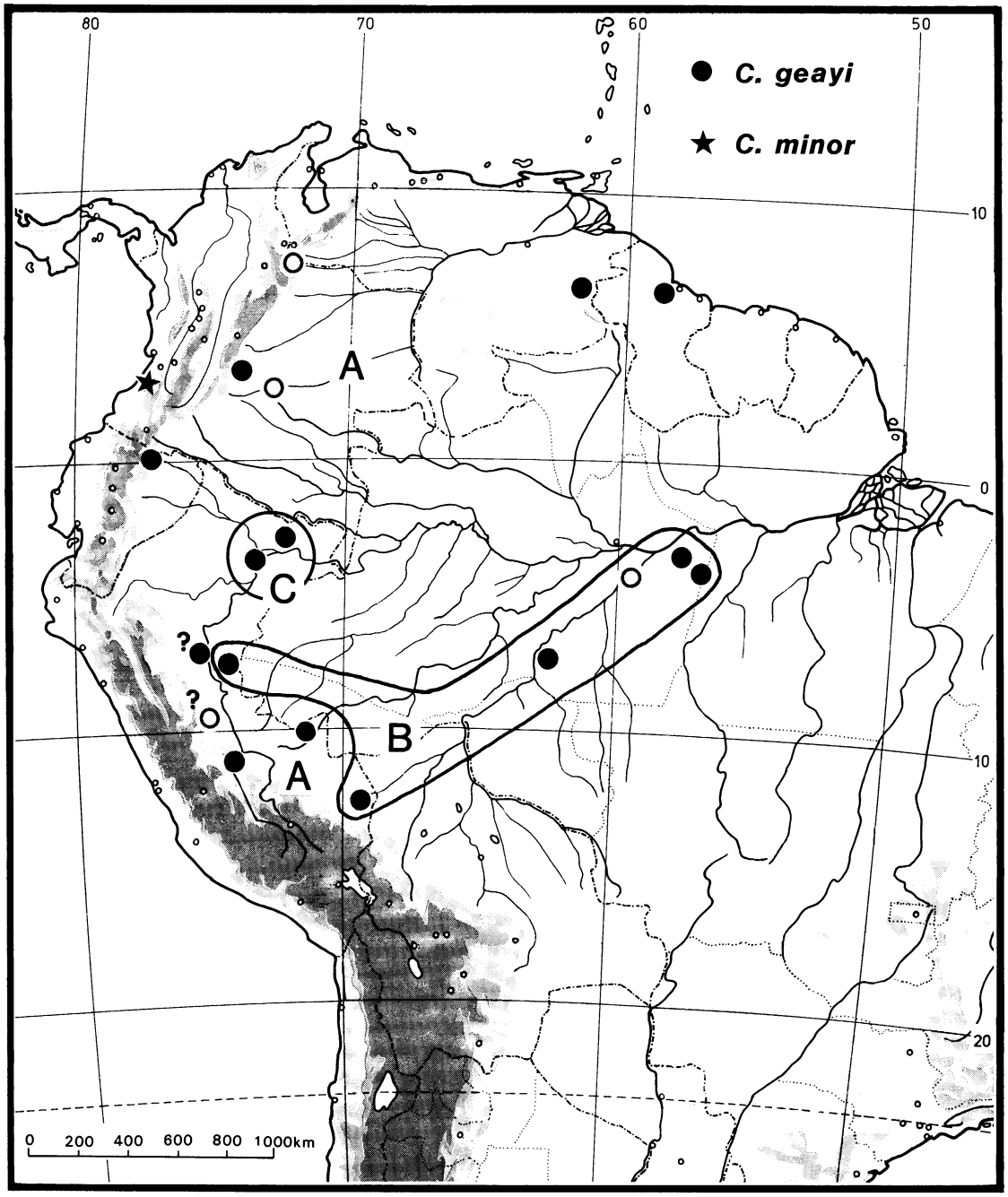


Fig. 3. Northern South America, showing type locality of *Ctenophryne minor*, new species from western Colombia, and localities for the widespread *C. geayi* east of the Andes. Open symbols are literature records.

Geographic variation in ventral color pattern of *Ctenophryne geayi*: **A.** Northern and western pattern of pale flecks or small spots (figs. 2D, 8). **B.** Southern pattern of large spots (fig. 9A–D). **C.** Intermediate pattern of pale flecks and one to several large spots (fig. 9E, F [also fig. 8E, see text]). Question marks at two southwestern localities indicate a literature record and a cleared and stained specimen for which ventral patterns are unknown.

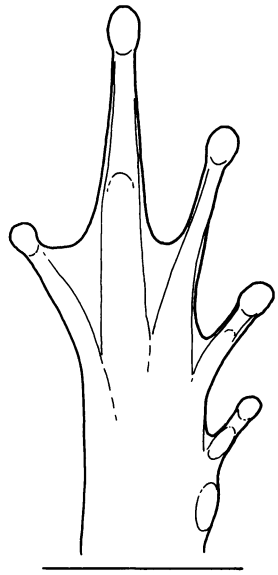


Fig. 4. Underside of right foot of *Ctenophryne minor*, new species (holotype). Scale line = 5 mm.

microhylid at present known to occur as far south in the Pacific lowlands as *C. minor*, is a large species (as large or larger than *C. geayi*) that is readily distinguished from *minor* by its uniformly black or dark grayish brown dorsal color and gray ventral color.

Description of Holotype

The female holotype is judged to be a subadult based on the following criteria: The ovaries contain numerous unpigmented ova in a range of approximately 0.1–0.7 mm; the flattened and highly convoluted oviducts are about 1 mm wide. The enlarging ova and, especially, the noticeably enlarged and convoluted oviducts indicate that the specimen was approaching maturity.

Measurements (in mm) and Proportions: Snout to vent length (SVL) 30.0, head width (HW) 10.6, tibia length (TL) 13.3, eye diameter (horizontal) 2.5, eye-naris distance (EN) from center of naris to anterior edge of eye 2.45, internarial distance (EN) between centers of nares 3.2, hand length (HL) from proximal edge of inner metacarpal elevation to tip of third finger 7.9, foot length from proximal edge of inner metatarsal elevation to tip of fourth toe 12.6. Proportions: TL/SVL 0.443, HW/SVL 0.353, Eye/SVL 0.083, EN/SVL 0.082, IN/SVL 0.107, EN/IN 0.766, Hand/SVL 0.263, Foot/SVL 0.420.

Morphology: Skin smooth above and below, only a faint, diagonal postocular fold. Head relatively narrow, scarcely narrower than body (fig. 2A). Snout seen from above essentially rounded with slight indication of a blunt point, rounded and slightly projecting in lateral view; nostrils widely spaced, lateral but easily visible from above, slightly closer to tip of snout than to eye. Loreal region flat, steeply sloping outward toward lip; canthus rostralis rounded. Eyes relatively small, width of upper eyelid about 33 percent of interorbital distance. No external sign of tympanum. Relative lengths of fingers 3 > 4 > 2 > 1, first about one-half length of second, tips rounded, not flattened or expanded, no terminal grooves; subarticular and metacarpal elevations very low, rounded, scarcely visible. Relative lengths of toes 4 > 3 > 5 > 2 > 1, tips flattened and slightly expanded but lacking terminal grooves; basal web between toes 1 and 2, about one-half webbed on outer sides of toes 2 and 3, slightly less than half on outer side of toe 4 but to base of disk on toe 5; subarticular elevations virtually absent; inner metatarsal tubercle low and elongate; no outer metatarsal tubercle (fig. 4).

Color Pattern: In life (fig. 1), the frog was grayish brown dorsally and black laterally, these two areas separated by a pinkish line extending from the groin to above the eye and onto the canthus rostralis. The grayish brown dorsum was not unicolor: there were a few scattered blotches of paler brown, a few scattered white dots middorsally, and sparse pale blue speckling dorsolaterally. The limbs were grayish brown like the dorsum, with a few narrow black crossbands that tended to have pale pinkish borders; thighs were sparsely speckled with pale blue dorsally. The ventral surfaces were black, with a pattern of very pale blue spots (fig. 2B). Extensive black suffusion nearly concealed the basically pale bronze of the iris.

The preserved specimen is dark and light brown (corresponding to the black and grayish brown seen in life) with white ventral spotting. The relatively large ventral spots are mostly in the range of about 1–2 mm in greatest diameter, with a maximum of 3.5 mm owing to coalescence.

OSTEOLOGY: As interpreted from an X-ray photograph, the skeletal features are those of *Ctenophryne* (see Carvalho, 1954): clavicle (and presumably the cartilaginous procoracoid) absent; posterior part of vomeropalatine absent; quadratojugal in contact with maxilla. Other discernable features include: premaxillary shelf deeply notched; 8 presacral vertebrae present; sacral diapophyses broadly expanded; coccyx without trace of diapophyses; terminal phalanges pointed. There are no teeth.

DISTRIBUTION AND HABITAT

Ctenophryne minor presumably is confined to rainforested lowlands west of the Andes, in extreme northwestern South America (fig. 3). It might conceivably occur in northwestern Ecuador, but the only known locality is in southwestern Colombia.

The Quebrada Guanguí area—the type locality—was described by Myers et al. (1978: 321–322) as having an elevational range of from 90 m (at the mouth of the *quebrada*) to about 200 m (hill tops), in:

> rough hilly country at the western foot of a northerly inclined spur of the Cordillera Occidental. The broken landscape (fig. 4) is the result of stream dissection of presumed Tertiary and Pleistocene sediments and gravels. Slopes are more often steep than gentle, and perpendicular surfaces are not uncommon. Hillside soils are gravelly in places. Drainage is by clear-water streams flowing over rock, gravel, and sand. . . . The region has a decidedly tropical wet climate (*Af* in the Köppen system). Rainfall data are lacking, but extrapolation from distant stations and orographic considerations suggest that the Quebrada Guanguí area receives a yearly rainfall probably in excess of 5 m. . . . There is no undisturbed forest along the larger streams, where small terraces and adjacent hillsides are either under cultivation, mainly for plantains, or in dense second growth. Inland, the native lowland rain forest (fig. 5) is relatively undisturbed but only of moderate height, probably due to the precipitous slopes. . . . The forest tends to be most open on gravelly slopes, some of which are quite wet due to seepage. Leaf litter is sparse.

No lakes or ponds were seen in this wet albeit hilly and well-drained country. Although a good sample was obtained of the rich herpetofauna (including > 40 species of anurans), it is virtually devoid of species requiring standing water for breeding. The frog *Smilisca phaeota*, an ubiquitous forest-edge species throughout its range, was found about a "puddle" of water in second-growth riverbank vegetation. *Ctenophryne minor* also may well breed in such small temporary bodies of water (but perhaps within the primary forest), but its general habitat (at the only known locality) appears quite different from that of *C. geayi*, which occurs mainly in low-relief, sluggishly drained country (e.g., see Duellman, 1978: fig. 4).

COMPARISON WITH *CTENOPHRYNE GEAYI*

Diagnostically significant comparisons are made above, but additional observations on proportions are pertinent. We have calculated the regressions of several standard measurements against SVL for 26 specimens of *C. geayi*: tibia length, head width, eye diameter, internarial distance, eye-naris distance, hand length, and foot length. These regressions (all but foot length) are plotted in figure 5, along with the measurements of the holotype of *minor*. In only two instances—foot length (not plotted) and eye-naris distance—is the plot for *minor* on the extrapolated line for *geayi* or virtually so. In all other proportions the plot for *minor* is well apart from the position predicted for a *geayi* of such small size. The differences are quantified in the ratios between SVL and the other measurements. In only one ratio (Foot/SVL) does *minor* fall within the *geayi* range, though in another (EN/SVL) *minor* is barely outside. The differences in proportions together with those of size and color pattern provide good evidence that *minor* is a species distinct from *geayi*.

Ctenophryne geayi Mocquard

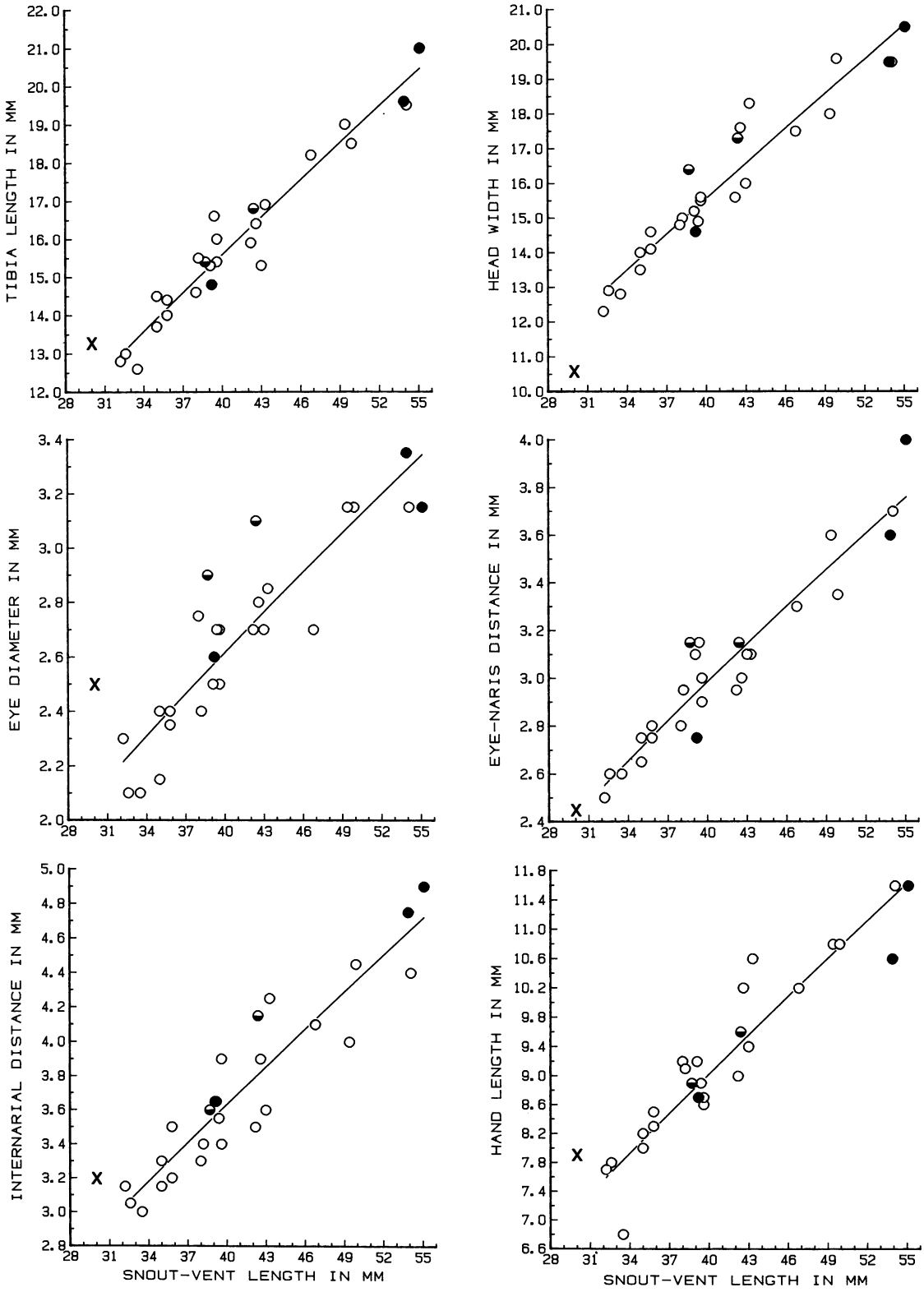
Figures 2C, D, 6–9

Ctenophryne Geayi Mocquard, 1904: 308 (type locality, "rivière Sarare en Colombie," holotype MNHN 03-84 [Guibé, 1950: 59]).

Lithodytes cinereus (not of Cope): A specimen of *C. geayi* apparently was mislabeled as holotype of this taxon; see Lynch (1988) for references and disposition of name.

HOLOTYPE: Not examined by us; the specimen was redescribed by Cochran and Goin (1970: 83–85).

DIAGNOSIS: See diagnosis of *C. minor*.


TIBIA LENGTH IN MM
HEAD WIDTH IN MM
EYE DIAMETER IN MM
EYE-NARIS DISTANCE IN MM
INTERNARIAL DISTANCE IN MM
HAND LENGTH IN MM
SNOUT-VENT LENGTH IN MM
SNOUT-VENT LENGTH IN MM

MEASUREMENTS AND PROPORTIONS: Fifteen adult males (nuptial pads present) range in size from 32.2 to 43.3 mm SVL. Eight adult females measure 42.4 to 55.1 mm, so considerable sexual dimorphism in size is apparent.

The only juvenile female (AMNH 44787) examined by us measures 39.2 mm and shows no evidence of approaching maturity: Its ovarian ova are ≤ 0.3 mm, and the oviducts are threadlike and only about 0.4 mm in diameter. Lynch (1988: 254) reported a somewhat larger measurement of 41.8 mm SVL for a juvenile female with dubious locality data.

Proportions for the entire sample ($N = 26$) are mean ± S.E. (range): TL/SVL 0.388 ± 0.003 (0.356–0.421); HW/SVL 0.388 ± 0.003 (0.360–0.424); Eye/SVL 0.065 ± 0.001 (0.057–0.075); EN/SVL 0.074 ± 0.001 (0.067–0.081); IN/SVL 0.090 ± 0.001 (0.079–0.98); EN/IN 0.826 ± 0.011 (0.729–0.933); Hand/SVL 0.225 ± 0.003 (0.197–0.245); Foot/SVL 0.407 ± 0.004 (0.378–0.443).

The regression coefficients for the various body measurements on snout-vent length are less than one. Hence, on average the lower ratios represent the larger individuals in this sample of specimens of all sizes and both sexes. Regression formulas (see fig. 5) are as follows:

$$\begin{aligned}
\text{TL} &= 0.619\text{SVL}^{0.874},\ r^2 = 0.918\\
\text{HW} &= 0.675\text{SVL}^{0.851},\ r^2 = 0.940\\
\text{EYE} &= 0.155\text{SVL}^{0.766},\ r^2 = 0.802\\
\text{EN} &= 0.208\text{SVL}^{0.722},\ r^2 = 0.902\\
\text{IN} &= 0.177\text{SVL}^{0.819},\ r^2 = 0.866\\
\text{HAND} &= 0.477\text{SVL}^{0.797},\ r^2 = 0.873\\
\text{FOOT} &= 0.580\text{SVL}^{0.905},\ r^2 = 0.913
\end{aligned}$$

MORPHOLOGY: Head narrower than rotund body. Snout blunt viewed from above, rounded and slightly projecting in profile; nostrils lateral but visible from above, moderately widely spaced, closer to snout tip than to eye. Loreal region moderately steeply sloping, flat; canthus rostralis rounded. Eyes small, upper eyelid about 33 percent of interorbital span. Tympanic ring barely visible externally, overlying skin undifferentiated. Relative lengths of fingers 3 > 4 > 2 > 1, first greater than half length of second, tips rounded, neither flattened nor expanded, no terminal grooves; subarticular and metacarpal elevations low, rounded. Relative lengths of toes 4 > 3 > 5 > 2 > 1, first less than half length of second, tips rounded, flattened, not or scarcely expanded, no terminal grooves; webbing variable—nearly full to less than half (see below); subarticular elevations rounded, very low; inner metatarsal elevation small, rounded, no outer elevation. A weak, diagonal postocular fold; occipital fold present or absent; skin otherwise smooth.

Male frogs show a fine-grained nuptial pad on the first two or three fingers, sometimes accompanied by a scattering of pointed tubercles. Males also possess a variably developed band of similar tubercles on the chin bordering the lower jaw. Duellman (1978: 190) stated that males lack nuptial excrescences. Possibly the development of the excrescences and pads varies with reproductive condition.

Two other morphological variables are noteworthy. Toe webbing is clearly sexually dimorphic, with males consistently having more extensive webbing than females (fig. 6). The relative degree of webbing may vary both ontogenetically and with reproductive condition, but the material is inadequate to support this inference.

Many species of microhylid frogs exhibit a transverse occipital fold (Zweifel, 1986: fig. 6). Among 20 specimens of *C. geayi* examined, a distinct fold is present in five, whereas the region of the fold is merely distinguished by pale pigment in most of the others. Nelson (1972: 112), discussing the function of this fold in *Gastrophryne* in protecting the frog's

←

Fig. 5. Regression of body measurements on snout-vent length in *Ctenophryne geayi* (circles), with *C. minor* (single X) included for comparison. Open circles represent the northern (and western) ventral pattern type of *C. geayi* (area A in fig. 3), closed circles the southern pattern type (area B), and half-filled circles the intermediate pattern type (area C). Overlap between the largest adult males and smallest adult females occurs at 42–43 mm SVL; the single specimen of *C. minor* is a subadult female of 30 mm SVL. See text for regression formulas.

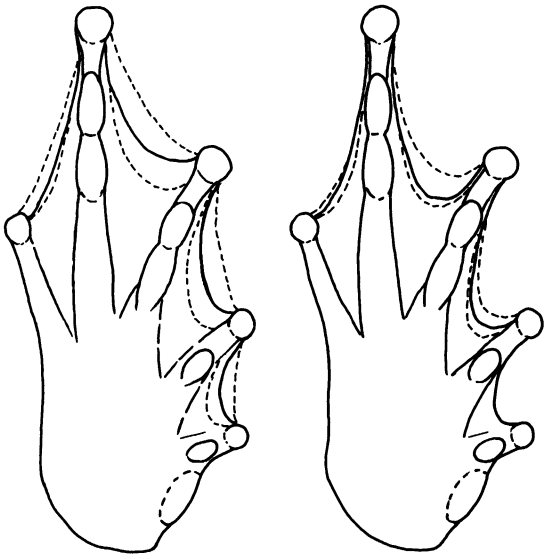


Fig. 6. Undersides of right hind feet of *Ctenophryne geayi*, showing variation in extent of webbing in males (left) and females (right). Solid line depicts approximate average webbing, broken lines show extents of minimum and maximum webbing.

eyes from attacks by ants, noted that "in frogs that have not been molested the fold is usually small or absent." Thus, though the ability to produce the fold may be a valid character, its expression in a living or preserved frog is variable.

COLOR AND PATTERN: A typical *Ctenophryne geayi* (adult male, KU 158526, Sta. Cecilia, Ecuador, fig. 2C, D) has the following color and pattern in preservative. Dorsal surfaces of the body, arms, and legs are nearly uniform medium brown with a scattering of tiny white flecks and a pale vertebral hairline. The lower part of the snout and the side of face including the lips are much darker brown than the dorsum, the color being most intense along the canthus rostralis. The upper edge of this dark area is bordered by a weak white line and the lips have tiny white spots. A diagonal skin fold from the posterior corner of eye to the arm insertion has a pale bordering line above. This line breaks above the arm but resumes and continues to the groin and along the anterior surface of the thigh. The lateral area below this light line is dark brown, unspotted, and continuous with the dark ventral ground color. The chin is almost black and lacks spots except marginally. The ground color of the remaining ventral areas, undersides of legs included, is dark brown. The chest, abdomen, and undersides of arms and thighs have numerous small, well-defined white spots, whereas the lower leg and tarsus have larger white spots. Above the level of the cloaca, the posterior of the thigh is the same brown as the dorsum; below that level it is dark brown like the venter with a pale upper border.

Variation in color pattern involves sexual dimorphism and individual and geographic variation. The chin is dark in males, pale and spotted like the chest in females, but no other sexual differences are evident. The dorsum may be slightly mottled rather than uniform and the vertebral light line absent or rarely replaced by a thin dark line. The brown of the upper arm may merge with that of the back, or the darker brown of the side of head and body may be narrowly continuous above the arm. A longitudinal light line may be present atop the thigh, and rarely also a diagonal dark mark. In addition to the ventral pale spotting, occasional specimens have a midventral light hairline crossed on the chest by a similar interbrachial line (fig. 8).

Duellman (1978: 190) described the color in life as pale brown dorsally, flanks and anterior and posterior surfaces of the thighs darker brown, throat dark grayish brown, other ventral surfaces dark brown with white flecks, and iris grayish bronze.

Size of the pale ventral spots is the only geographically variable aspect of coloration that we have noted (see Geographic Variation in Ventral Pattern below).

LARVA: Undescribed.

HABITAT AND HABITS: Information is limited mainly to that provided by Duellman (1978) from Ecuador and Schlüter (1980, 1984) from Peru. The former reported males calling from under leaves at the edge of a semipermanent pond in primary forest. Schlüter described the same calling habit, and emphasized association of calling with heavy rainfall. Aichinger (1987: 587), who spent time at the same Peruvian site previously worked by Schlüter, tabulated *C. geayi* among anuran species with a breeding-season duration of about "4 months . . . mainly during the rainy season," but presumably he did not

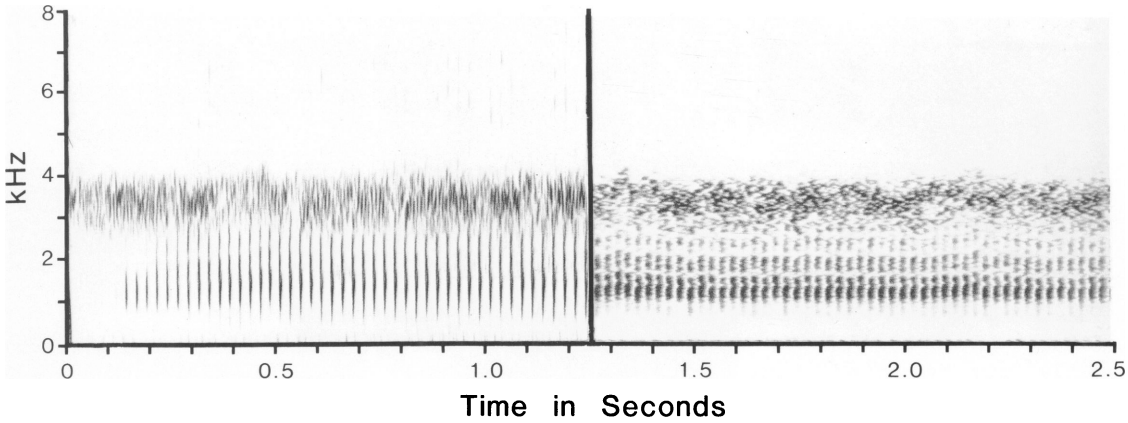


Fig. 7. Advertisement call of *Ctenophryne geayi*: consecutive wide-band (300 Hz filter) and narrow-band (45 Hz) displays of the beginning of a 4.8 sec call. Recorded by W. F. Pyburn at junction of Río Cafre and Río Guaviare, Vaupes [now Guaviare], Colombia, on June 28, 1969, air 27.7°C (from copy on AMNH herpetology reel 172).

mean to imply that breeding was constant during this period.

CALL: Nelson (1973: 163, fig. 3D, table 3) described the call of *Ctenophryne geayi*, from southern Colombia, as a "prolonged trill" with a length of 4.6–4.7 sec, dominant frequency 1100–1300 Hz, and pulse rate 37–39 per sec. He also estimated the pulse length at 0.03 sec—a measurement apparently based on narrow band (45 Hz filter) sound spectrograms, which give relatively poor time resolution. A spectrogram (fig. 7) illustrating both narrow (45 Hz) and wide (300 Hz) displays reveals the pulses to be essentially clicks, less than 0.01 sec long. (The recording used in preparing fig. 7 was made by William F. Pyburn, and was one of those analyzed by Nelson [loc. cit.], who deposited a copy in the AMNH herpetology tape library).

Duellman (1978: 190) described the call of Ecuadorian frogs as a "long, low-pitched, toad-like trill."

Schlüter (1980) also described and illustrated the call based on material from Panguana, Peru, some 1300 km south of Nelson's Colombian locality. Schlüter contrasted his characterization of the call as a "rattle" with Nelson's "trill," and pointed to differences in their respective sound spectrograms, specifying lower frequency limits of 1000 vs. 500 Hz. It appears to us that the difference between the spectrograms was misinterpreted, as Schlüter used a wide-band display and Nelson narrow band. Comparison of the wide- and narrow-band displays in figure 7 illustrates the point.

However, part of the difference perceived by Schlüter may relate to the pulse rate. Four calls of a Colombian frog average 39.9 pulses/sec, range 39.2–40.8) at an air temperature of 27.7°C. A call illustrated by Schlüter (1980: fig. 11) shows a faster rate, about 44.5/sec, at a lower air temperature, 23°C. If these calls are typical of the two populations at these temperatures, the difference could have systematic implications. The Colombian recording, incidentally, was made at a locality well within the range of the northern ventral pattern type of *C. geayi*, but we do not know the pattern type of the Peruvian population (see Geographic Variation below). More recordings of *Ctenophryne* with temperature and pattern data are needed.

GEOGRAPHIC VARIATION IN VENTRAL COLOR PATTERN

Ctenophryne geayi exhibits two or possibly three geographically correlated types of ventral patterns, as follow.

A. NORTHERN (AND WESTERN) PATTERN TYPE: Frogs from the northern and western part of the range—Guyana to Ecuador and south to central Peru—have a ventral pattern of pale flecks or very small spots, rarely as large as 1 mm and more often less than half

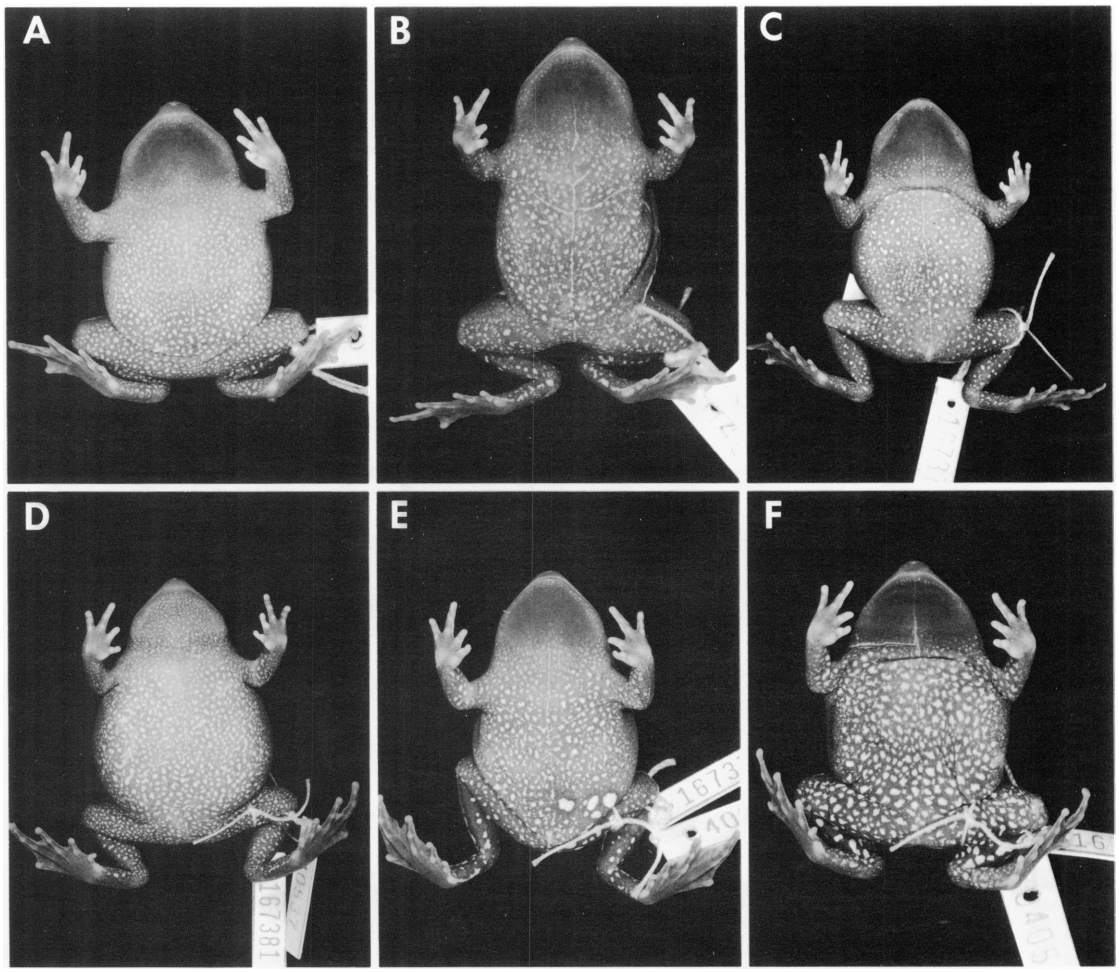


Fig. 8. Intrapopulational variation in ventral color pattern in a northern sample of *Ctenophryne geayi*: The pattern of pale dense flecking or small spots seems characteristic of northern and western *C. geayi*; of a series of 11 frogs (KU 167374–167384) from the same locality, however, one specimen (E) has a cluster of distinctly larger spots (compare fig. 9E, F). See also figure 2D for another example of the northern pattern type.

Not to scale, specimens shown 0.74–1.14 times life size. **A–C**, (KU 167377-79); **D**, (KU 167381); **E**, (KU 167375); **F**, (KU 167382), all from 13 km S, 1 km E Puente Cuyuni, eastern Venezuela.

that size (figs. 2D, 8). The holotype of *C. geayi* (from the northernmost locality mapped in fig. 3) evidently has the northern type of pattern described here, inasmuch as Cochran and Goin (1970: 84) said that its "entire ventral surface is *flecked* [italics ours] with pale spots, these being a little larger on the breast."

At least within some northern populations, however, individual specimens may have a uniform pattern of larger small spots measuring up to about 1.5 mm: Three of four specimens from Santa Cecilia, Ecuador, are alike in having numerous flecks and small spots < 1 mm (as in fig. 2D), whereas the fourth and largest specimen (KU 105256, 52 mm SVL) has many spots measuring about 1.5 mm. Similar variation is seen in a population sample from eastern Venezuela (fig. 8), in which one figured specimen (8F) has many spots of approximately 1.5 mm.

Two Peruvian specimens from the southwestern part of the range (KU 197048, Balta, Río Curanjo; USNM 233990, Kamahéni, Río Tambo) have the ventral spots as small as in

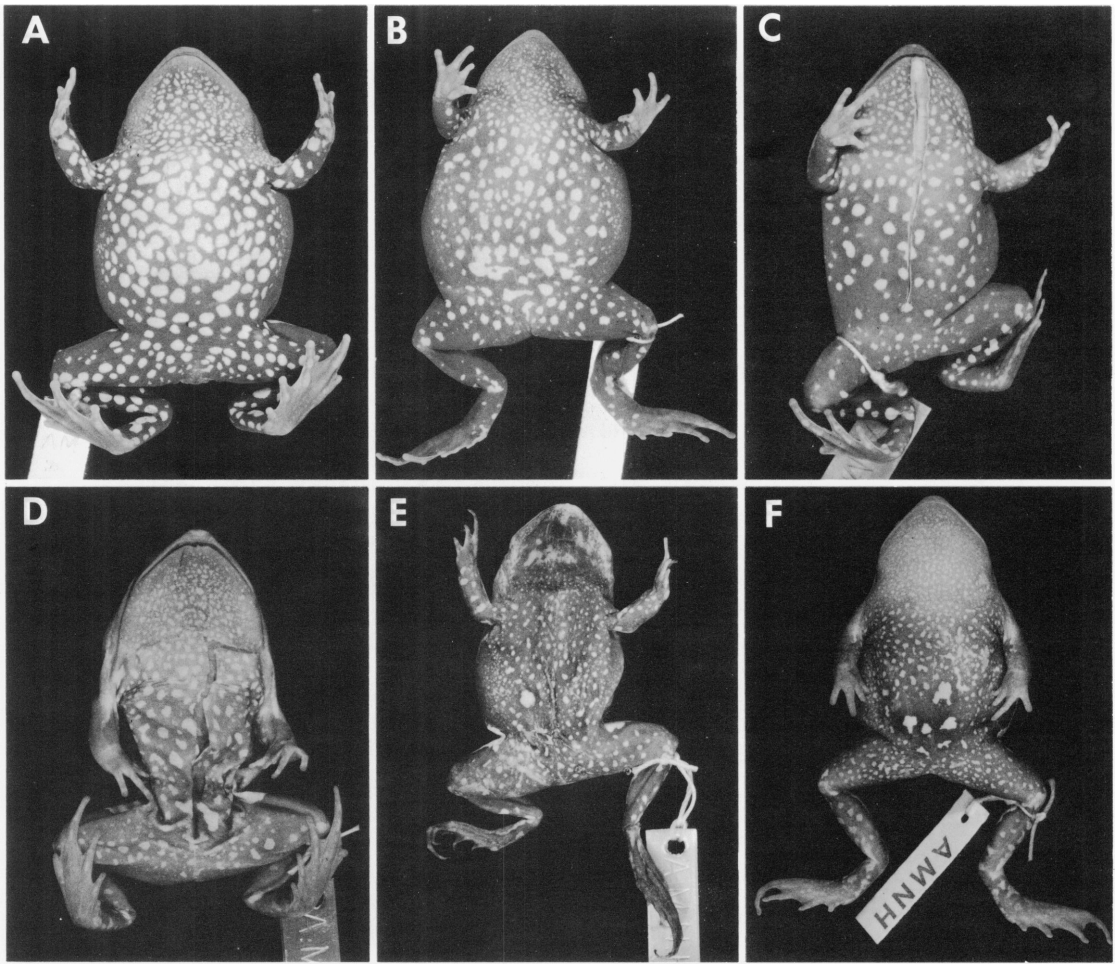


Fig. 9. Ventral color patterns in southern *Ctenophryne geayi*: Large spotted specimens shown in A–D are from localities south of the Amazon River, in north-central Brazil (A–C) and east-central Peru (D), and represent the pattern type termed "southern" in this paper. Specimens with intermediate patterns, in E, F, are from localities just north of the upper Amazon River, in northeastern Peru (also compare fig. 8E and see text).

Not to scale, specimens shown 0.80–1.21 times life size. **A**, Manjuru, Brazil (AMNH 73547); **B**, Maués, Brazil (AMNH 76183); **C**, Rio Livramento region, Brazil (AMNH 44787); **D**, between headwaters Río Utoquinia and Río Tapiche, Peru-Brazil frontier (AMNH 42685); **E**, Iquitos, Peru (AMNH 42887); **F**, Estirón, Río Ampiyacu, Peru (AMNH 115783).

most northern specimens. A few of their ventral markings slightly exceed 1 mm but most are ≤ 0.5 mm, in marked contrast to other southern specimens, which have the following pattern.

B. SOUTHERN PATTERN TYPE: Specimens from the southern half of the Amazon basin, in north-central Brazil (fig. 9A–C), have distinctly larger spots, of which an appreciable number are at least 1.5 mm (fig. 8C) up to a maximum of about 5 mm (fig. 9A). Spots up to about 4 mm (fig. 9C) also characterize two specimens from widely separated localities in eastern Peru (AMNH 42685, Peru-Brazil frontier; KU 205775, Cuzco Amazonico). These large spotted specimens are from localities geographically close to two other Peruvian specimens (see above) having the northern pattern type of pale flecking. Unfortunately, nothing is known about intra-

populational variation in this region, and the ventral pattern is unknown for two other localities in east-central Peru (as indicated by question marks in the distribution map, fig. 3).

C. INTERMEDIATE PATTERN TYPE: Four individuals from just north of the Amazon River, at Iquitos (AMNH 42663) and Estirón (AMNH 115783–84, USNM 200631) in northeast Peru, have pale flecked venters similar to those of most other specimens seen from the northern half of the Amazon basin—except in having, on the middle or posterior part of the venter, one to several distinctly larger spots measuring up to 2–3.5 mm (fig. 9E, F).

Geographic significance is suspected because all four specimens from this pair of localities have the same basic pattern. But, inasmuch as this pattern occurs also as intrapopulational variation in northern *geayi* (based on a single specimen, shown in fig. 8E), there is a degree of ambiguity to any correlation that might be assumed for this "intermediate" pattern type. Specimens of the three pattern types do not appear to differ in body proportions (fig. 5).

DISTRIBUTION

Ctenophryne geayi is widely distributed in northern South America east of the Andes (fig. 3), in lowland rain forest below 500 m elevation. It occurs from the Guayanan region southwestward through the western two-thirds of the Amazon Basin, and northward along the eastern Andes at the extreme western edge of the Orinoco drainage. Dunn (1949: 18) commented on the type locality, which is the northernmost locality plotted in figure 3.

Our distribution map (fig. 3) for *Ctenophryne* is based on the following literature records and specimens examined: **BRAZIL:** *Amazonas*: Municipio de Borba [on Rio Madeira at 4°25′S, 59°35′W] (Carvalho, 1954: 7); Rio Livramento region, 62°22′W, 7°17′S (AMNH 44787); Manjuru, 4°S, 57°W (AMNH 73547); Maués, 3°24′S, 57°43′W (AMNH 76183). **COLOMBIA:** *Guaviare* [formerly part of *Vaupes*]: junc. Río Cafre and Río Guaviare, about 20 km W San José del Guaviare, 2°37′N, 72°51′W (Nelson, 1973: 169). *Meta*: Serranía de la Macarena (USNM 157817). [*Norte de Santander*]: "rivière Sarare en Colombie," [= Río Sarare—the type locality—about 7°15′N, 72°10′W] (Mocquard, 1904: 9; Dunn, 1949: 18; Cochran and Goin, 1970: 83). **ECUADOR:** *Napo*: Santa Cecilia, 340 m, 00°02′N, 76°59′W (KU 105256, 158526–158528). **GUYANA:** *Essequibo*: Kartabo, 6°23′N, 58°42′W (AMNH 23119, 71399, USNM 129533). **PERU:** *Huánuco*: Río Yuyapichis (or Llullapichis), Panguana, 260 m, 9°37′S, 74°56′W (Schlüter, 1984: 171; Toft and Duellman, 1979: 73). *Junin*: Kamahéni, Río Tambo, about 11°15′S, 73°50′W (USNM 233990). *Loreto*: Iquitos, 100 m (AMNH 42887); Pampa Hermosa, Río Cushabatay, 150 m (AMNH 42663 [cleared and stained, but, for illustration of habitus and color pattern in dorsal view, see Dunn, 1949: 19]); Río Ampiyacu, Estirón (AMNH 115783, 115784, USNM 200631). *Madre de Dios*: Cuzco Amazonico, 15 km E Puerto Maldonado, 200 m (KU 205775). [*Ucayali* (formerly part of *Loreto*)]: Río Curanja, Balta, 300 m, 10°04′S, 71°15′W (KU 197048); Peru-Brazil frontier, [between headwaters] Utoquinia-Tapiche [Peruvian tributaries of Río Ucayali] (AMNH 42685). **VENEZUELA:** *Bolívar*: 13 km S, 1 km E Puente Cuyuni, 140 m (KU 167374–167384).

SYSTEMATIC IMPLICATIONS

It has long been realized (e.g., Boulenger, 1913: 1019) that the lowland rain forests of western Colombia and northwestern Ecuador contain a highly endemic anuran fauna, elements of which are found also in lower Central America. Lynch (1979: 191–192) tabulated only 13 (of 126) species of this "trans-Andean" fauna as occurring also in lowland tropical forests east of the Andes—but even so it bears emphasizing that at least half of this short list comprises apparent composite "species" and misapplied names (e.g., *Bufo typhonius*, *Hyla rubra*, *Leptodactylus bolivianus*, *L. wagneri*, *Rana palmipes* [see Hillis and de Sá, 1988]). Lynch (op. cit.: 191) recognized such taxonomic problems when he predicted that there probably "exist very few 'widely distributed' species of forest amphib-

ians . . . [and that] distinctions among different forest faunas will become greater."

The western Colombian species described herein as *Ctenophryne minor* is one of several recent additions to the large endemic fauna of the Pacific lowlands.[4] Although there was no previous reason to suspect the occurrence of *Ctenophryne* there, the existence of an endemic species is quite in keeping with the overall pattern of endemism on the Pacific side of northwestern South America. If our generic placement is correct, *minor* is the presumed sister species of *Ctenophryne geayi* as currently defined

Our brief survey of *Ctenophryne geayi*, however, raises the possibility that *geayi* might be a composite. At the current stage of knowledge, it seems useful to emphasize the existence of a northern and western population of *geayi* (s.s.) characterized by pale ventral flecking or small spots, and a southern population characterized by relatively large ventral spots. A third discernible ventral pattern (figs. 8E, 9E, F)—an apparent mixture in single specimens of northern and southern patterns—might represent no more than normal intrapopulational variation in northern *geayi* (as suggested by fig. 8), but we have seen too few specimens to make a satisfactory decision. Possible differences in the call (pulse rate, see above) conceivably could also be indicative of differentiation between northern and southern populations of *geayi*, although there are no obvious differences in body proportions (fig. 5) that would support the existence of more than a single taxon.

The type locality of the trans-Andean *Ctenophryne minor* is geographically closest to northern populations of *C. geayi* (fig. 3), but the large-spotted ventral pattern of the holotype (fig. 2B) is more similar to *geayi* specimens from south of the Amazon River. Both northern and southern *geayi*, however, tend to have the pale ventral markings more densely arranged than in the so far unique specimen of *Ctenophryne minor*.

[4] Additional lowland endemics (below 1000 m) described since Lynch's account (supra cit.) include *Eleutherodactylus muricatus* Lynch, *E. tenebrionis* Lynch, *E. zygodactylus* Lynch and Myers, *Epipedobates erythromos* (Vigle and Miyata), *Phyllobates terribilis* Myers, Daly, and Malkin, and *Physalaemus coloradorum* Cannatella and Duellman. Some species of intermediate elevations, such as the recently described *Centrolenella balionota* Duellman, extend below 1000 m, so the definition of "lowland" is not clearcut.

REFERENCES

Ahl, Ernst
1935. Beschreibung einer neuen Engmaulkröte der Gattung *Ctenophryne*. Zool. Anz. 112(9–10): 254–255.

Aichinger, M.
1987. Annual activity patterns of anurans in a seasonal Neotropical environment. Oecologia (Berlin) 71: 583–592.

Boulenger, G. A.
1913. On a collection of batrachians and reptiles made by Dr. H. G. F. Spurrell, F.Z.S., in the Choco, Colombia. Proc. Zool. Soc. London 1913, pt. 4: 1019–1038 + pls. 102–108.

Carvalho, Antenor Leitão de
1954. A preliminary synopsis of the genera of American microhylid frogs. Occas. Pap. Mus. Zool. Univ. Michigan 555: 1–19 + pl. 1.

Cochran, Doris M., and Coleman J. Goin
1970. Frogs of Colombia. U. S. Natl. Mus. Bull. 288: xii + 655 pp.

Duellman, William E.
1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 65: 352 pp.

Dunn, Emmett Reid
1949. Notes on South American frogs of the family Microhylidae. Am. Mus. Novitates 1419: 21 pp.

Frost, Darrel
1987. A replacement name for *Glossostoma* Günther, 1900 (Anura: Microhylidae). Copeia 1987(4): 1025.

Guibé, Jean
1950. Catalogue des types d'amphibiens du Muséum National d'Histoire Naturelle. Paris: Imprimerie Nationale, 71 pp.

Hillis, David M., and Rafael de Sá
1988. Phylogeny and taxonomy of the *Rana palmipes* group (Salientia: Ranidae). Herpetol. Monogr. 2: 1–26.

Lynch, John D.
1979. The amphibians of the lowland tropical forests. *In* W. E. Duellman (ed.), The South American herpetofauna: its origin, evolution, and dispersal. Univ. Kansas Mus. Nat. Hist. Monogr. 7: 189–215.

1988. *Lithodytes cinereus* Cope, 1885, a neglected junior synonym of *Eleutherodactylus fenestratus* (Steindachner), 1864 (Amphibia: Leptodactylidae). Copeia, 1988(1): 254–256.

Mocquard, F.
1904. Description de quelques reptiles et d'un batracien nouveaux de la collection du muséum. Bull. Mus. Hist. Nat. (Paris) 6: 301–309.

Myers, Charles W., John W. Daly, and Borys Malkin
1978. A dangerously toxic new frog (*Phyllobates*) used by Emberá Indians of western Colombia, with discussion of blowgun fabrication and dart poisoning. Bull. Am. Mus. Nat. Hist. 161(2): 307-366 + color pls. 1-2.

Nelson, Craig E.
1972. Systematic studies of the North American microhylid genus *Gastrophryne*. J. Herpetol. 6(2): 111–137.
1973. Mating calls of the Microhylinae: descriptions and phylogenetic and ecological considerations. Herpetologica 29(2): 163–176.
1985. Microhylinae (part). *In* Darrel R. Frost (ed.), Amphibian species of the world. A taxonomic and geographical reference, pp. 375–391. Lawrence, Kansas: Allen Press and Assoc. Syst. Coll.

Schlüter, Andreas
1980. Bio-akustische Untersuchungen an Microhyliden in einem begrentzen Gebiet des tropischen Regenwaldes von Peru (Amphibia: Salientia: Microhylidae). Salamandra 16(2): 114–131.
1984. Ökologische Untersuchungen an einem Stillgewässer im tropischen Regenwald von Peru unter besonderer Berücksichtigung der Amphibien. Printed doctoral dissertation, Univ. Hamburg, 300 pp.

Toft, Catherine A., and William E. Duellman
1979. Anurans of the lower Río Llullapichis, Amazonian Perú: a preliminary analysis of community structure. Herpetologica 35(1): 71–77.

Zweifel, Richard G.
1986. A new genus and species of microhylid frog from the Cerro de la Neblina region of Venezuela and a discussion of relationships among New World microhylid genera. Am. Mus. Novitates 2863: 24 pp.
1989. Identity of a supposed South American microhylid frog, *Ctenophryne marmorata*. Copeia 1989(1): 229–231.