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The Cloud Forest *Colostethus* (Anura, Dendrobatidae) of a Region of the Cordillera Occidental of Colombia

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ABSTRACT.—**Three species of *Colostethus* were found at 1800 m in the cloud forest of the Pacific slopes of the Cordillera Occidental of Colombia, including *C. abditaurantius*, *C. fraterdanieli*, and a new species. Sonagrams are given for all three species. Chromatic sexual dimorphism in *C. abditaurantius* is described. Range extensions derived from material in the Colección de Anfibios y Reptiles of the Universidad del Valle are given for *C. lehmanni*, which is placed in the Cordillera Occidental and in southern Colombia. The *C. ramosi* group is named for the clade delimited by the synapomorphy of black, apparently glandular tissue on the ventral surface at the distal end of the upper arm and often extending distad along the inner surface of the lower arm (=black arm band) in adult males.**

RESUMEN.—**En estudios herpetológicos a los 1800 m en un bosque nublado de la vertiente del Pacífico de la Cordillera Occidental de Colombia, se encontraron tres especies de *Colostethus: C. abditaurantius*, *C. fraterdanieli*, y una nueva especie. Se presentan sonogramas para las tres especies. Se describe el dimorfismo sexual cromático de *C. abditaurantius*. Con base en los ejemplares examinados de la Colección de Anfibios y Reptiles de la Universidad del Valle, se reportan ampliaciones de los límites de distribución de *C. lehmanni*, que se registra en la Cordillera Occidental y en el sur de Colombia. Se nombra el grupo *C. ramosi* para el clado delimitado por la sinapomorfia de tejido aparentemente glandular negro en la superficie ventral de la parte distal del brazo, frecuentemente extendiéndose distalmente por la superficie interior del antebrazo (=banda negra del brazo) en machos.**

The dendrobatid genus *Colostethus* Cope, 1866 is a widely distributed assemblage of roughly 100 species united by plesiomorphy. Most of the species groups that have been proposed (and given generic rank in some cases) lack unambiguous synapomorphies and are reflective only of phenetic similarity (Coloma, 1995). While the aposematic/toxic dendrobatids have received much attention in recent years, resulting in a greater understanding of their biology and evolution, basic data on distribution, natural history, and systematics are unavailable for most *Colostethus*. A large number of species appear to be highly endemic, but for many this is probably an artifact created by the lack of distribution records in the literature. Such is the case for the nominal species reported herein.

Specimens of the following nominal species of *Colostethus* have been reported from the Cordillera Occidental (including the Pacific foothills): *C. agilis* Lynch and Ruiz-Carranza, 1985; *C. alacris* Rivero and Granados Díaz, 1990; *C. betancuri* Rivero and Serna, 1991; *C. brachistriatus* Rivero and Serna, 1986; *C. breviquartus* Rivero and Serna, 1986; *C. chocoensis* (Boulenger, 1912); *C. furviventris* Rivero and Serna, 1991; *C. imbricolus*, Silverstone, 1975; *C. inguinalis* (Cope, 1868); *C. lacrimosus* Myers, 1991; *C. latinasus* (Cope, 1863); *C. mertensi* (Cochran and Goin, 1964); *C. nubicola* (Dunn, 1924); *C. pratti* (Boulenger, 1899); *C. talamancae* (Cope, 1875); and *C. yaguara* Rivero and Serna, 1991. In this paper we provide accounts for three more *Colostethus*, including one new species, and report localities in the Cordillera Occidental for a fourth species.

MATERIALS AND METHODS

The study site is known as Hacienda San Pedro, about 6 km (by road and trail) south of El Queremal, Municipio de Dagua, Departamento del Valle del Cauca, Colombia (3°29'N, 76°42'W), at 1800 m on the Pacific slopes of the Cordillera Occidental. This area represents an extension of the protected forests of Parque Nacional Natural Los Farallones de Cali. Much of the area has been cleared for pasture, but there remain many fairly extensive, often interconnected sections of relatively undisturbed forest along the main streams and smaller creeks.

Calls were recorded using a Sony WM D6C Professional Walkman and a Sony ECM 909 microphone. Recordings were digitized and edited using CSRE 4.5 pc-based signal analysis software. Call and note duration was taken from expanded waveforms. Call rate was measured directly from tapes with a stopwatch. Frequencies were obtained through fast Fourier transform (window widths 512 and 1024 points).

All collected material was killed in Chloretone solution, fixed in 10% formalin, and stored in 70% ethanol or formalin. At present, all material is deposited in the Colección de Anfibios

y Reptiles of the Universidad del Valle, although some paratypes will eventually be distributed among different institutions. Specimens were measured to 0.1 mm with dial calipers under a dissecting microscope. Unless otherwise specified, measurements are given only for adults and are expressed in mm. Adult females were diagnosed as having differentiated ova and enlarged, convoluted oviducts; sexual maturity in males was confirmed by the presence of testes and open vocal slits.

Type material at the Natural History Museum of Los Angeles County was examined and compared directly with material collected at the study site. Additional comparisons were made with specimens in the collection at the Universidad del Valle and the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia, original descriptions and subsequent literature. Appendix I includes only those species for which accounts are provided or whose range is extended in this paper. Diagnoses are based on examined material and are intended to complement original descriptions. Color descriptions are derived from the first author's notes taken on live specimens in the field. Colombian distribution data have been taken from examined material and from original descriptions only; although Rivero and Serna (1989) give general distribution patterns for Colombian *Colostethus*, they do not specify localities (other than those published in the original descriptions) or list examined specimens for the species discussed herein. Staging of larvae follows Gosner (1960); description of larval morphology follows Altig (1970).

The following collection abbreviations appear throughout the text: AMNH (American Museum of Natural History), BM (British Museum of Natural History), ICN (Instituto de Ciencias Naturales), LACM (Natural History Museum of Los Angeles County), UVC (Colección de Anfibios y Reptiles, Universidad del Valle).

Other nominal species of anurans collected at the study site include *Gastrotheca antomia, G. dendronastes, Hyla alytolylax, H. columbiana, Eleutherodactylus babax, E. brevifrons, E. calcaratus, E. cerastes, E. deinops, E. ervthropleura, E. gracilis, E. juanchoi, E. mantipus, E. molybrignus, E. orpacobates, E. palmeri, E. platychilus, E. thectopternus, E. w-nigrum, Centrolene geckoideum, C. robledoi, Cochranella ignota, C. griffithsi, C. ruizi,* and *C. savagei.*

Species Accounts

Colostethus abditaurantius Silverstone
Fig. 1

Colostethus abditaurantius Silverstone, 1975: 1–6.

Holotype adult female LACM 72000, "Quebrada la Gracia, Bello, Departamento de Antioquia, Colombia, about 1450 m."

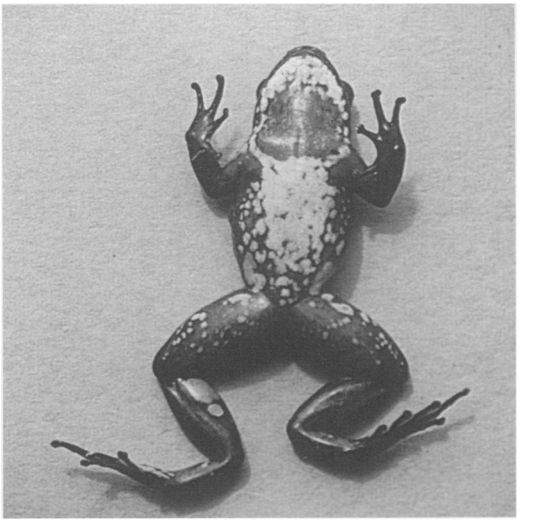

FIG. 1. *Colostethus abditaurantius* male UVC 12197, showing ventral coloration in life (photo by Erik R. Wild). Note the absence of iridophores on the throat and chest, contrasting with the white belly.

Diagnosis.—Snout–vent length (SVL): males: 23.4–28.5 ($\bar{x}$ = 27.6; N = 19), females: 29.0–34.8 ($\bar{x}$ = 31.1; N = 12); oblique lateral, dorsolateral, and ventrolateral stripes (OLS, DLS, and VLS respectively) absent; toes extensively webbed; weak outer metatarsal fold present; first finger shorter than second when appressed; third finger of males not swollen; ventral coloration dimorphic: throat and chest of mature males dark, transparent, free of iridophores, contrasting with pure white of rest of venter (see below), females ventrally immaculate white; skin of dorsum and venter smooth; legs indistinctly patterned with dark transverse banding dorsally; bright orange axilla, groin, and calf spots present; testes white.

This diagnosis disagrees on a single point with Silverstone's (1975) original description: male ventral coloration/sexual dimorphism (see Fig. 1). In all mature males the throat region is dark relative to the rest of the white venter. Essentially there are two ways in which dark coloration is produced on white ground in *Colostethus.* First, the dark pattern can be created by the presence of melanophores, which gives origin to the gray, black, and spotted throats in many male *Colostethus.* Second, the dark condition can be attained by the absence of iridophores from an otherwise white area. In *C. abditaurantius,* the throat is a translucent, purplish-black color in life (see Fig. 1); in preservative, the dark area is creamy white or pale yellow, in

contrast to the pure white of the surrounding area. We have also observed this pattern of male ventral coloration in several other riparian *Colostethus.*

Silverstone (1975) based his description on just two specimens, the female holotype LACM 72000 and the male paratype LACM 71999 (although the type series contains a third specimen, PAS 1003.71). Due probably to the fact that he did not personally collect the type series (Silverstone-Sopkin, pers. comm.) and the small number of specimens in the series, Silverstone (1975) erred in his description of "throat of male not uniformly dark, not contrasting with color of belly" (p. 2) and "throat, breast and belly . . . white" (pp. 4) in life. While the throat is not strongly contrasting with the ventral coloration in preservative, in most cases one can detect the lack of pigmentation on the throat (e.g., Silverstone's [1975:3, his fig. 2] photograph of the male paratype). Additionally, in reproductively active males (i.e., large, calling) throat coloration is more marked; if the male paratype was not reproductively active, the dark throat may have been less evident.

Discussion of Similar Species.—The species most easily confused with *Colostethus abditaurantius* from the Pacific slopes of the Cordillera Occidental is *C. agilis.* Lynch and Ruiz-Carranza (1985) omitted *C. abditaurantius* from the diagnosis in their description of *C. agilis.* Both species have extensive webbing, are of similar size, and lack defined OLS, DLS, or VLS (*C. agilis* often has several white spots considered homologous to the OLS by Lynch and Ruiz-Carranza, 1985). The two species are readily distinguished in life, based primarily on the characteristic large orange axilla, groin, and calf spots (absent in *C. agilis*). In preservative, the two are most easily distinguished by the swollen third finger in male *C. agilis,* absent in *C. abditaurantius.* Additionally, these species are para- or allopatric; *C. agilis* is reported from higher elevations, from 2190–2600 m (Lynch and Ruiz-Carranza, 1985), as opposed to 1450–2000 m for *C. abditaurantius.*

Colostethus lacrimosus and *C. chocoensis,* both without VLS, OLS, or DLS and with extensively webbed toes, are found on the Pacific slopes of the Cordillera Occidental but are easily distinguished by the absence of the bright orange spots, smaller size, and presence of a light oblique post-ocular stripe in *C. lacrimosus.* Also, *C. lacrimosus* and *C. chocoensis* are found at much lower elevations; *C. chocoensis* is restricted to below 800 m, and *C. lacrimosus* to below 640 m.

Color in Life.—The dorsum is dark golden brown, with diffuse dark brown or black spotting and transverse banding. In many specimens, a short, narrow golden or bronze line extends from the posterior corner of the eye to above the arm insertion. The venter is white, usually with a bluish hue, immaculate in female adults and with black reticulations in juveniles and sub-adults; the throat of adult males is dark, translucent purplish-black, free of iridophores and therefore contrasting with the white of the rest of the venter. Bright orange axilla, groin, and calf spots are present. The scutes of all fingers and of toes I, II, and III are white. A line of white dots, varying in number from one or two to many, extends around the upper lip. The legs have dark brown bands dorsally; ventrally they are free of white pigmentation with a brown wash around the edges of the thighs. Toe webbing is not pigmented. The plantar and palmar surfaces are brown. Small white spots are scattered along the flanks (not in a line homologous to the OLS as in *Colostethus agilis*).

Distribution.—*Colostethus abditaurantius* occurs both in the Cordillera Central and Occidental from 1450–2000 m. In the Cordillera Central, this species is known from the western slopes, while it has been collected on both the eastern and western flanks of the Cordillera Occidental. Available data indicate that its range extends from northern Antioquia south to Valle del Cauca in both Cordilleras.

Natural History.—*Colostethus abditaurantius* is strictly riparian, found either physically immersed with the head out of the water, or sitting at the water's edge. The preferred habitat is that of shallow (<5 cm depth), slow-flowing tributaries of the main streams, although it is also common to find this species under rocks and in the slow flowing water of the protected banks and back-eddies of the larger streams, though they are not as abundant. When disturbed, this species immediately dives into the water and hides in the substrate or, more commonly, among the rocks or in the multitude of tiny cavities at the water's edge. They are extremely agile in the water, often swimming some distance to disappear in the substrate or rocks.

Males actively defend their territories by calling and chasing out invaders. They call from partially submerged leaves and rocks, from within tiny caves, or from small waterfalls. Depending on the substrate of the stream, males are often found calling from well formed, smooth cavities in the mud of the stream-bank. Due to the shape and size of these cavities, it is possible that the frogs themselves may construct or at least modify them.

Females are also territorial, defending territories consisting of a large rock or an area at the water's edge. When another female enters her territory, the resident immediately chases the invader out; no physical contact has been observed.

Calls.—Based on a recording of UVC 11746

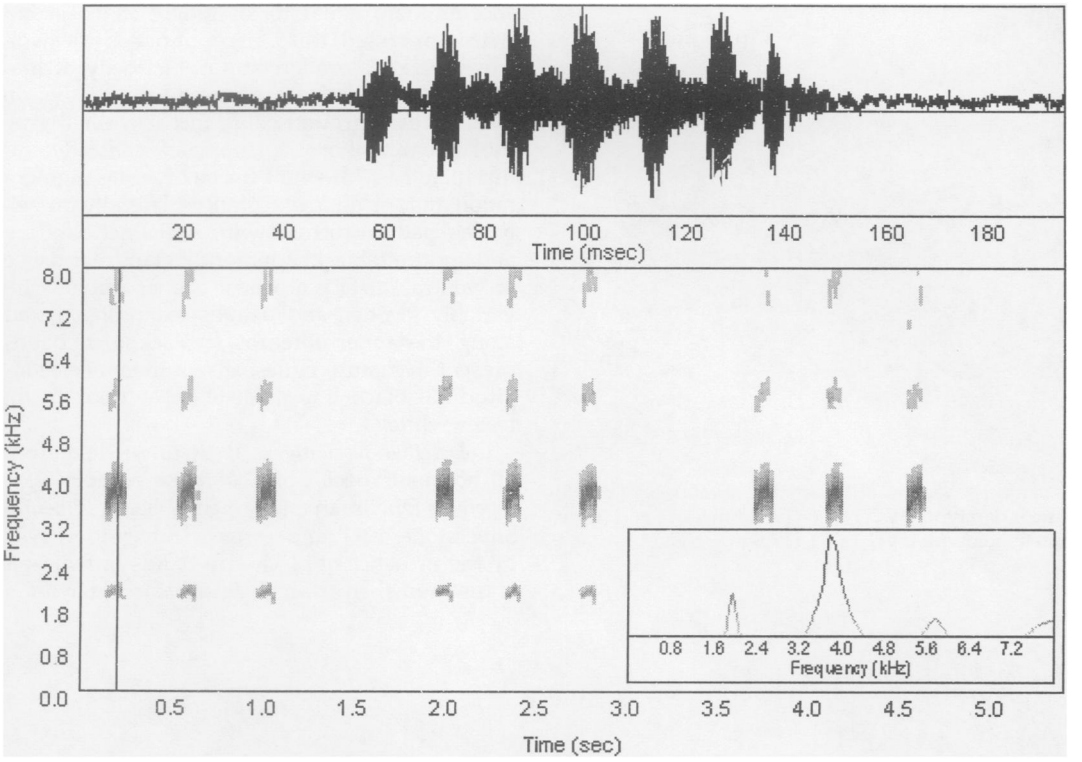

FIG. 2. Audiospectrogram and expanded waveform of *Colostethus abditaurantius* UVC 11746. The inset shows the cross-section at the position of the cursor. The waveform corresponds to the first call of the first series of three, and is accordingly composed of seven well defined pulses (subsequent calls contain only six pulses).

(SVL = 29.2), made 11 Feb. 1995 at 1115 h at 23.0 C air temperature from a distance of ca. 1 m. The frog was observed calling from within a tiny cave that extends some 30 cm into the bank of a shallow, slow-flowing stream. The recording includes 220 calls in 3.62 min of continuous tape (=60.8 calls/min). The call is a single croak usually emitted in series of two or three, with a variable pause between series. A sample of 17 calls taken from within a longer series was analyzed to determine acoustic characteristics (see Fig. 2). The first call of every series and isolated calls consist of seven pulses and have a duration of 94–98 msec (N = 7, $\bar{x}$ = 95.5, SD = 1.61), while all subsequent calls consist of six notes of 78–84 msec (N = 10, $\bar{x}$ = 81.1, SD = 2.00). For the 17 calls, pulse rate ranges from 71.5–76.6 pulses/sec ($\bar{x}$ = 73.7, SD = 1.61). The fundamental frequency was measured at 1906 and 1937 Hz. The emphasized frequency falls between 3718 and 3781 Hz; two higher harmonics occur at 5531–5718 Hz and 7312–7968 Hz, although in some cases the highest harmonic is absent.

Colostethus fascianigrus, sp. nov.
Figs. 3–4

Holotype.—UVC 11781 (field number TG 0159), an adult male collected in leaf litter on 1–2 Feb. 1995 by Taran Grant along the Quebrada Seca, Hacienda San Pedro, about 6 km south of El Queremal, Municipio Dagua, Departamento del Valle del Cauca, Colombia, 3°29′13″N, 76°42′20″W, at 1800 m on the Pacific slopes of the Cordillera Occidental.

Paratopotypes.—Adult males (12): UVC 11587 (collected 9–11 Sept. 1994 by Fernando Castro-H.'s herpetology class); UVC 11804, 11808–10, 11814–15, 11820, and 11845 (29–30 Mar. 1995 by Taran Grant and Wilmar Bolívar-G.). Adult females (10): UVC 11553 (26 Aug. 1994 by Taran Grant); UVC 11785–87 (1–2 Feb. 1995 by Taran Grant); UVC 11805–06, 11811–13, and 11817 (29–30 Mar. 1995 by Taran Grant and Wilmar Bolívar-G.).

Diagnosis.—SVL: males 16.6–19.7 ($\bar{x}$ = 18.1; N = 36); females 17.3–21.5 ($\bar{x}$ = 19.8; N = 29); OLS complete, DLS and VLS absent; toe webbing absent; outer metatarsal fold absent; first finger

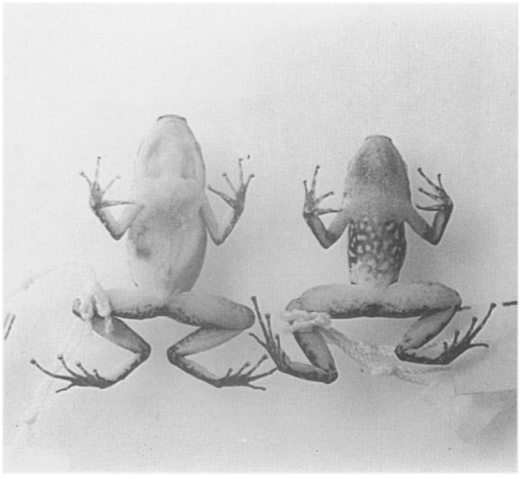

FIG. 3. Venters of *Colostethus fascianigrus* (left) female paratype UVC 11806 (19.1 mm SVL) and (right) male holotype UVC 11781 (17.8 mm SVL).

shorter than, equal to, or longer than second when appressed; third finger of males not swollen; ventral coloration dimorphic: belly of mature males with large discrete white spots on black or gray ground color, throat washed gray (not prominent in life), females ventrally immaculate or with slight traces of white pigmentation and/or dark reticulations laterally on belly; leg pattern diffuse, with indistinct banding and spotting; black, apparently glandular tissue on ventral surface at distal end of upper arm, variably swollen and usually extending distad along the inner forearm (=black arm band) present in mature males, absent in females; longitudinal black line present on anterior thigh; testes white.

Colostethus fascianigrus is distinguished from all nominal species of *Colostethus* except *C. exasperatus* Duellman and Lynch, 1988, *C. lehmanni* Silverstone, 1971, and *C. ramosi* Silverstone, 1971 by the presence of black arm bands in males; it is distinguished from *C. exasperatus* in having a

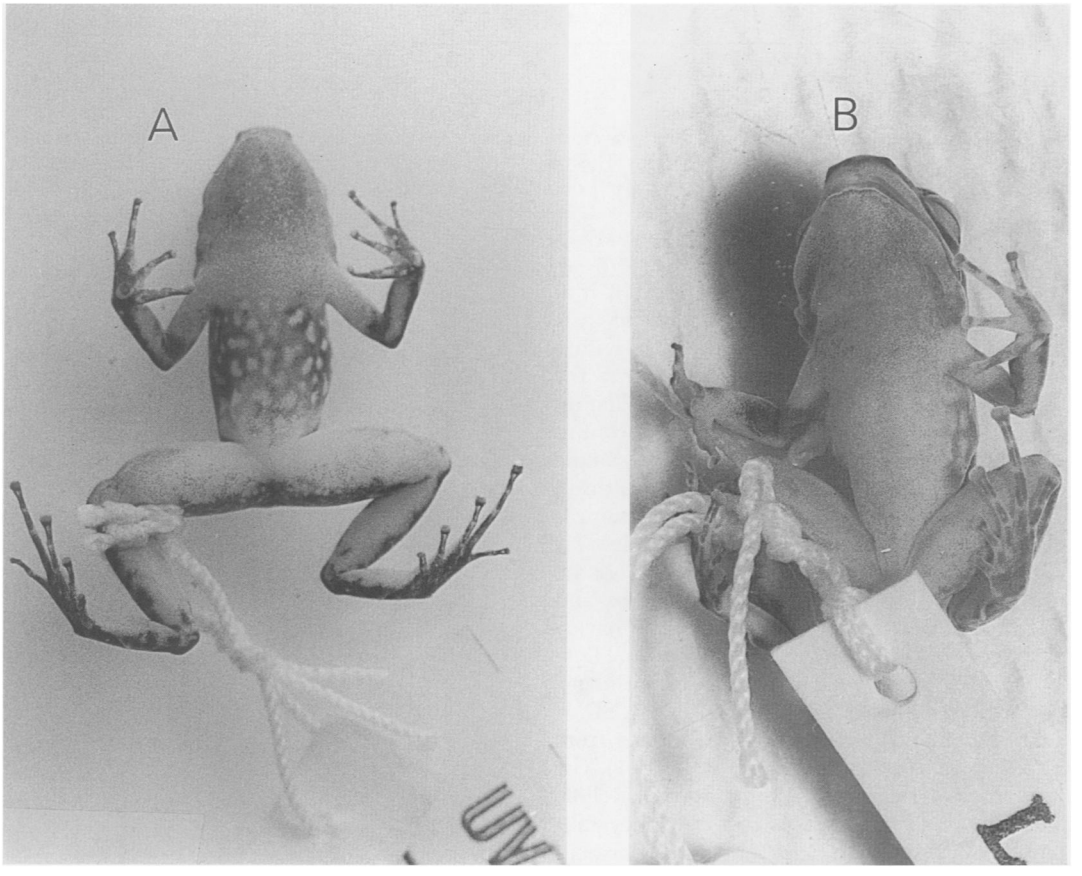

FIG. 4. Venters of related species (A) *Colostethus fascianigrus* male holotype UVC 11781 and (B) *C. lehmanni* male holotype LACM 44156 (photo by P. A. Silverstone-Sopkin). Note the swollen black arm band synapomorphy and the extent of spotting in both.

complete OLS (partial in *C. exasperatus*), in lacking a DLS (present in *C. exasperatus*), and from *C. exasperatus, C. lehmanni,* and *C. ramosi* in having large white spots on dark ground color on the belly of males (brown spots in male *C. exasperatus* and immaculate in male and female *C. lehmanni* and *C. ramosi*).

Discussion of Similar Species.—We have observed the black arm band in males of two other nominal species from Colombia, *Colostethus lehmanni* (including the holotype LACM 44156, as described by Silverstone [1971] and seen in Fig. 4B), and *C. ramosi.* Additionally, Coloma (1995: 29) reports the presence of "a swollen black gland on the inner surface of the elbow" in *C. exasperatus.*

Colostethus lehmanni is described as having "lower sides of body brown with white spots" (Silverstone, 1971:3); in many of the UVC specimens the white spots are fused into a wavy VLS. *Colostethus lehmanni* never has white spots on a black belly as in *C. fascianigrus* (see Fig. 3). The calls of *C. fascianigrus* and *C. lehmanni* are quite distinct, the former consisting of a cricket-like "chirp" (here used as a strictly imitative word, i.e., not a chirp call as defined by Myers and Daly [1976:228]) of two or three notes repeated frequently but sporadically, with an emphasized frequency of around 5 kHz (see below), while the latter is a peep of a single note repeated at regular intervals at least 15 times with an emphasized frequency of ca. 4 kHz (at 16.6 C air temperature).

The black arm band is also present in *Colostethus ramosi,* as observed in the male paratype LACM 44148. Silverstone (1971) separated this species from *C. lehmanni* based on two characters, (1) the black throat in males (as opposed to gray in *C. lehmanni*) and (2) the absence of a longitudinal black line on the anterior surface of the thigh (present in *C. lehmanni*). While the throat of most *C. lehmanni* is indeed gray, in some specimens the throat has been observed to be as black as that of the male paratype of *C. ramosi* (e.g., UVC 6233 and 6293). The remaining character is not strong, as thigh marking tends to be quite variable in *Colostethus,* and suggests that these taxa may be conspecific. Until additional material from the type locality of *C. ramosi* can be examined, we are reluctant to formally synonymize these species and therefore continue to recognize them both. Regardless, *C. fascianigrus* is distinguished from *C. ramosi* by the presence of large white spots on dark ground color on the belly of males.

Outside of the *Colostethus ramosi* group (see Discussion), *C. fascianigrus* is compared with those species that lack toe webbing and DLS and VLS and have complete OLS and ventral spotting in males. In Colombia this includes *C. subpunctatus* (Cope, 1899), which differs from *C. fascianigrus* in having small black spots or reticulate pattern on the belly, legs, and often throat in both males and females, having a pale proximoventral calf spot, often having a vertebral stripe, having the entire tympanum dark, and in lacking the black arm band and gray wash on the throat in mature males.

Two species from Ecuador also resemble *Colostethus fascianigrus. Colostethus delatorreae* Coloma, 1995 is also from the western slopes of the Andes, but is found at higher elevations than have been recorded for *C. fascianigrus* (i.e., 2340–2500 m for *C. delatorreae* versus 1600–1960 m for *C. fascianigrus*). *Colostethus delatorreae* differs from the new species in the presenting a VLS and two small black spots at the base of the arms (both absent in *C. fascianigrus*); also, the tibia is proportionately longer in *C. delatorreae* (49% of SVL in holotype; Coloma, 1995) than in *C. fascianigrus* (42–46% of SVL in type series).

The other Ecuadorian species that phenetically resembles *Colostethus fascianigrus* is *C. pulchellus* (Jiménez de la Espada, 1875), as defined by Coloma (1995; see also Edwards, 1974b). In addition to differences in size (maximum SVL of *C. pulchellus:* males to 21.5, females to 24.4; *C. fascianigrus:* males to 19.7, females to 21.5) and the presence of discrete markings on the chest and gular region in some populations of *C. pulchellus* (absent in all *C. fascianigrus*), these two species are clearly distinguished by their calls, based on differences in both temporal and spectral parameters. Coloma (1995) describes the call of *C. pulchellus* as a buzz consisting of 4–6 notes with an emphasized frequency of 2700–3000 Hz (at 24–30 C), while that of *C. fascianigrus* is a chirp consisting of two or three notes with an emphasized frequency of roughly 5 kHz (see below).

Colostethus nubicola is of similar size, has a complete OLS, and is also found on the Pacific slopes of Colombia. However, the venter of *C. nubicola* is either immaculate or the throat and often the chest and belly are dark; the belly of *C. nubicola* never has white spots on black ground. Male *C. nubicola* have the third finger swollen and do not have the black arm band, present in *C. fascianigrus.* Also, *C. nubicola* has a VLS in life and generally is found at lower elevations.

Colostethus fascianigrus, at first glance in the field, can be confused with juvenile *C. fraterdanieli* Silverstone, 1971, although the two are easily distinguished once collected based on differences in webbing, ventral coloration, the black arm band, and the longer head in *C. fraterdanieli* (see full account below).

Measurements of Holotype.—SVL 17.8; forearm length from proximal edge of palmar tubercle

to outer edge of flexed elbow 4.2; hand length from proximal edge of palmar tubercle to tip of third finger 4.8; tibia length between outer edge of flexed knee and heel 8.1; foot length from proximal edge of outer metatarsal tubercle to tip of fourth toe 7.6; head width between angles of jaws 6.1; head length from angle of jaws to tip of snout 5.4; eye length from posterior to anterior corner 2.4; eye to naris from anterior corner of eye to center of naris 1.6; distance between centers of nares 2.6; snout length from anterior corner of eye to tip of snout 2.9; interorbital distance 2.0; approximate diameter of tympanum 1.3.

Description of Holotype.—Adult male, vocal slits present, testes white, third finger not swollen; maxillary and premaxillary teeth present; tongue rounded (not notched); head width between angles of jaws 34% of SVL and 1.1 times greater than head length; inter-orbital distance 33% of head width; canthus rostralis poorly defined, gently rounded; loreal region slightly concave; snout sloping, dorsally rounded with nares protruding laterally, acutely rounded, almost wedge-shaped laterally; eye–nares distance 67% of eye length and 55% of snout length; dorsum posteriorly tubercled, light brown, upper eyelids and dorsal pattern (=poorly defined spotting and striping) black; OLS complete, visible dorsally, bordered above and below by black; arms dorsally yellowish with dark wash; arms ventrally lighter, but still washed with melanophores, black arm band extends ventrally around distal end of upper arm and distad along inner surface of forearm, slightly swollen; appressed fingers I and II equal in length; fingers not fringed, except inner edge of third finger which has a weak fringe; hand moderate in length, 27% of SVL, 1.1 times longer than forearm; large elliptical palmar tubercle on base of palm, distally dark; smaller, elongated thenar tubercle on edge at base of finger 1; a single large subarticular tubercle on fingers I and II, two on III and IV, with distal tubercles being smaller and less protuberant; tympanum well defined, anteroventral $\frac{2}{5}$ visible, tympanum diameter 54% of eye length; black band extends around snout (narrow at tip), through nares, along loreal region, through eye, forming lower border of OLL above, extending obliquely through upper $\frac{1}{5}$ of tympanum, above arm insertion, and continuing along flanks, where it is interrupted by discrete white spots (as on belly); sub-ocular stripe yellowish with dark wash, extending anteriorly from arm insertion and borders black band above, rising obliquely through lower $\frac{1}{5}$ of tympanum to eye and extending around snout along-upper lip; venter smooth; throat and chest washed dark on light ground; belly has large (ca. 2 times diameter of disk of toe III), well defined white spots on black ground; groin ventrally immaculate; legs relatively long, heel of adpressed leg extends to anterior edge of eye, tibia length 46% of SVL; legs ventrally washed gray; plantar surface gray; foot length 43% of SVL; small, round, protuberant metatarsal tubercle at base of foot, in line with toe III; larger, flattened, slightly elliptical inner metatarsal tubercle, wider than toe I; toes I and II each have one well developed subarticular tubercle; III has two, with the proximal being well developed while the distal is non-protuberant and smaller; IV lacks well developed tubercles, although there is slight swelling projecting below each phalangeal joint; toe V has a small, non-protuberant subarticular tubercle at the base, and another better developed tubercle distally; tarsal fold (=keel) prominent, well defined but relatively short, curved, arising from inner edge approximately $\frac{1}{5}$ tarsal length from distal end of tarsus, and extending proximally a little more than $\frac{1}{5}$ tarsal length; outer metatarsal fold absent; toes free of webbing, but with a weak, barely visible fringe; legs dorsally tubercled, washed black on yellowish ground with poorly defined black bands and spots, no well defined light stripes on posterior or anterior surfaces of thighs; finger and toe discs moderate in size (=approximately 1.5 times width of digits).

Range of Proportions for Type Series (Including Holotype).—Forearm/SVL 0.21–0.24; hand/SVL 0.23–0.27; hand/forearm 1.1–1.2; tibia length/SVL 0.42–0.46; foot length/SVL 0.39–0.43; head width/SVL 0.32–0.35; head width/head length 1.0–1.1; inter-orbital distance/head width 0.31–0.37; eye–naris distance/snout length 0.55–0.63; eye-naris distance/eye length 0.63–0.73; tympanum diameter/eye length 0.44–0.58.

Color in Life.—The dorsum is brown with yellow and orange tinges and large, poorly defined black spotting and marbling; the legs are dorsally yellow, with dark brown, diffuse transverse bars and posterior and anterior longitudinal stripes. Venter (except belly) entirely transparent yellow with faint dark wash, legs often with tiny white spots on posterior (inner if legs are extended) edge of thighs. The belly has white spots on a black ground in adult males, is white in adult females, occasionally with faint white spots laterally in adult females, and is white in juveniles. The lower lip is white. A prominent black arm band, often swollen and extending distad along the forearm, is present in mature males. The large metacarpal tubercle is dark (gray or brown) distally and light (white or creamy yellow) proximally. The flanks are light brown in adults and transparent yellow in juveniles.

Larvae.—Based on UVC 11784 (lot of three

[originally five, two lost during capture, *fide* Milton Reyes] Stage 26 larvae collected with male UVC 11783) and UVC 11846 (lot of four Stage 25 larvae collected with male UVC 11845). Means are given first for UVC 11784 followed by UVC 11846 in parentheses.

2(2)/3 rows of denticles (row 2 interrupted by beak), all equal in length; first anterior row notched medially, all posterior rows slightly curved medially; mouth emarginate; papillae small, single complete row on posterior labium, one or two rows of papillae on lateral margin of anterior labium, one of which extends along the anterior labium; anterior labium bare medially; beak serrated; upper jaw weakly notched medially; lower jaw "V"-shaped; jaws wide (heavily keratinized for nearly the entire length of jaw); mouth oriented anteroventrally; eyes situated dorsally; body compressed dorsoventrally, elliptical in dorsal aspect; nostrils positioned dorsolaterally, directed anterolaterally; anus dextral; spiracle sinistral; melanophores present across venter posterior to mouth (in preservative); mouth small, ca. ⅓ width of body; low-finned tail, depth: $\bar{x}$ = 2.3 (2.5); total length: $\bar{x}$ = 16.0 (13.0); body length: $\bar{x}$ = 5.9 (5.1); width at midbody: $\bar{x}$ = 3.5 (3.2).

Etymology.—Derived from Latin *fascia,* meaning band or stripe, and *nigrum,* black, in reference to the swollen black arm band in mature males.

Distribution.—The *Colostethus fascianigrus* material in UVC is relatively extensive. Localities are all in the Cordillera Occidental from elevations of 1600–1960 m on both the eastern and Pacific slopes. The material examined shows this taxon to occur from extreme southern Chocó (4°44'N) to southern Valle del Cauca (3°29'N).

Natural History.—Colostethus fascianigrus is terrestrial. This species has been observed only on the ground in the leaf litter or in water when depositing larvae (see below). Like its sympatric congeners, *C. fascianigrus* is extremely quick and agile, responding to danger by hopping a short distance and hiding in the leaf litter or in soil and roots at the base of larger plants.

Males call sporadically from leaf litter. Cephalic amplexus was observed between a single pair, with the male calling while clasping the female; the pair quickly separated and hopped off. The role of amplexus is unknown in this species, i.e., whether it represents aggression, an aspect of courtship, or if amplexus is maintained through ovoposition.

Males transport four or five larvae to at least Stage 26. A single male was observed depositing larvae in a small, shallow, still pool of water on the forest floor. After nearly two hours at the water's edge, the male immersed his entire body, with just the head out of the water; after ca. 10 min, some of the larvae were observed swimming from his back. It is not known if larvae are usually deposited in stages or all together (both methods have been reported for dendrobatids; see Silverstone, 1976; Wells, 1980a, b); the frog may have left before all of the larvae could slide off his back simply because he was disturbed by a sudden downpour of rain.

Calls.—UVC 11814 (SVL = 17.8) emitted two series of calls while amplexing an uncollected female in leaf litter on 29 Mar. 1995 at 1520 h at 18.0 C air temperature. These series are identical to advertisement calls emitted under normal circumstances, as confirmed by extensive field observations of calling males and the unvouchered recording described below. The first series contains eight calls in 4.8 sec, and the second series 11 calls in 11.0 sec; the longer series of 11 calls was analyzed to determine acoustic properties (see Fig. 5). All calls consist of two notes. Call duration ranges from 77–85 msec (N = 11, $\bar{x}$ = 80.2, SD = 2.44), and note duration from 10–17 msec (N = 22, $\bar{x}$ = 12.3, SD = 1.62). Notes are non- or only weakly pulsatile. The emphasized frequency ranges from 4968–5187 Hz. Harmonics are weak; when discernible, the fundamental frequency occurs at roughly 2700 Hz, and a higher harmonic sometimes occurs at ca. 7300–7900 Hz. Frequency modulation within notes is minimal, but the frequency of the second note is usually (N = 9) 30–160 Hz higher than the first (in the two remaining calls both notes have the same frequency). In the first 10 calls, both notes exhibit emphasized frequencies above 5 kHz, while in the eleventh the first note lies at 4968 Hz and the second at 5125 Hz.

An uncollected but visually identified individual was recorded on tape TG-A 003 from 75 cm distance positioned ca. 2 m from a shallow, slow-flowing stream on 30 Mar. 1995 at 1304 h at 19.0 C. Two series of calls were recorded, the first consisting of 28 calls given in 53 sec, and the second of 36 calls in 60 sec. Of the 28 calls in the first series, 25 are composed of three notes, while the remaining calls contain only two; all calls in the second series consist of two notes. Calls composed of three notes have a duration of 153–156 msec, while those of two notes have the same duration as those given by UVC 11814 (i.e., ≈80 msec). Emphasized frequencies for all calls in both series fall between 4750 and 5187 Hz. Notes are given in rising frequency in both two- and three-note calls. The first note has most of its energy at around 4750–4850 Hz, while subsequent notes are all above 5 kHz. There is a difference of 30–125 Hz between second and third notes. Harmonic separation is better in this recording, with fundamental frequencies occuring between 2343 and 2625 Hz

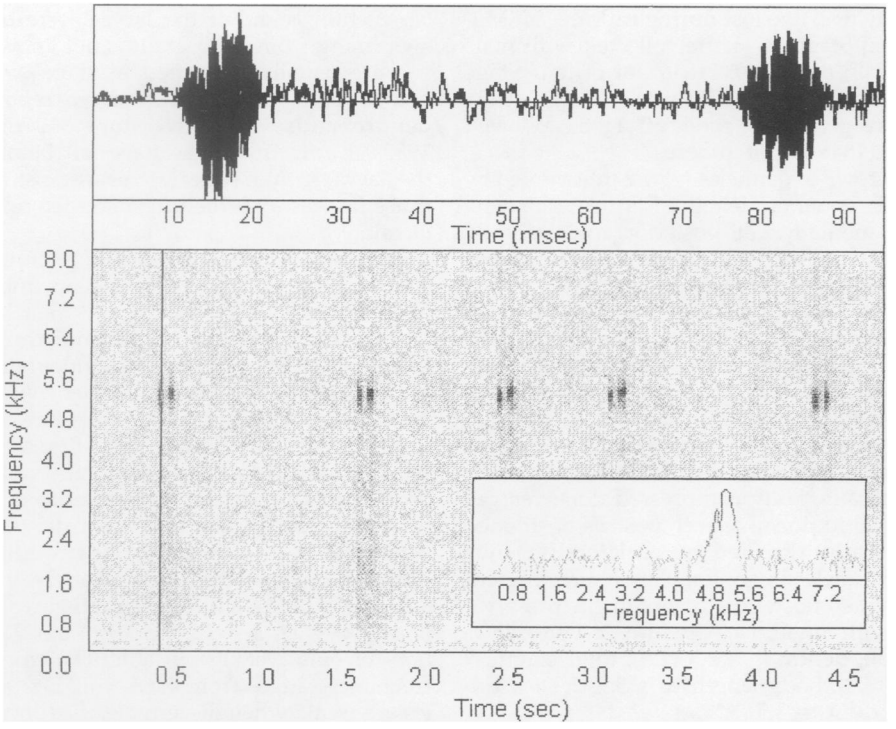

FIG. 5. Audiospectrogram and expanded waveform of *Colostethus fascianigrus* UVC 11814. The inset shows the cross-section at the position of the cursor. The waveform shows the two notes of the first call.

and the higher harmonic between 7062 and 7968 Hz.

Colostethus fraterdanieli Silverstone

Colostethus fraterdanieli Silverstone 1971: 4–6. Holotype adult male LACM 44164, "Antioquia: Santa Rita (near Río Nare), 1890–1910 m" Colombia.

Diagnosis.—SVL: males: 20.0–24.9 ($\bar{x}$ = 22.9; N = 9), females: 22.7–27.0 ($\bar{x}$ = 25.1; N = 21); OLS complete, DLS and VLS absent; toes II–III and/or III–IV basally webbed; weak outer metatarsal fold present; first finger longer (usually), equal to, or shorter than second when appressed; third finger of males swollen; ventral coloration dimorphic: throat of mature males spotted dark on light ground (usually), white in females; abdomen of males and entire venter of females immaculate white; legs with well defined transverse dark bars extending dorsally on thighs between longitudinal dark stripes bordering well defined anterior and posterior longitudinal light stripes (yellow in life) present on anterior and posterior thigh; lower lip dark (black or brown in preservative); testes pure black or with black reticulations on white ground.

The dark lower lip is not pointed out by Silverstone (1971), but is present in all specimens examined including all type specimens (based on direct examination and photographs of unexamined types).

Discussion of Similar Species.—Silverstone (1971) included at least three morphotypes from different localities in the type series, consisting primarily of variations in pattern and coloration. Much of the variation he described has been observed within the population at Hacienda San Pedro. The spotting on the throat of mature males ranges from heavy to almost absent; as has been suggested of the extent of swelling of the third finger (Myers et al., 1991), the extent of spotting may also be under hormonal control, varying with the reproductive activity of the male. The pattern on the thighs is generally well defined, but in some specimens it is more diffuse, with the yellow posterior stripe being broken into a series of spots. The variation is not representative of several sympatric species, as other aspects of adult morphology, larval morphology, and the call are constant throughout the population. *Colostethus fraterdanieli* does not have "dos manchas oscuras en el pecho" as reported by Rivero and Serna (1986:528) and was correctly placed by Rivero (1990) in his *C. inguinalis* group (group IV).

In recent years, several similar taxa have been

described, including *Colostethus alacris, C. brachistriatus, C. yaguara,* and an un-named species found in Edwards' unpublished dissertation (1974a:223–229). Edwards' work (1974a) appears to have had great influence in the classification of the above nominal species, yet he only examined *C. fraterdanieli* material collected with the holotype (deposited at LACM), and his color description is that given by Silverstone (1971) for the male holotype; it is therefore not known whether Edwards or the subsequent authors took into account the extent of variation of *C. fraterdanieli* sensu Silverstone. In addition to color and pattern, other morphological characters weighted heavily, such as relative finger length, vary within populations, as observed at Hacienda San Pedro and in the type series (see Discussion). With the exception of *C. yaguara,* which does not have the third finger swollen in males (but the type series only contains one male, and the variability of this character within populations must be considered [see Myers et al., 1991:18; see also Discussion for comments on sex determination]), the recently described species may prove to be conspecific with *C. fraterdanieli.*

Color in Life.—Legs ventrally yellow; bright yellow axilla and groin spots; OLS light golden brown, yellow at groin; OLS bordered by thick black line below, below which flanks break into reticulate pattern, fading into white of venter; sub-ocular stripe light, cream to golden brown, with or without small black spots; throat of mature males has black spots on white ground, immaculate white in females; iris flecked gold/orange; black lower lip line extends from angles of jaws around lip, either joined or not anteriorly; dorsum brown with green and orange or golden tinges; inner forearm and fingers I and II white; basal toe webbing yellow; palmar and plantar surfaces gray; thigh markings bright yellow, black banding on brown ground; top of feet yellow; scutes of toes I–IV white; scutes of fingers I–III white.

Larvae.—Based on a lot of eight Stage 25 larvae UVC 11855, collected with male UVC 11854 near a small pool of water at the study site.

2(2)/3 rows of denticles (row 2 interrupted by beak), all equal in length; mouth emarginate; single complete row of papillae on posterior labium and laterally, anterior labium bare medially; beak serrated; upper jaw not notched medially; lower jaw V-shaped; jaws wide; mouth oriented anteroventrally; eyes situated dorsally; body compressed ventrolaterally, elliptical from above; nostrils situated dorsolaterally, oriented anteroventrally; anus dextral; spiracle sinistral; ventral area posterior to mouth distinctly free of melanophores (in preservative), contrasting with dark surrounding area; mouth small, ca. ¼ width of body; tail depth: $\bar{x}$ = 2.7; total length: $\bar{x}$ = 13.6; body length: $\bar{x}$ = 5.0; width at midbody: $\bar{x}$ = 3.3.

Distribution.—*Colostethus fraterdanieli* is known from the western flanks of the Cordillera Central and from both the western and eastern sides of the Cordillera Occidental. Hacienda San Pedro is the southernmost confirmed locality; however, should the potentially synonymous taxa prove to be conspecific its range would extend to at least central Cauca. *Colostethus fraterdanieli* occurs at elevations between 1800 and 2500 m.

Natural History.—*Colostethus fraterdanieli* is terrestrial, confined to the forest floor. All metamorphosed specimens were collected out of the water, to a maximum of approximately 30 m from water. Their first reaction to threat is to leap into leaf litter or to hide among the roots and loose soil at the base of trees and bushes, as in *C. fascianigrus.*

Colostethus fraterdanieli calls frequently from leaf litter on the forest floor. The advertisement call consists of a single peep repeated at a constant rate up to more than 300 times. The encounter call consists of a softer peep repeated three to five times, answered and repeated by each male (see below). In some cases, males will simply chase out intruders without vocalization. No physical contact has been observed. Female aggression has not been observed.

Males transport up to 12 larvae on their backs, depositing them in small, still pools and shallow, slow-flowing streams; deposition of larvae has not been observed.

Calls.—UVC 11728 (SVL = 21.8) was recorded 2 Feb. 1995 at 1115 h at 21.0 C air temperature, beginning at a distance of 30 cm and gradually reduced to 10 cm. The frog called from leaf litter 45 cm from a stump. At one point, a conspecific juvenile approached the calling male. The male responded by moving toward the juvenile and assuming a higher position on a fallen leaf and continuing to call; the juvenile subsequently disappeared into the surrounding leaf litter. Six hundred and seventy-nine calls were given at a rate of 120.4 calls/min. A sample of 15 calls in series taken from the middle region of a continuous series of 119 calls reveals that calls consist of a single non- or weakly pulsatile note of 45–49 msec duration ($\bar{x}$ = 47.8, SD = 1.04) (see Fig. 6). The emphasized frequency ranges from 3593–3656 Hz, and two harmonics occur at approximately 5500 and 7400 Hz. Notes are weakly modulated from lower to higher.

UVC 11729 (23.9 SVL) was recorded on the same date at 1150 h at 25.0 C air temperature. The frog was partially concealed between a pair of fallen leaves and was calling across a depression ca. 2 m across and 0.5 m deep. Fifty-two calls were given at a rate of 132.8 calls/min. In

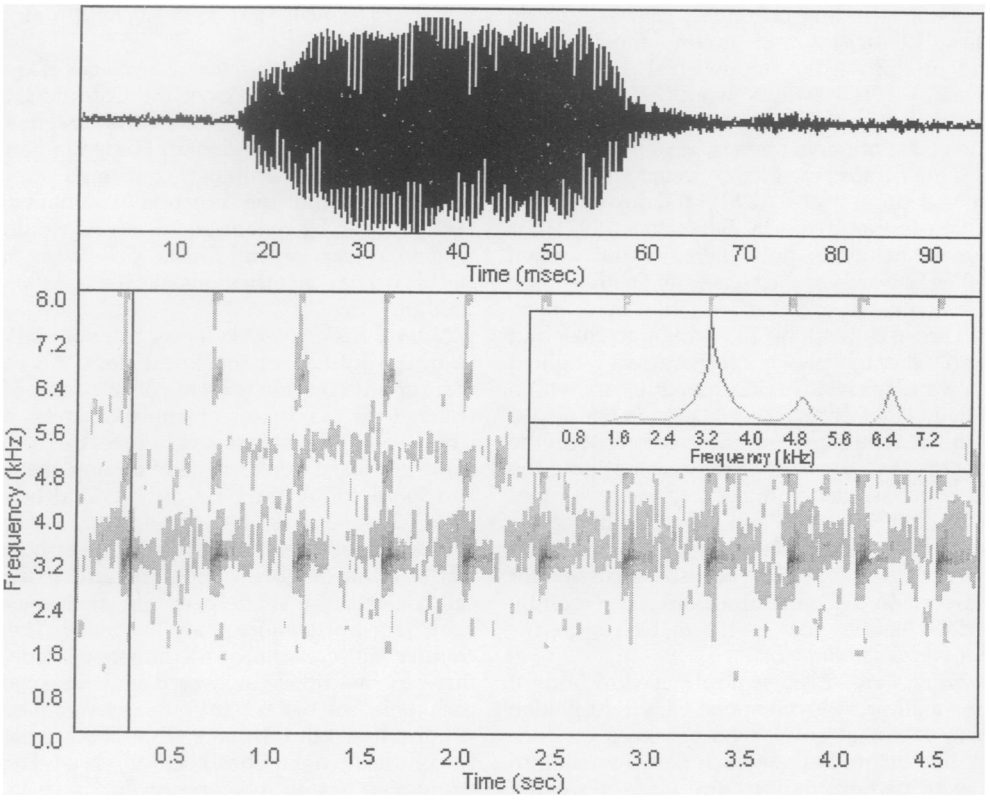

FIG. 6. Audiospectrogram and expanded waveform of *Colostethus fraterdanieli* UVC 11729. The inset shows the cross-section at the position of cursor. The waveform corresponds to the first call.

a sequence of 15 calls, each has a duration of 38–49 msec ($\bar{x}$ = 43.6, SD = 2.50). The emphasized frequency lies between 3156 and 3250 Hz, with weak harmonics occurring at ca. 4800 and 6400 Hz. Calls are non-pulsatile and weakly frequency modulated from lower to higher.

On 30 Mar. 1995, UVC 11830 and an uncollected (but positively identified) frog were recorded producing encounter calls in leaf litter. The recording was made 15 cm from the voucher specimen. Calls are composed of 3–5 non-pulsatile notes. Call duration ranges from 454–726 msec, depending on the number of notes. Note duration ranges from 43–65 msec, with the first note always shortest. Spectral analysis shows that the emphasized frequency falls within the range of the emphasized frequencies of the advertisement call but that harmonic separation is poor.

DISCUSSION

Characters.—Of the *Colostethus fraterdanieli* collected at the study site, three specimens (UVC 11730, 11733–34) with well developed vocal slits (i.e., apparently not artifacts due to mishandling) do not present the swollen third finger. At first, this was interpreted as variation in the expression of the swollen third finger in males; however, examination of the gonads revealed that all three are adult females. This illustrates the importance of direct examination of gonads in sex determination of *Colostethus*, rather than relying on secondary sex characteristics alone. Combined with the variation in the expression of the swollen third finger reported by Myers et al. (1991), this provides a warning against drawing taxonomic conclusions based on samples consisting of only one or a few males (e.g., Rivero and Serna, 1991).

Variation in relative lengths of appressed first and second fingers is observed in *Colostethus fascianigrus* and *C. fraterdanieli*. The holotype of *C. fraterdanieli* (LACM 44164) is reported by Silverstone (1971) to have the first finger slightly shorter than the second; however, the hands are twisted due to preservation, and when the fingers are straightened it is revealed that finger I is slightly longer than finger II. Regardless, variation in this character is observed within the type series at LACM (e.g., LACM 44165 has finger I slightly shorter than finger II, while in LACM 44168 finger I is much longer than finger

II). No variation has been seen in *C. abditaurantius,* with all material exhibiting the first finger shorter than the second. This character has been used consistently in *Colostethus* diagnoses and has been weighted heavily in some cases (e.g., Rivero and Serna, 1986); however, due to the variation observed in the expression of this character, taxonomic conclusions based on limited series should be avoided.

The biological significance of the black arm band in males of *Colostethus exasperatus, C. fascianigrus, C. lehmanni,* and *C. ramosi* is unknown. Although histological evidence is unavailable, it seems glandular in nature, is usually slightly swollen, and in extreme cases forms a tubercle-like projection. In most specimens, the tissue extends distad along the inner surface of the lower arm to form a black, swollen patch of skin (see Fig. 4B). The expression of this character only in males and the variation in the extent of swelling (from almost flat to tubercle-like) suggest that it may be analogous to the swollen third finger in many other dendrobatids, with both characters under hormonal control and used in amplexus.

Community Ecology.—Unlike many other dendrobatids (specifically *Dendrobates* and *Phyllobates* in captivity), no inter- or intraspecific larval cannibalism has been observed either in the field or in captivity (a mixed colony of 15 *Colostethus fascianigrus* and *C. fraterdanieli* tadpoles was maintained in a small aquarium in the laboratory). Larvae are found in quite high concentrations in ground water. Larvae of *C. fascianigrus* and *C. fraterdanieli* are deposited by males in the same bodies of water. *Colostethus abditaurantius* larvae have not been collected, but adults inhabit the same pools where larvae of *C. fascianigrus* and *C. fraterdanieli* were collected and it is therefore assumed that all three species are larval competitors.

Two definite micro-habitat preferences were observed: riparian (*Colostethus abditaurantius*) and terrestrial (*C. fraterdanieli* and *C. fascianigrus*). The two terrestrial species are both confined to the leaf litter of the forest floor, probably only rarely coming in contact with their riparian congener. The calls of these two species are very different; the emphasized frequency of *C. fraterdanieli* lies at approximately 3.2 kHz and is composed of a single peep repeated at a constant rate up to more than 300 times, while the emphasized frequency of *C. fascianigrus* occurs at ca. 5 kHz and consists of a cricket-like chirp of two or three notes emitted sporadically. The call of *C. abditaurantius* is a short croak usually repeated in series of two or three with an emphasized frequency of 3.7–3.8 kHz.

The only other anuran heard calling diurnally at Hacienda San Pedro was *Hyla columbiana,* a primarily nocturnal species known to often call diurnally as well. However, diurnal calling was observed only once, and it was weak and ceased within a few minutes. Regardless, the call of *H. columbiana* shares no appreciable affinities with any of the *Colostethus* calls at Hacienda San Pedro.

Systematics.—Due to the uniqueness of the black arm band in dendrobatids, we suggest that it is synapomorphic and propose the *Colostethus ramosi* group for *C. exasperatus, C. fascianigrus, C. lehmanni,* and *C. ramosi.* The monophyly of this group is further supported by biogeography and a host of unpolarized character states such as size and proportions, hand and foot morphology, and testes coloration. Relationships within and between groups cannot be resolved until a complete phylogenetic analysis of the basal portion of the dendrobatid clade is undertaken, leaving these taxa in a four-branch polytomy that arises from the huge polytomy that comprises *Colostethus.*

We have not seen *Colostethus exasperatus,* and its placement in the *C. ramosi* group is based on Coloma's (1995:29) description of "a swollen black gland on the inner surface of the elbow" and our conversations with Luis A. Coloma. While sharing the black arm band synapomorphy and the above unpolarized character states, *C. exasperatus* differs in body striping, namely in the presence of a DLS (absent in the other species) and only a partial OLS (complete in the other species). If our hypothesis of monophyly is correct, then the different combinations of body stripes are homoplastic in *Colostethus.*

The closest relatives of *Colostethus abditaurantius* and *C. fraterdanieli* remain unknown, although according to Rivero and Serna's (1989) arrangement they are placed in the *C. fuliginosus* (group VI) and *C. inguinalis* (group IV) groups, respectively.

Distribution.—The discovery of populations of *Colostethus abditaurantius, C. fraterdanieli,* and *C. lehmanni* on the western slopes of the Cordillera Occidental is not surprising. The pattern of populations on the western flanks of the Cordillera Central and in the Cordillera Occidental is observed repeatedly; *Eleutherodactylus erythropleura, E. gracilis, E. mantipus, E. thectopternus, E. wnigrum, Cochranella ruizi, C. savagei,* and *Centrolene geckoideum* all show the same pattern.

Available data indicate that *Colostethus fascianigrus* has a somewhat limited distribution confined to the Cordillera Occidental in Valle del Cauca and Chocó, extending across a little over 1° latitude. However, considering the range extensions of *C. lehmanni* (occurring throughout much of the Colombian Andes), *C. abditaurantius* and *C. fraterdanieli* (both ranging into the Cordillera Occidental), this may be more reflective of the paucity of locality data than real distribution.

Colostethus lehmanni apparently replaces *C. fascianigrus* at higher elevations. Immediately above the study site of Hacienda San Pedro, at 1960 m, occasional calls of *C. lehmanni* can be heard, but they are much less abundant than *C. fascianigrus* calls. As elevation increases, *C. lehmanni* calls become more abundant and *C. fascianigrus* less so, until reaching 2020 m, at which point no *C. fascianigrus* can be detected.

Coloma (1995) reported the presence of *Colostethus lehmanni* in Ecuador, but questioned the assignment of the Ecuadorian specimens to this taxon due to its absence between the type locality in Colombia and the localities in Ecuador, leaving a huge gap in the distribution. The UVC material essentially fills the gap, providing locality records to southern Colombia, and thus supporting the notion that the Ecuadorian and Colombian populations represent a single species. Of interest is the difference in elevational distribution; Coloma (1995:38) reported Ecuadorian *C. lehmanni* as occurring between 1460 m, lower than any of the known Colombian populations, and 2120 m, much lower than the 2800 m upper limit in Colombia. Due to the morphological uniformity described by Coloma (1995) and observed in the examined material, additional data (e.g., vocalizations) are required to determine if this nominal taxon is comprised of several cryptic species.

Conservation.—At the time that this study was carried out, all three species of *Colostethus* found at the study site were extremely abundant despite the habitat fragmentation and alteration. Calls of all three have been heard from the trails in all of the haciendas surrounding the study site. However, they are strictly confined to the forest relics, which are being reduced almost continuously. Recent visits to Hacienda San Pedro indicate that fluctuations in activity and/or abundance are occurring, although we have not detected any major habitat alterations. In some cases, particularly in *C. abditaurantius*, local extinctions appear to have taken place, although it is just as likely that the frogs are simply inactive due to unfavorable environmental conditions. We have noted similar disappearances of other previously common species (e.g., several centrolenids), but we feel that any speculations as to the factors influencing activity or abundance would be premature at this point. It does seem clear that our collecting is not the predominant factor, as local demes that were only heard and were never sampled are now absent as well.

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APPENDIX I

Specimens Examined

Colostethus abditaurantius (73). COLOMBIA: Departamento de Antioquia: Quebrada Altagracia, Bello, 1450 m, LACM 71999 (paratype), 72000 (holotype); Parque Nacional de las Orquídeas, 1480–1540 m, ICN 19483–94. Departamento de Risaralda: Municipio Pereira, Parque Regional Ucumarí, UVC 10172, 10793–94. Departamento del Choco: Municipio San José del Palmar, Alto del Oso, Quebrada la Guagua and neighboring stream, UVC 9282–93. Departamento del Valle del Cauca: Parque Natural El Topacio Pana, UVC 6265; Municipio Tuluá, Quebrada la Leona, Reserva Municipal "La Leona," Cordillera Central, UVC 11673, 11725–26, 11755–66; Municipio La Cumbre, Vereda Chicoral, Corregimiento Bitaco, ca. 1800 m, UVC 10020–22, 10895, 10897; Municipio Dagua, 6 km S El Queremal, Hacienda San Pedro, 3°29′13″N, 76°42′20″W, 1800 m, UVC 11548, 11743–56, 11837–39, 12197; Municipio Dagua, El Queremal, above Hacienda San Pedro, on the trail to La Lulera (3°28′8″N, 76°42′3″W), 1950 m, UVC 12198–200; Municipio Dagua, El Queremal, above Hacienda San Pedro, La Lulera, 3°28′8″N, 76°42′3″W, 2000 m, UVC 12201.

Colostethus fascianigrus (70, not including 23 type specimens listed in text). COLOMBIA: Departamentos del Chocó: Cerro Torrá, 1625–1700 m, UVC 6965; 6 km W El Boquerón, 26 km from El Cairo, ca. 1700 m. Departamento del Valle del Cauca: Reserva Forestal de Yotoco, ca. 1600 m, UVC 7580, 7582, 7621, 8554–56, 8558–62, 9890, 10327–33, 10910; Municipio La Cumbre, Vereda Chicoral, Corregimiento Bitaco, ca. 1800 m, UVC 10006, 10022; San Antonio, La Horqueta, near Cali, ca. 1900 m, UVC 7111; Municipio Dagua, El Queremal, road to Berrequín, 1770 m, UVC 7587–94; Municipio Dagua, 6 km S El Queremal, Hacienda San Pedro, 3°29′13″N, 76°42′20″W, 1800 m, UVC 11332, 11384, 11549–50, 11554, 11788–95, 11807, 11816, 11818–19, 11821–22, 11846 (lot of three back-riding tadpoles); Municipio Dagua, El Queremal, above Hacienda San Pedro, 1960 m, UVC 12221–23, 12346; Municipio Dagua, W El Queremal, UVC 11783–84 (lot of three back-riding tadpoles); Municipio Florida, Hacienda Los Alpes, UVC 6974–76, 10981–82, 10984–85; km 18 on Cali-Buenaventura road, Finca la Zingara, UVC 11997, 11999; km 21 on Cali-Buenaventura road, ca. 1900 m, UVC 11466–67, 11469.

Colostethus fraterdanieli (42). COLOMBIA: Departamento de Antioquia: Santa Rita (near Río Nare), 1890–1910 m, LACM 44164 (holotype), 44165–66, 44168–69 (paratypes). Departamento de Caldas: Municipio Santa Rosa de Cabal, UVC 7380. Departamento del Cauca: Reserva Natural El Guayabo, UVC 6163, 6271, 6273–74. Departamento del Valle del Cauca: Peñas Blancas, UVC 6266, 6268; Municipio Dagua, 6 km S El Queremal, 3°29′13″N, 76°42′20″W, 1800 m, UVC 11551, 11555–56, 11728–42, 11823–32, 11854, 11855 (lot of eight back-riding tadpoles).

Colostethus lehmanni (54). COLOMBIA: Departamento de Antioquia: Santa Rita (near Río Nare), 1890–1910 m, LACM 44154–55 (paratypes), 44156 (holotype), 44157–61 (paratypes); Frontino, Corregimiento Nutibara, 16.5–17 km from Nutibara, 1900 m, ICN 16280–82, 16286. Departamento del Valle del Cauca: Parque Nacional Natural los Farallones de Cali, Campamento de Corea, UVC 6192, 6216, 7314; Parque Nacional Na-

tural los Farallones de Cali, Campamento de Corea, 2580 m, UVC 6199–200, 6213, 6233; Parque Nacional Natural los Farallones de Cali, Campamento de Corea, 2800 m; Municipio La Cumbre, Vereda de Chicoral, UVC 10898; Vereda de Pance, 2100 m, UVC 11213–14; Municipio Tuluá, Reserva Municipal "La Leona," Cordillera Central, ca. 1800 m, UVC 11870; Municipio Buga, Nogales, Finca Chupaderos, "El Hospital,"Cordillera Central, 2400 m, UVC 11871; Municipio Dagua, El Queremal, above Hacienda San Pedro, La Lulera, 3°28'8"N, 76°42'3"W, 2020 m, UVC 12225; Municipio Dagua, above Hacienda San Pedro, clearing near Quebrada la Esperanza, 2020 m, UVC 12345. Departamento del Cauca: Municipio Popayán, Vereda Santillana, UVC 6283–95. Departamento de Chocó: Cerro Torrá, 1625–1700 m, UVC 6966, 6968; Municipio San José del Palmar, 4 km below El Boquerón, 24 Km W El Cairo, ca. 1800 m, UVC 10114; 6 km below El Boquerón, ca. 1700 m, UVC 10144–49. Departamento de Nariño: Municipio Ricaurte, Reserva La Planada, 1800 m, UVC 7061–66.

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The Effects of Size on the Diets of Six Sympatric Species of Postmetamorphic Litter Anurans in Central Amazonia

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ABSTRACT.—**All species of diurnal leaf-litter anurans in central Amazonia changed the type and size of their prey as they grew. Postmetamorphic individuals of all species ate principally mites and collembolans, and larger frogs ate larger prey of other types. The shift in prey types was not a passive effect of selection for larger prey. There was a strong relationship between electivity for prey types and frog size, independent of electivities for prey size, in six of the seven species. This study showed that most species in the community had strong ontogenetic changes in diet composition and electivity for prey types, and these changes did not conform to simple models of the effects of predator size and diet quality.**

Change in diet with ontogeny has often been studied in fish (reviewed in Werner and Gilliam, 1984; Osenberg et al., 1992; Sheldon and Meffe, 1993). In anurans and reptiles, change in diet has been related to changes in selection for the type or size of prey (Schoener and Gorman, 1968; Pengilley, 1971; Labanick, 1976; Rose, 1976; Mushinsky et al., 1982; Christian, 1982; Dominguez and Salvador, 1990; Donnelly, 1991; Simon and Toft, 1991; Lima and Moreira, 1993). However, most of these studies have focused on one or two species (Lynch, 1985 is an exception). Consequently, little is know about change in diet with ontogeny in multi-species assemblages. However, the selection for prey size is not independent of selection for prey type because different types of arthropods have different mean sizes. The smallest arthropods available for anurans and lizards are principally mites and collembolans. The most abundant arthropods of intermediate sizes are ants, termites, and beetles, and the largest arthropods are orthopterans, butterflies, and spiders (Schoener and Janzen, 1968; Dominguez and Salvador, 1990; Lima and Moreira, 1993). Therefore, variation in the taxonomic composition of the diet with the stage of growth of individuals is expected as a passive side effect of the capacity to ingest larger prey. Lima and Moreira (1993) demonstrated that the shift in prey types with growth was not just a passive effect of selection for larger prey in the leaf-litter frog, *Colostethus stepheni*. For that species, there was a strong relationship between electivity for prey types and frog size, independent of electivities for prey size.

To test whether size-independent shifts in electivity are a general phenomenon in leaf-litter frogs or are restricted to *C. stepheni*, I studied the diet of postmetamorphic individuals of six species of diurnal leaf-litter frogs that occur syntopically with *C. stepheni* in Reserva Florestal Adolpho Ducke in Central Amazônia.

MATERIALS AND METHODS

Study Area and Distribution of the Species.—The study was conducted in a 10,000-ha tropical rainforest reserve, Reserva Florestal Adolfo Ducke (Reserva Ducke), located 25 km northeast of Manaus, Amazonas, Brazil (03°08'S;