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A NEW AMAZONIAN SPECIES OF *COLOSTETHUS* WITH SKY BLUE DIGITS

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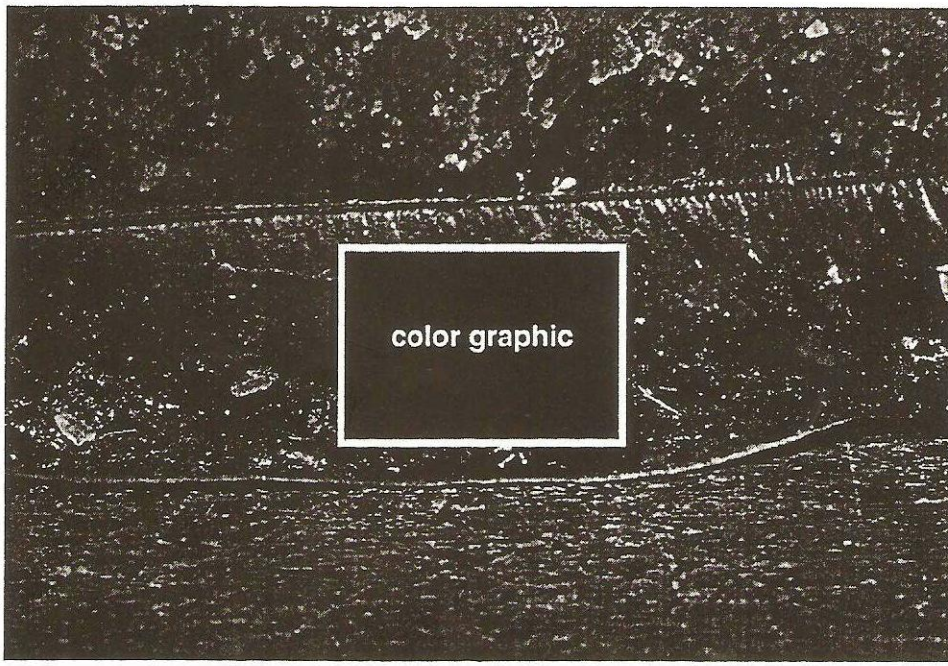
ABSTRACT: We describe a new species of *Colostethus* that is unusual in that males have blue digits on the hands and blue toe discs; females have blue discs on the fingers and toes but lack blue digits. The new species occurs in lowland tropical rainforest south of Manaus, Amazonas, Brazil, in the municipality of Careiro, at km 12 on the road to Autazes. Six species of *Colostethus* occur in the vicinity of Manaus; two, *C. stepheni* and *C. marchesianus*, occur north of the Amazon River, and four, including the new species and three undescribed species, occur south of the river. Four of these six species have small body size; i.e., adult male SVLs are ≤18.0 mm. Two of the species, both undescribed, from south of the Amazon have adult male SVLs ≥19.5 mm. Calls of all six species are unique; calls are produced either continuously, as in the case of the new species, *C. marchesianus*, and one of the large undescribed species south of the Amazon river, or in bouts of varying lengths. The function of the blue digits in males of the new species is unknown but may be associated with visual communication during reproductive behavior. Blue toes or discs were present only in adults during the breeding season.

Key words: Anura; *Colostethus*; Dendrobatidae; Breeding coloration; Vocalization; New species; Amazon rainforest; Amazonas; Brazil; Visual communication; *Colostethus caeruleodactylus* new species

The genus *Colostethus* as currently recognized consists of 99 small ground-dwelling species that inhabit the leaf litter of Neotropical forests (Frost, 1999). These frogs are cryptically colored with shades of brown; many are similar in appearance and difficult to identify (Duellman and Simmons, 1988). Although much remains to be learned about the systematics of dendrobatid frogs, most workers think that the species of *Colostethus* (sensu lato) comprise the basal portion in Dendrobatidae (Coloma, 1995; Grant et al., 1997). The derived clades in this family, for example, *Phyllobates*, *Minyobates*, and *Dendrobates*, differ from *Colostethus* in having mostly brilliant-colored species that have toxic alkaloids in their skin (Daly et al., 1987; Myers, 1987; Myers et al., 1991).

The genus *Colostethus* occurs on the islands of Martinique and Tobago and from southern Nicaragua south to northern Bolivia and southeastern Brazil. The greatest diversity of this group is in the Andean regions of Colombia, Ecuador, and Peru (Duellman, 1999). In a recent review of *Colostethus* in Ecuador, Coloma (1995) recognized 31 species in that country, five of which were new. As further indication of the number of unknown species in this genus, Coloma (1995) reported a total of 92 described species, whereas Frost (1985) listed 63 described species. Thus, 29 new species were described in a 10-yr period from 1985 to 1995.

Colostethus is an abundant leaf-litter frog of Amazonian lowland rainforests. Until recently, Amazonian forests were thought to be homogenous over large areas, harboring relatively few species within various clades of frogs, including *Colostethus* (Caldwell, 1996). In recent years, the complexity of the Amazonian forests has been recognized (Tuomisto et al., 1995), and, similarly, many species of frogs once thought to extend throughout the Amazon basin have been recognized as species complexes (Heyer et al., 1996). Amazonian Brazil will undoubtedly prove to have more species of *Colostethus* than now recognized.



crop most background from around frog.

FIG. 1.—A male *Colostethus caeruleodactylus*, showing sky blue fingers and discs. Photo by W. E. Magnusson.

During field work in the municipality of Careiro, along the road to Autazes at km 12, in Amazonas, Brazil, one of us (A. P. Lima) discovered a locality in which seven species of dendrobatids, including four apparently undescribed species of *Colostethus*, were found. Herein, we describe one of these species that is patterned like many other *Colostethus*, with the exception of having sky blue fingers and discs on the hand and similarly colored toe discs (Fig. 1).

MATERIALS AND METHODS

All specimens of the new species and those used for comparison in this paper were deposited in the herpetology collection of the Instituto Nacional de Pesquisas da Amazonia (INPA) in Manaus, Brazil, and in the Oklahoma Museum of Natural History (OMNH). Specimens were initially fixed in 10% formalin and subsequently transferred to 70% ethanol for permanent storage. Measurements (in mm) of preserved specimens were made with digital calipers or with a micrometer on a dissecting microscope. Measurements were taken in the same manner as described in Duellman and Simmons (1988), with the exception that head width was measured at the level of the angle of the jaws. Color in life was taken from field notes of A. P. Lima. Calls were recorded using a Sony WM-D6C tape recorder and analyzed using version 1.2.1 of Canary, a sound analysis program from the Cornell Laboratory of Ornithology. We have followed the format used by Duellman and Simmons (1988) with slight modification by Coloma (1995) for presentation of the character states of the new species.

SPECIES DESCRIPTION

Colostethus ***caeruleodactylus*** sp. nov.

Holotype.—INPA 7238, an adult male, collected by Albertina P. Lima on 1 May 1998, from approximately 40 km S Manaus, elevation 50 m, Amazonas, Brazil (3°

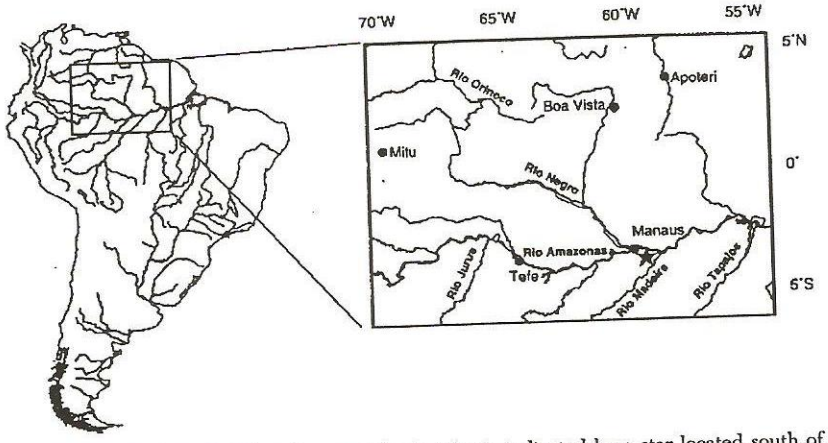


FIG. 2.—The type locality of *Colostethus caeruleodactylus* is indicated by a star located south of the city of Manaus.

37′ 10.4″ S, 59° 86′ 78.4″ W), in the municipality of Careiro, at km 12 on road to Autazes, in leaf litter in lowland terra firme forest (Fig. 2).

Paratypes.—Males, INPA 7229–32, INPA 7234–35, OMNH 35837–40, OMNH 35842–43; females, INPA 7236–37, OMNH 35841, OMNH 35844. All paratypes were collected at the type locality by Albertina P. Lima on 20 April and 1 May 1998.

Diagnosis.—Fifteen characteristics were defined by Duellman and Simmons (1988) and modified slightly by Coloma (1995) as useful in diagnosing species of *Colostethus*. These characters in *C. caeruleodactylus* are: (1) small size; mean (±SE) SVL of 12 adult males was 15.5 ± 0.4 mm (range 15.0–16.3 mm); mean SVL of five adult females was 16.1 ± 0.6 mm (range 15.4–16.8 mm); (2) disc on Finger III slightly wider than width of finger; (3) Finger I slightly longer than Finger II; (4) lateral fringes on fingers absent; (5) disc on Toe IV wider than width of digit, but not greatly expanded; (6) fringes on toes absent; (7) outer metatarsal fold absent; (8) basal webbing on foot only between Toes II and III and between III and IV; webbing formula II2–3 ¾III2 ½–3 ¾IV; (9) dorsolateral stripe absent or very diffuse; (10) oblique lateral stripe diffuse, barely visible, and restricted to the inguinal area; (11) no definite ventrolateral stripe, but white irregular blotches present ventrolaterally from snout to middle of body; (12) throat usually unpigmented but may have a few faintly pigmented areas; females with less dark pigment on chin or upper chest than males; (13) belly immaculate in both sexes; (14) Finger III of adult male not swollen; (15) testes white.

Three additional characters that have been useful in diagnosing other species of *Colostethus* are absent in *C. caeruleodactylus*: enlarged recurved teeth on the maxillary and premaxillary (Myers et al., 1991); black band on the forearm (Grant and Castro, 1998); and the medial lingual process (Grant et al., 1997).

In addition to *C. caeruleodactylus*, five other species of *Colostethus* are known from the vicinity of Manaus; two occur north of the Amazon River and three, like *C. caeruleodactylus*, occur south of the river. Three of the species, like *C. caeruleodactylus*, are small species, defined as male SVL ≤ 18.0 mm, and two have male body size ≥ 18.0 mm. Of these five species, two are described and three are not.

All six species in the vicinity of Manaus have distinct calls (our personal observations). Data on the calls of the two described species, *C. stephani* and *C. marchesianus*, are presented and compared with *C. caeruleodactylus* in Table 1. Fur-

TABLE 1.—Call characteristics of three species of *Colostethus* in the vicinity of Manaus, Amazonas, Brazil. Data for *C. marchesianus* and *C. stepheni* taken from the literature. Calls cont. = Calls continuous.

Species	Mean male size (mm)	Calls cont.	No. calls/min.	No. notes/call	Frequency (kHz)	Mean call duration (s)	Note duration (s)
C. caeruleodactylus	15.5	Yes	150.0	1	5.54–6.64	0.062	0.062
C. stepheni[1]	15.9	No	—	7–9	3.7–4.5	0.350	0.02
C. marchesianus[2]	18.0	Yes	360	1	4.5–7.0	—	—

[1] Data from Martins (1989).
[2] Data from Juncá (1998), advertisement call 2, described as emitted during territorial advertisement, courtship, and antagonistic interactions.

ther data on the calls and morphology of the three undescribed species will not be presented here.

The two described species, *C. stepheni* and *C. marchesianus*, are small species that occur north of the Amazon River in the Manaus region; *C. caeruleodactylus*, which occurs south of the river, does not overlap in distribution with these two species and the Amazon River most likely affords an effective barrier. In comparison, however, *C. caeruleodactylus* differs from *C. stephani* in that the latter has a complete oblique lateral stripe (referred to as a dorsal stripe in Martins, 1989), a dark brown granular dorsum, and lateral fringes on Finger III; further, reproductive males have a swollen third finger. The calls of *C. stephani* and *C. caeruleodactylus* are distinct (Table 1). From *C. marchesianus*, *C. caeruleodactylus* differs in life by having blue digits on the hand and blue discs on the toes in males, and blue discs on the fingers and toes of females. In preservative, the blue coloration of the fingers of the male changes but is distinct from all other body surfaces by being dark gray; under a microscope, evenly spaced light areas are surrounded by a dark gray interstitium. The calls of *C. marchesianus* and *C. caeruleodactylus* are distinct (Table 1).

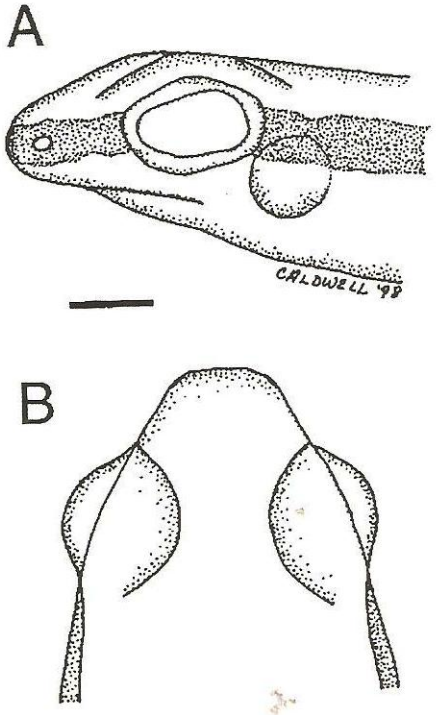


FIG. 3.—*Colostethus caeruleodactylus*. Head shape of holotype in (A) lateral view and (B) dorsal view. Scale bar = 1 mm.

Although not found at the type locality of *C. caeruleodactylus*, *C. brunneus* is widespread in the Amazon region (Frost, 1999). *Colostethus caeruleodactylus* differs from *C. brunneus* in that the latter is larger (mean ± SE SVL of five adult males was 18.2 ± 0.73 mm, range 15.5–19.7 mm; SVL of 24 females was 19.7 ± 0.17 mm, range 17.6–21.2), has an "hourglass" pattern on the back, which is never present in *C. caeruleodactylus*, and lacks blue digits or discs in life and dark gray digits in preserved males.

Description of the holotype.—An adult male, 15.0 mm SVL; body slender; head longer than wide; head length 44.8% of SVL; head width 33.6% of SVL; snout bluntly rounded in lateral view (Fig. 3A), truncate in dorsal view (Fig. 3B); loreal region flat; nostrils lateral, slightly protuberant, directed posterolaterally; canthus rostralis smoothly rounded, not obvious;

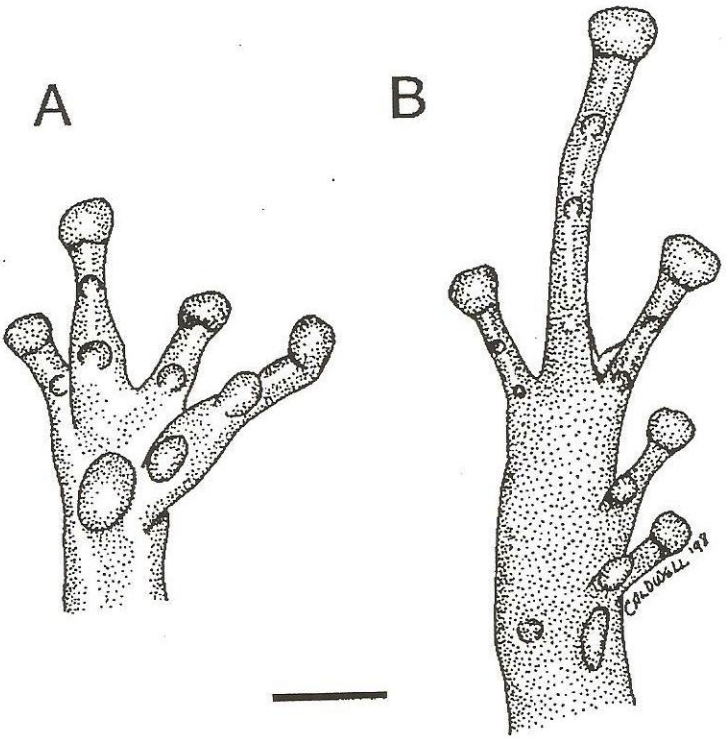


FIG. 4.—*Colostethus caeruleodactylus*. (A) Right hand and (B) right foot of holotype. Scale bar = 1 mm.

snout short; head broadly rounded from interorbital area to snout; internarial distance 41.6% of head width; eye–nostril distance 75.4% of eye length; slightly raised supratympanic fold, obscuring posterodorsal aspect of tympanum; anteroventral margin of tympanum distinct; tympanum nearly round, directed slightly posterolaterally, 47.3% of eye length; tympanum 0.3 mm from eye.

Choanae large, round; odontophores absent; tongue attached anteriorly, nearly twice as long as wide; lingual process absent (see Grant et al., 1997, for description of character); vocal sac and vocal slits present; premaxilla and maxilla with minute medially recurved teeth.

Skin of dorsum smooth with slightly raised round granules, more abundant on posterior one-half of dorsum; skin on upper surfaces of legs slightly granular; skin on belly slightly granular; anal opening directed posteriorly at level of upper thigh; skin on posteriomedial surfaces of thighs evenly granular; no enlarged warts near anus.

Forelimb slender, skin smooth, no ulnar fold; Finger I slightly longer than Finger II when fingers appressed; Finger III > I > II > IV; palmar tubercle nearly round, at least three times larger than oval thenar tubercle; no supernumerary tubercles; subarticular tubercles of Fingers II, III, and IV round, slightly raised; oval, raised subarticular tubercle of Finger I larger than others; fingers without distinct lateral fringe; Finger III not swollen, but slightly flattened and barely keeled; webbing between fingers absent; tips of digits expanded slightly, digits with cleavages along the dorsal midline; scutes present but inconspicuous (Fig. 4A).

Hind limbs stout; tibia length 47.4% of SVL; foot length 44.5% of SVL; no outer

metatarsal fold; inner tarsal fold weak, with a slightly raised, dark brown, curved protuberance located proximally one-third of distance from foot; this weak fold extends half-way to inner metatarsal tubercle; inner metatarsal tubercle elliptical, raised, length three times width, about twice as long as bluntly rounded conical outer metatarsal tubercle; supernumerary tubercles absent; subarticular tubercles small, round, those of Toes I and II largest; basal subarticular tubercle of Toe IV absent; tip of digits slightly expanded into pads; cleft along midline separates inconspicuous scutes atop digits; toes lack lateral fringes; slight webbing between Toes II and III and between III and IV only; relative length of toes: Toe IV > III > V > II > I (Fig. 4B).

Measurements (mm) of the holotype.—SVL 15.0, tibia length 7.1, foot length 6.7, head length 6.7, head width 5.1, tympanum length 1.0, eye length 2.0, eye–nostril distance 1.5, third finger disc 0.5, fourth toe disc 0.6.

Variation among type specimens.—All adult males with sky blue fingers, including discs, on the hand and sky blue toe discs on the foot in life; females have sky blue discs on fingers and toes. In females, the chin is white with only a small amount of pigment (appearing as stippling when magnified) around the distal edges of the chin. Males have predominantly white chins but vary from having no or only a small amount of pigment at the tip of the chin (six individuals) to slightly heavier stippled pigment in the center of the chin (six individuals). The bellies of all males and females are white with no pigmentation. The dark brown lateral stripe becomes diffuse in the groin to a greater degree in some individuals than in others.

The basal subarticular tubercle on the right foot is absent in 14 of 17 specimens. In two specimens, the tubercle is present on both the right and left feet, whereas in two others, it is present on one side but absent on the other. Mature ova in females are dark brown.

Measurements (mm), including mean followed by maximum and minimum size, of 12 males: SVL 15.5 (15.0–16.3); tibia length 7.2 (6.9–7.6); head length 6.5 (6.0–6.9); head width 5.2 (4.7–5.7); tympanum length 1.0 (0.9–1.1); eye length 2.2 (2.0–2.4); third finger disc 0.37 (0.30–0.45); fourth toe disc 0.52 (0.49–0.60). Same measurements of five females: SVL 16.1 (15.4–16.8); tibia length 7.5 (7.1–7.7); head length 6.6 (6.4–7.2); head width 5.2 (4.8–5.6); tympanum length 1.0 (0.9–1.1); eye length 2.2 (2.2–2.3); third finger disc 0.37 (0.34–0.42); fourth toe disc 0.56 (0.51–0.60).

Color in life.—Dorsum light brown with small darker brown granules; upper surfaces of legs same color as dorsum but lacking granules; no definite dorsolateral stripe; oblique lateral stripe present as a narrow diffuse area only in the groin region; no definite ventrolateral stripe, but irregular blotches of white pigment extend from snout to groin; throat, chest, and belly white; throat has small area of black stippled pigmentation at distal margin of chin; entire digits of hands sky blue; digits of feet brown with sky blue only on dorsal surfaces of discs. Dorsal part of iris of eye yellow with tiny black flecks; remainder of iris dark brown. Testes white.

Color in preservative.—Dorsum light brown with darker brown pustules; dark brown stripe extending from snout laterally to groin, becoming slightly diffuse at groin; diffuse, pale oblique lateral stripe only in groin; brown triangular area on anterior surface of proximal thigh; upper surfaces of legs brown; upper arm light brown, forearm light tan; posterior surfaces of thighs and shanks brown, without pattern; ventral surfaces including chin, venter, and upper arms white with small amount of black pigmentation at distal edge of chin; ventral surfaces of legs and forearms with slight pigmentation. In preservative, fingers, which are sky blue in life, are dark gray and distinct from all other body surfaces; under a microscope, evenly spaced tiny light circles are surrounded by a dark gray interstitium.

Call characteristics.—Males of *C. caeruleodactylus* have calls consisting of a single note produced at a constant rate for several minutes. The call of one frog from the type series was recorded (specific

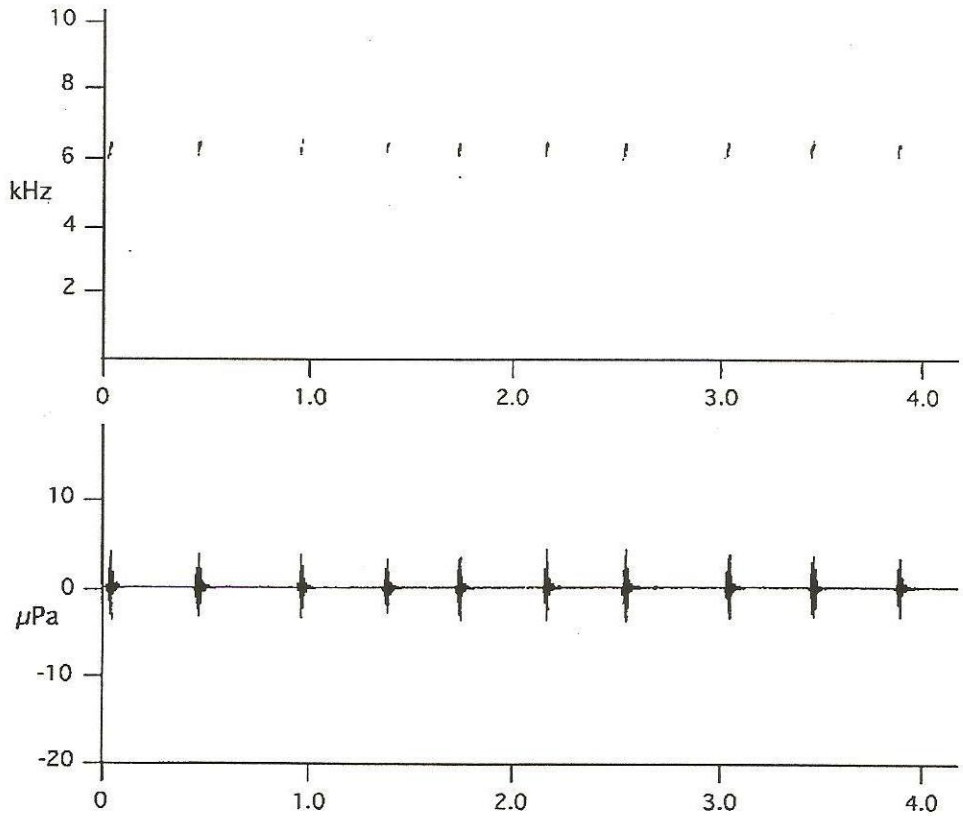


FIG. 5.—Sound spectrogram (upper panel) and waveform (lower panel) of the continuous call of *Colostethus caeruleodactylus*.

specimen number not available, Tape No. JPC 23, recorded by A. P. Lima); air temperature was 24 C. During a 5-min recording, the individual called for 3 min 55 s, paused for 5 s, then called again for 2 min 16 s (Fig. 5); some individuals have been observed to call for up to 15 min with only brief pauses (A. P. Lima, personal observation). In comparison, *C. marchesianus* also produces continuous calls, but at a faster rate, and *C. stepheni* produces calls in intermittent bouts (Table 1). Of the three undescribed, sympatric species of *Colostethus* south of the Amazon river, two produce bouts of calls, and the third produces continuous notes, but at a faster rate and lower frequency than *C. caeruleodactylus* (unpublished data).

Distribution.—The species is known only from the immediate type locality, which is a large (4 × 6 km) isolated forest fragment, bordered on the south by small farms and on the north by a large lake, Lago Tucunaré, which is fed by Rio Autaz Mirim. The locality is slightly disturbed primary lowland forest intersected by deeply cut stream beds. Trees of commercial value were removed and other trees with less commercial value were used for local construction projects. Although this selective logging has occurred, the forest retains a closed canopy, with temperature and moisture regimes similar to undisturbed forest (our personal observations).

Natural history.—The frogs were abundant while reproducing during the wet

season, particularly during April and May. Sporadic visits to the site throughout the year have indicated that the frogs are difficult to observe during the dry season, which extends from June to December or January, depending on the onset of the rainy season. During the wet season, males called from positions on tops of leaves in leaf litter, small twigs, or other short vegetation at ground level. Males called primarily in late afternoon from a distance of about 2 m apart. The frogs were observed on small hillsides near large flooded ravines that form throughout the forest as a result of rising water during the rainy season.

Etymology.—The name is derived from the Latin *caeruleus*, meaning sky blue, and the Greek *daktylos*, meaning finger. The name is in allusion to the sky blue digits of the male frog during the breeding season.

Discussion

Males of this species are unusual in having sky blue digits on the hand and on the dorsal discs of the fingers and toes. The blue color is sexually dimorphic; in males, all fingers, from base to tip, are blue (Fig. 1), whereas in females, only the discs of the digits are blue. Frogs encountered outside the breeding season (June, July, and August, which also is the dry season) and juveniles did not have blue digits; those observed in December and January as the first rains began, had pale blue digits.

The blue digits of the male are obvious when frogs are seen in the leaf litter. The function of the coloration is unknown at present, but because the blue fingers develop in males only during the breeding season, we hypothesize that the color may be used for sexual recognition. A number of species of frogs are known to use a combination of vocal and visual communication during reproduction (Haddad and Giaretta, 1999). Various species of frogs in several unrelated clades use the toes, feet, or legs in visual communication, and behaviors may include foot flagging, toe undulations, and leg extensions (Lindquist and Hetherington, 1996). A few species of dendrobatids are known to use some form of visual communication. Males of *Colostethus stepheni* guarding nests sway the body back and forth in response to intruding males (Juncá et al., 1994); territorial females of *Mannophryne trinitatis* pulsate their bright yellow throats as a warning to intruders (Wells, 1980); and *Epipedobates parvulus* performs leg-stretching displays (Wevers, 1988). Thus, visual displays are known in other dendrobatids, and it seems probable that the blue digits in *C. caeruleodactylus* function in some kind of visual display; however, further research is needed to ascertain the nature and context of the display.

Dendrobatidae is renowned for the brilliant coloration and poison skin of the derived genera, including some species in the genera *Epipedobates* and *Phyllobates*, and nearly all species in the genera *Minyobates* and *Dendrobates* (Myers, 1987; Myers and Daly, 1983). *Colostethus* and *Mannophryne* are two of the basal genera and include species with non-poisonous skin marked dorsally and laterally with shades of brown, dark brown, and white. Some species of *Mannophryne* have bright yellow throats; other species of *Colostethus* have yellow venters and/or orange to yellow dorsolateral stripes, in addition to other color and pattern variants (see Coloma, 1995, for color pattern examples). Although blue is common in some species of *Dendrobates* (e.g., *D. azureus*), we are not aware of other species of *Colostethus* that have sky blue digits and toe discs as in *C. caeruleodactylus*.

Resumo

Nós descrevemos uma espécie nova de *Colostethus* que é única porque os machos têm dedos azuis nas mãos e discos azuis nos dedos das mãos e pés. As fêmeas têm discos azuis nos dedos ds mãos e dos pés, mas seus dedos não são azuis. Esta espécie nova vive nas terras baixas de floresta amazônica ao sul de Manaus, Amazonas, Brasil, no município do Careiro, no Km 12 na estrada para Autazes. Cinco outras espécies de *Colostethus* vivem nas vizinhanças de Manaus: duas, *C. stepheni* e *C. marchesianus*, ocorrem ao norte do rio Amazonas, e quatro, incluindo a espécie nova

e três outras espécies ainda por descrever, ocorrem ao sul desse rio. Quatro destas seis espécies têm corpos pequenos: o comprimento da região anterior à região cloacal (CRAC) dos machos é inferior a 18,0 mm. Duas das espécies por descrever, ambas oriundas do sul do rio Amazonas, têm machos com um CRAC maior do que 19,5 mm. O coaxar de cada uma das seis espécies é único. Um coaxar pode ser emitido ou episodicamente, em episódios de duração variada, ou continuamente como no caso da espécie nova, no de *C. marchesianus* e no de uma das espécies maiores ainda por descrever do sul do rio Amazonas. A função dos dedos azuis dos machos é desconhecida, mas podem estar associados com comunicação visual durante o comportamento reprodutivo. A cor azul foi vista somente en adultos durante o período de reprodução, porém, nosso conhecimento é insuficiente para determinar em quais estágios de vida a espécie tem dedos azuis.

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Literature Cited

Coloma, L. A. 1995. Ecuadorian frogs of the genus *Colostethus* (Anura: Dendrobatidae). University of Kansas Natural History Museum, Miscellaneous Publication 87:1–72.

Caldwell, J. P. 1996. Diversity of Amazonian anurans: the role of systematics and phylogeny in identifying macroecological patterns. Pp. 73–88. *In* A. Gibson (Ed.), Neotropical Biodiversity and Conservation. Occasional Publication of the Mildred E. Mathias Botanical Garden, No. 1.

Daly, J. W., C. W. Myers, and N. Whittaker. 1987. Further classification of skin alkaloids from Neotropical poison frogs (Dendrobatidae), with a general survey of toxic/noxious substances in the Amphibia. Toxicon 25:1023–1095.

Duellman, W. E. 1999. Distribution patterns of amphibians in South America. Pp. 255–328. *In* W. E. Duellman (Ed.), Patterns of Distribution of Amphibinas: a Global Perspective. Johns Hopkins University Press, Baltimore, Maryland, U.S.A.

Duellman, W. E., and J. E. Simmons. 1988. Two new species of dendrobatid frogs, genus *Colostethus*, from the Cordillera del Cóndor, Ecuador. Proceedings of the Academy of Natural Sciences of Philadelphia 140:115–124.

Frost, D. R. (Ed.). 1985. Amphibian Species of the World. A Taxonomic and Geographical Reference. Allen Press and the Association of Systematics Collections, Lawrence, Kansas, U.S.A.

———. 1999. Amphibian Species of the World [on line]. Ver. 2.1. 15 November 1999. American Museum of Natural History, New York, New York, U.S.A. (http:/research.amnh.org/herpetology/amphibia/index.html)

Grant, T., and F. Castro. 1998. The cloud forest *Colostethus* (Anura, Dendrobatidae) of a region of the Cordillera Occidental of Colombia. Journal of Herpetology 32:378–392.

Grant, T., E. C. Humphrey, and C. W. Myers. 1997. The median lingual process of frogs: a bizarre character of Old World ranoids discovered in South American dendrobatids. American Museum Novitates 3212:1–40.

Haddad, C. F. B., and A. A. Giaretta. 1999. Visual and acoustic communication in the Brazilian torrent frog, *Hylodes asper* (Anura: Leptodactylidae). Herpetologica 55:324–333.

Heyer, W. R., J. M. Garcia-Lopez, and A. J. Cardoso. 1996. Advertisement call variation in the *Leptodactylus mystaceus* species complex (Amphibia: Leptodactylidae) with a description of new sibling species. Amphibia-Reptilia 17:7–31.

Juncá, F. A. 1996. Parental care and egg mortality in *Colostethus stepheni*. Journal of Herpetology 30: 292–294.

———. 1998. Reproductive biology of *Colostethus stepheni* and *Colostethus marchesianus* (Dendrobatidae), with the description of a new anuran mating behavior. Herpetologica 54:377–387.

Juncá, F. A., R. A. Altig, and C. Gascon. 1994. Breeding biology of *Colostethus stepheni*: a dendrobatid with a nontransported nidicolous tadpole. Copeia 1994:747–750.

Lindquist, E. D., and T. E. Heatherington. 1996. Field studies of visual and acoustic signaling in the "earless" Panamanian golden frog, *Atelopus zeteki*. Journal of Herpetology 30:347–354.

Martins, M. 1989. Nova especie de *Colostethus* da Amazonia central (Amphibia: Dendrobatidae). Revista Brasileira de Biologia 49:1009–1012.

Myers, C. W. 1987. New generic names for some Neotropical poison frogs (Dendrobatidae). Papéis Avulsos de Zoologia (São Paulo) 36:301–306.

Myers, C. W., and J. W. Daly. 1983. Dart-poison frogs. Scientific American 248:120–133.