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## Spotted Poison Frogs: Descriptions of Three New *Dendrobates* from Western Amazonia, and Resurrection of a Lost Species from “Chiriqui”

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### ABSTRACT

A color pattern of pale spots on a dark ground has independently arisen in several lineages of small dendrobatid frogs. Such a pattern seems to be autapomorphic in *Dendrobates maculatus* W. Peters, 1873, which has not been recognized as a valid taxon since its original description; it is here removed from the synonymy of the common *D. auratus*. The only known specimen of *maculatus* is the holotype that was collected over a century ago, purportedly in “Chiriqui,” which then included both Atlantic and Pacific sides of extreme western Panama. Except in color pattern, *D. maculatus* is a relatively plesiomorphic species that, unlike other Central American *Dendrobates*, retains maxillary teeth, finger 1 > 2, and vestigial foot webbing. Its closest relationships remain to be determined.

A pale-spotted pattern (yellow on black) also is autapomorphic in *Dendrobates vanzolinii*, new species, an easily recognized frog that occupies a fairly large range in east-central Peru and adjacent Brazil. Its range at least partly overlaps that of *D. quinquevittatus* Steindachner, 1864, and some specimens of *vanzolinii* have been recorded under that name. Although *D. quinquevittatus* is indeed a widespread and variable species, it is nonetheless a composite of at least five species as

currently recognized. *Dendrobates fantasticus* and *D. reticulatus*, both described by Boulenger (“1883” [1884]), have been wrongly placed in the synonymy of *quinquevittatus*.

A population sample assigned to *D. reticulatus* was obtained sympatrically with *D. quinquevittatus*; the specimens are readily distinguished by color pattern, body size, and size of hands and finger discs. A distinctive reticulated pattern on the limbs seemingly provides a synapomorphy that unites at least four Amazonian species, namely *quinquevittatus*, *fantasticus*, *reticulatus*, and *vanzolinii*, with the first species seeming to occur sympatrically with the last three. Color patterns are divergent in this monophyletic group, with *D. vanzolinii* being the only spotted species.

A fifth frog that has been mentioned in print under the name *quinquevittatus* is *Dendrobates captivus*, new species, which is known only from three specimens collected by Harvey Bassler in 1924 and 1929, at the mouth of the Río Santiago, 177 m. (upper Río Marañón), Department of Amazonas, Peru. *Dendrobates captivus* occurs sympatrically with *quinquevittatus*, from which it is easily distinguished by a lineate spotted pattern, nonreticulated limbs, and smaller hand. There is no demonstrably close relationship with

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the *quinquevittatus* group on the basis of present evidence.

The sister species of *captivus* may be *Dendrobates mysteriosus*, new species, from higher in the Marañón drainage (mountain forest NW mouth Río Chinchipe, 900 m. elev., Dept. Cajamarca, Peru). This species is known from only a single

specimen, also obtained by Harvey Bassler, in 1929. It differs from *captivus* in an irregular pattern of larger spots, larger size, and larger hand. Points of resemblance include similarly spotted thighs and well-developed first digits of hands and feet (as compared with *quinquevittatus*).

## INTRODUCTION

The four species of poison frogs described or redescribed in this paper share little in common except small size and color patterns of pale dorsal spots on a darker ground. This kind of color pattern is not common within the Dendrobatidae, even though the group is renowned for brilliant warning colorations. It might be expected that an unusual shared pattern would be indicative of close relationship, but the present patterns lack any detailed correspondence that would suggest homology. A pattern of pale spots seems to have been separately derived in at least three lineages among the four species treated herein, as follows:

1. *Dendrobates maculatus*: This century-old name must finally be recognized as belonging to a valid species, which presumably waits to be rediscovered somewhere in western Panama. I am unable at this time to demonstrate a close relationship with any other known dendrobatid. Unlike the other species to be discussed, *D. maculatus* retains the plesiomorphic characters of maxillary teeth, long first finger, and relatively small finger discs. Such characters at one time would have caused this species to be placed in the genus *Phyllobates*, which, however, has been redefined to include only the true poison-dart frogs (Myers, Daly, and Malkin, 1978, p. 331; Daly et al., 1980). *Dendrobates* is presently used as a "collective group," to include a mixture of plesiomorphic and apomorphic species whose phyletic relationships are still under study.

2. *Dendrobates vanzolinii*: Specimens of this new species have been confused with *D. quinquevittatus*, but the two seem to be sympatric in at least part of the range of *vanzolinii*, which appears to maintain its distinct

tive spotted pattern over many thousands of square kilometers in east-central Peru and adjacent Brazil. The two species probably are closely related, however. Together with two others (*D. fantasticus*, *D. reticulatus*), they share small size and distinctively reticulated limbs, with the latter character (fig. 1) serving as a recognizable synapomorphy that segregates these frogs into a monophyletic group, although the dorsal color patterns are quite divergent.

3–4. *Dendrobates captivus* and *D. mysteriosus*: These new species are known only from their type localities in the upper Marañón drainage of eastern Peru. Their seemingly allopatric distribution is consistent with the possibility that they are sister species, although the actual evidence for such a relationship is slight and in need of corroboration. The specimens on which the descriptions are based were obtained by Harvey Bassler in 1929, near the end of his extraordinary decade of exploration in Amazonian Peru. It is appropriate that he already is commemorated in the name *Dendrobates bassleri* Melin, otherwise it would be my greatest pleasure to rectify the situation at this time. The type specimens of *D. captivus* have been mentioned previously in the literature under the name *D. quinquevittatus*, which occurs sympatrically with *captivus*.

Before going on to the separate species accounts, it is pertinent to comment on the problem of *Dendrobates quinquevittatus*—a widespread Amazonian species of which the present paper constitutes a partial revision. Several *Dendrobates* undergo truly fantastic interpopulational variation in different characters, most noticeably those of color and color pattern. The very distinctiveness of

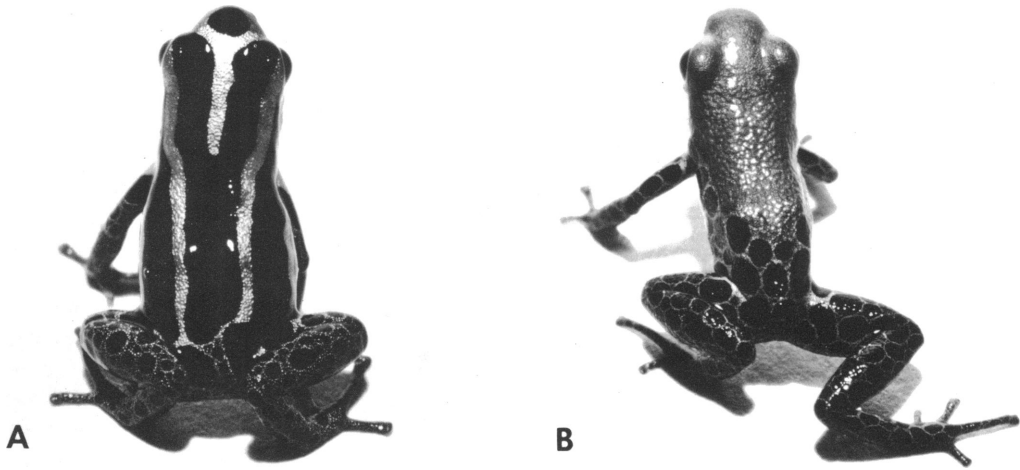


FIG. 1. A. *Dendrobates quinquevittatus* (AMNH 103608, adult ♂ 16.5 mm. SVL). B. *Dendrobates reticulatus* (AMNH 103638, adult ♀ 15.2 mm. SVL). Both from 3 km. SSW Mishana, 150 m. elev., Río Nanay drainage, Dept. Loreto, Peru. The pale reticulum on the limbs is considered to be a synapomorphy that unites these species with *D. fantasticus* and *D. vanzolinii*, new species (compare fig. 7A).

some populations can be a real “hindrance in judging whether they are in fact conspecific,” whereas uniquely colored “sibling species” may go unnamed for the same reason (Myers and Daly, 1976, p. 223). Silverstone (1975) was well aware that some species are highly variable, and so he was appropriately conservative in his recognition of taxa. However, it goes almost without saying that errors will be made in monographing such a difficult group. New material, as well as closer attention to morphological details and evidence of sympatry, convinces me that *Dendrobates quinquevittatus* Steindachner,<sup>2</sup> *sensu* Silverstone, is a

composite of five or more species of distinctively colored frogs. Two of these species (*D. captivus*, *D. vanzolinii*) are named herein. For a third, the name *Dendrobates reticulatus* Boulenger was recently resurrected in order to record the taxonomic distribution of a new skin toxin (alkaloid no. 247, Myers and Daly, 1980, pp. 20, 22). No

<sup>2</sup> Silverstone (1975, p. 33) credited “Fitzinger in Steindachner” as the author of this name. Inspection of the original description of *quinquevittatus* reveals that Steindachner (1864, pp. 260, 262, pl. 15, fig. 2) is the sole author of the name for nomenclatural purposes, since he alone is responsible for publishing the name and a validating illustration. Exactly the same situation pertains in the case of *Dendrobates galactonotus*, except that a specimen was actually described rather than illustrated under that name. Steindachner published both label names in the synonymy of *Dendrobates tinctorius*, but in the text he clearly recognizes them as

“Varietäten,” and the names *quinquevittatus* and *galactonotus* have always been legally available for that reason. Hoogmoed and Gorzula (1979, p. 189) reached the same conclusion concerning the authorship of *Dendrobates leucomelas*, a third valid species whose name was first published by Steindachner in the synonymy of *D. tinctorius*. The only difference is that Steindachner clearly regarded *leucomelas* as a synonym of the variety *auratus*, using the name “*Dendrobates tinctorius* var. *auratus*” (p. 288) for the illustration of a specimen generally regarded as the holotype of *D. leucomelas* (see Silverstone, 1975, p. 26). Of the aforesaid names, only *leucomelas* was first published as a true synonym, and it alone would have been unavailable for that reason under article 11(d), of the 1961 International Code of Zoological Nomenclature. Fortunately, article 11(d) was amended in the 1964 Code, and *leucomelas* is available for the reasons given by Silverstone (*loc. cit.*), but with corrected authorship.

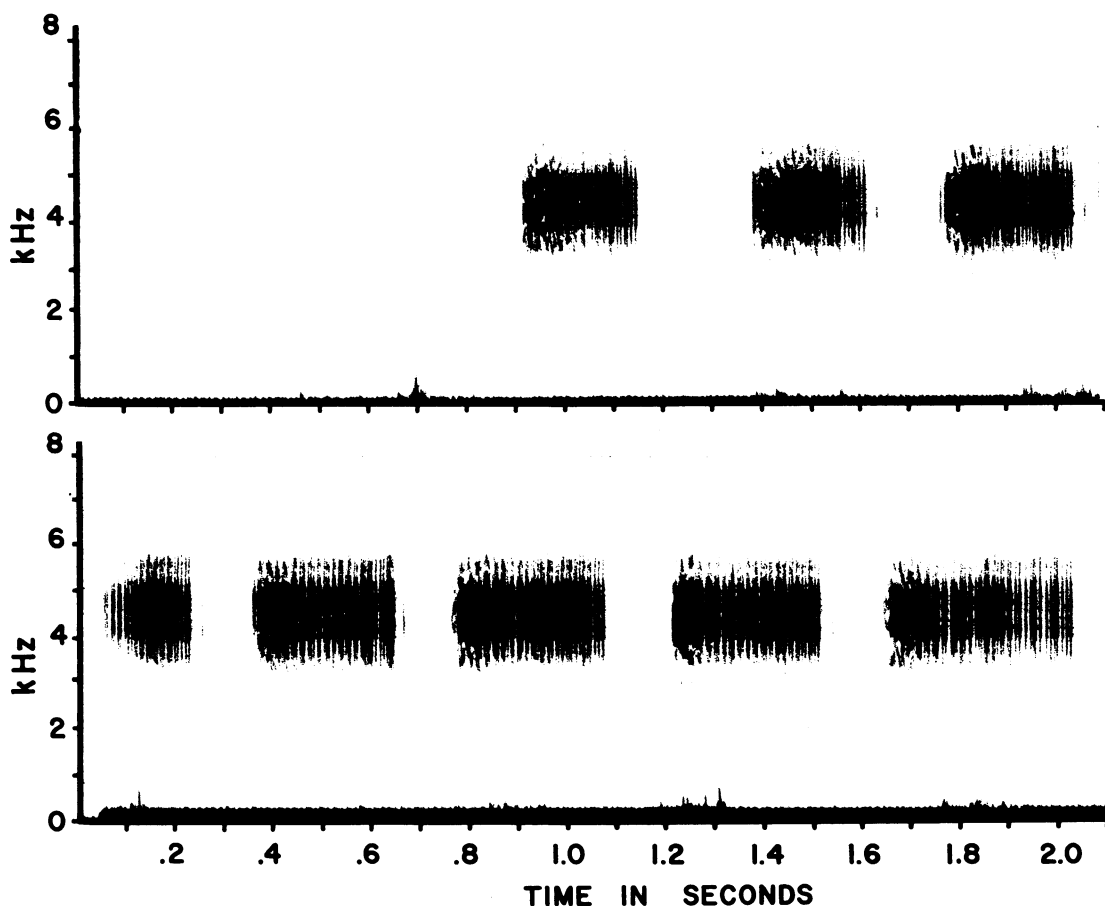


FIG. 2. Beginning (top) and end (bottom) of 7.4-seconds-long buzz call of *Dendrobates reticulatus*, from 3 km. SSW Mishana, Río Nanay, Loreto, Peru. Specimen (one of AMNH 103638–53) recorded calling from plastic bag, at 25.6° C., April 22, 1977 (wide-band, 300-Hz, spectrogram, from AMNH reel 210). The call is a long train of variably pulsed short buzzes of variable duration. This species lacks a vocal sac (at least in the Mishana population, with 41 adult males examined).

evidence was presented that *reticulatus* is a distinct species, and so I briefly diagnose it here. Pending reanalysis of the entire *quinquevittatus* complex, my use of the name *D. reticulatus* is based on Silverstone's comments on the type series of *reticulatus* and on his association of this name with a "*quinquevittatus*" pattern type in the Iquitos region (see Silverstone, 1975, p. 34, fig. 14A).

In 1977 John Daly and I obtained a sizable sample of *D. reticulatus* in rain forest 3 km. south-southwest of Mishana, Río Nanay

drainage (about 35 km. SSW Iquitos), Loreto, Peru (AMNH 103619–103673, 103704–103707 [nurse frogs with tadpoles]), and a smaller sample of *D. quinquevittatus* at the same locality (AMNH 103605–103615). There was no question of their distinctiveness, as intrapopulational variation in color patterns was relatively slight and certainly nonoverlapping. The specimens of *quinquevittatus* had metallic *golden orange* stripes on a black body, whereas *reticulatus* had the top of the head and back a bright metallic *reddish or*

ange (fig. 1), occasionally with a few black spots within this area. Each had a reticulum of pale blue over the limbs and venter, but the chin spot was golden yellow in *quinquevittatus* and reddish orange in *reticulatus*.<sup>3</sup> There are obvious differences in size:

*D. quinquevittatus* (Adult SVL in mm.)

6♂ 14.9–17.2,  $\bar{X} = 16.10 \pm 0.32$ ; 3♀ 16.0–18.4,  $\bar{X} = 17.47$

*D. reticulatus*

24♂ 13.7–14.9,  $\bar{X} = 14.37 \pm 0.07$ ; 29♀ 13.9–16.6,  $\bar{X} = 15.11 \pm 0.10$

*Dendrobates reticulatus* has absolutely smaller hands and finger discs than sympatric *quinquevittatus*, as is immediately apparent upon casual comparison. Relative difference in hand sizes is reflected in the ratio of hand length (from proximal edge of palmar tubercle to tip of longest finger)/greatest head width, as follows:

*D. quinquevittatus* (Adult Hand Length/Head Width)

0.81–0.92 ( $\bar{X} = 0.864$  in 5♂, 0.887 in 3♀)

*D. reticulatus*

0.67–0.83 ( $\bar{X} = 0.773 \pm 0.007$  in 23♂, 0.748  $\pm 0.007$  in 27♀)

The differences in hand size may be correlated with behavioral differences, as it was our impression that *reticulatus* is less of a climber than the large-handed *quinquevittatus*. Although *reticulatus* was seen up to two meters above ground on the sides of trees, individuals were not found sleeping in arboreal bromeliads, as were several specimens of *quinquevittatus*. Both species were heard to give buzz calls, although I was able to record only *reticulatus* at this locality (fig. 2). Interestingly, vocal slits are lacking in two of the six adult male *quinquevittatus* and in all the adult male *reticulatus* ( $N = 41$ , including 17 skinned carcasses not included in

measurements above). In some species (e.g., *D. bombetes* and *Phyllobates terribilis*), either the left or the right vocal slit not uncommonly fails to develop, but I have not previously noticed male dendrobatids that lack them entirely.

## REDESCRIPTION OF A LOST SPECIES FROM PANAMA

*Dendrobates maculatus* W. Peters,  
new combination

Figures 3, 4A

*Dendrobates trivittatus* (Spix) var. *maculata* W.

Peters, 1873, p. 617. Holotype: ZMB 7815, said to have been obtained by Moritz Wagner in "Chiriqui" [then including both Atlantic and Pacific versants of extreme western Panama].

*Dendrobates auratus* (not of Girard). Part (name in synonymy): Dunn, 1931, p. 393; 1941, p. 88. Savage, 1968, p. 759. Silverstone, 1975, p. 40.

**ETYMOLOGY:** The epithet *maculatus*, meaning "spotted," is the past participle of the Latin *maculo*. Peters rendered it "*maculata*" as a feminine modifier of the Latin for "variety."

**DEFINITION AND DIAGNOSIS:** A small dendrobatid (one adult female less than 20 mm. SVL). Body and limbs brown (?) with bright spots (yellow or red?), some about as large as eye; lacking stripes and probably lacking concealed flash marks. Teeth present. Fingers long, the appressed first finger slightly longer than second; finger discs only slightly expanded, less than 1.5 times finger width. Slight basal webbing between toes 2–4.

*Dendrobates maculatus* appears to be distinguishable from all other dendrobatids by its spotted color pattern in combination with small size and with the appressed first finger being at least as long as the second.

**MEASUREMENTS (IN MM.) OF HOLOTYPE:** The holotype (fig. 3) is an adult female as revealed by the presence of large ovarian ova. Length from snout to vent 18.9; tibia length from heel to fold of skin on knee 8.0; greatest width of body 7.0; greatest head width (between angles of jaws) 5.8; head width between edges upper eyelids 5.4; approximate width of interorbital area 2.0; head length from tip of snout to angle of jaw

<sup>3</sup> In no case is the chin spot enlarged to cover all the underside of the head, which, in addition to size and other differences, seems sufficient to separate *reticulatus* from *Dendrobates fantasticus* Boulenger, another name that should be removed from the synonymy of *D. quinquevittatus* (see Boulenger, "1883" [1884]; Silverstone, 1975, p. 32).



FIG. 3. *Dendrobates maculatus* W. Peters. Dorsal and ventral views of holotype (ZMB 7815) from "Chiriqui,"  $\times 2.9$ . It is the only known specimen, found over a century ago.

5.2; tip of snout to center of naris 0.7; center of naris to anterior edge of eye 1.6; distance between centers of nares 2.7; eye length from anterior to posterior edge 2.8; horizontal diameter of tympanum (posteriorly indistinct) about 1.2; corner of mouth to lower edge of tympanic ring 0.3; length from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger 4.6; width of disc of third finger 0.5; width of third finger (penultimate phalanx) below disc 0.4; width of discs of third and fourth toes both 0.6; width of third and fourth toes below discs both 0.4.

#### REDESCRIPTION OF HOLOTYPE

The type and only known specimen of *Dendrobates maculatus* is an adult female of 18.9 mm. SVL. Both sides of the lower jaw are broken, the left arm is broken at the elbow, and the carcass is a little soft. Otherwise, this century-old specimen is well preserved. An incision was made on the left side in order to examine a gonad (=mature

ovary), but the specimen is otherwise undissected. Premaxillary and maxillary teeth are present, the latter extending posteriorly only to the level of the choanae.

The skin is smooth overall (but skin granulation of dendrobatids is sometimes lost in preservative). The habitus is typical of many dendrobatids: Body somewhat wider than head (body width overemphasized in fig. 3, showing specimen pressed under glass). Head width greatest between angles of jaws, but distance between outer edges of upper eyelids nearly as great (see Measurements). Greatest head width 83 percent of greatest body width and 31 percent of SVL. Snout sloping, rounded in lateral profile, slightly truncate in dorsal or ventral aspect. Nares situated near tip of snout and directed posterolaterally; both nares visible from front and from below but not from above. Canthus rostralis rounded; loreal region seemingly vertical and flat (although snout region somewhat pliant due to long preservation). Inter-

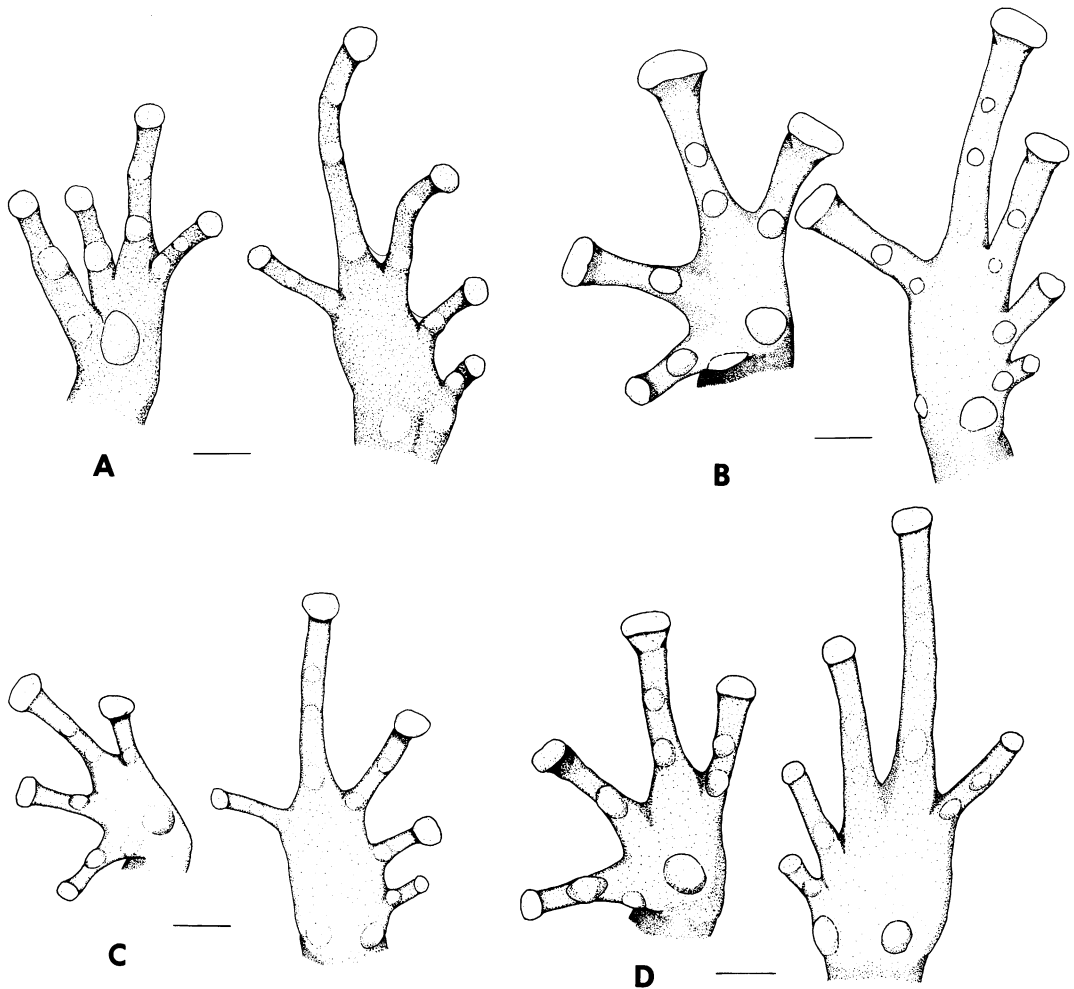


FIG. 4. Left hands and right feet (left foot in D) of holotypes, drawn to same scale (lines = 1 mm.). A. *Dendrobates maculatus* (adult ♀ 18.9 mm. SVL); note plesiomorphic features of long first finger and vestigial webbing between toes 2–3 and 3–4. B. *Dendrobates vanzolinii* (adult ♂ 17.5 mm. SVL). C. *Dendrobates captivus* (adult ♂ 15.4 mm. SVL). D. *Dendrobates mysteriosus* (subadult ♀ 17.6 mm. SVL).

orbital area wider than upper eyelid. Length of snout shorter than eye length (snout/eye = 0.82; center naris–edge eye/eye = 0.57). Tympanum circular, its area less than 50 percent of eye, concealed posterodorsally.

Relative length of appressed fingers  $3 > 1 > 2 > 4$ ; all digits relatively long (fig. 4A); fingers 1, 2, and 4 nearly equal when appressed, with disc of second finger overlap-

ping that of first and disc of fourth reaching disc of first; third finger distinctly longer. Finger discs expanded very slightly, with disc of third being 1.25 times wider than distal end of adjacent phalanx. A large elliptical outer metacarpal tubercle on median base of palm, a smaller inner metacarpal tubercle on base of first finger, and one or two subarticular tubercles on fingers (one each on fingers 1, 2, and two each on fingers 3, 4); some

tubercles poorly defined, all low, with rounded surfaces (fig. 4A).

Hind limbs of moderate length, with heel of appressed limb reaching eye; tibia 42 percent of SVL. Relative lengths of appressed toes  $4 > 3 > 5 > 2 > 1$ ; first toe short, reaching base of subarticular tubercle of second toe, and with barely expanded disc; other toes with distinct, slightly expanded discs (slightly larger than finger discs), those on third and fourth toes 1.50 times wider than adjacent phalanges. Small, low and rounded, inner and outer metatarsal tubercles. One to three nonprotuberant subarticular tubercles (one each on toes 1, 2, two each on 3, 5, and three on 4), some being poorly defined. A low, obliquely aligned tubercle on middle of tarsus (no tarsal ridge between tarsal tubercle and inner metatarsal tubercle). Hands and feet lacking supernumerary tubercles and lateral fringe—but slight basal webbing present between toes 2–3 and 3–4 (fig. 4A).

Dorsal ground color of body and limbs is a faded brown (perhaps medium or dark brown in life, although the possibility of a reddish hue cannot be discounted). Several dozen pale spots<sup>4</sup> are scattered dorsally and laterally over body and limbs and atop the head (fig. 3). These spots vary from roughly one-fourth of eye size to about the same size as the eye; many are edged in brown of a darker hue than the intervening ground color and were presumably dark-rimmed also in life.

The venter is a very pale brown, turning medium brown (less faded?) on the chin. The broken lower jaw is deflected downward, creasing the base of the throat and thus con-

cealing a transverse dark brown marking between throat and chest; although this marking resembles one found normally in some *Colostethus*, it is likely the result of differential fading (other areas concealed from light, i.e., axillae and creases behind knees, are also a relatively dark, unfaded brown). In keeping with the original description (fn. 4), there is an indication of a few large pale spots on the undersides of the thighs and a vague suggestion that there was at least one pale spot or blotch on the belly. There are no concealed flash marks in axillae or on the hind limbs, nor is there any discernible mark in the now faded groin region.

#### DISCUSSION

*Dendrobates maculatus* is defined by a suite of mainly plesiomorphic characters, including first finger longer than second, digital discs barely expanded, basal toe webbing present, and teeth present. None of these character states has been previously noted for a recognized species of *Dendrobates* in Central America. I have therefore entertained an uneasy thought that "Chiriqui" might be an erroneous locality, particularly since the collector (Moritz Wagner) was also placed in Amazonian Ecuador as the collector of *Phyllobates chalcus* (from "Pastasathal" *vide* Peters, 1873, p. 609). However, *Dendrobates maculatus* does not seem particularly close to known South American dendrobatids, which would not be surprising if it were an early isolate in Central America. Furthermore, Moritz Wagner certainly traveled in western Panama, as evidenced by his own writings (Wagner, 1863a, 1863b, 1863c).

The only other *Dendrobates* having toe webbing are the species of Silverstone's (1976) "*Phyllobates*" *femoralis* group, which occur in Amazonia and in the adjacent Pacific drainage from Peru north to western Colombia. But, if the vestigial webbing is plesiomorphic, as thought, it is of no help in corroborating a relationship, and, for that matter, the autapomorphic color pattern of *D. maculatus* is of no help either (members of the *femoralis* group tend to be primitively striped; none has a spotted body). Data obtained from the holotype seem only to con-

<sup>4</sup> The pale spots were golden yellow over a century ago, but it is not clear whether this color was noted from life or from the preserved specimen. The spots were said to be present ventrally as well as dorsally; the ground color was not mentioned. The original description of the holotype (Peters, 1873) is brief enough to be given in full: "Der erste Finger ist, wie bei den typischen Exemplaren, etwas länger als der zweite. Oben und unten mit mehr oder weniger zahlreichen goldgelben Flecken gezeichnet." By "typischen Exemplaren," Peters meant specimens of *Dendrobates trivittatus*, of which, for reasons unknown to me, he considered *maculatus* a variety.



firm that *Dendrobates maculatus* is a distinct species, with relationships yet to be determined.

Some dendrobatids have extremely small geographic ranges, which, together with secretive or arboreal habits in some cases, is likely to hinder discovery or rediscovery. *Dendrobates maculatus*, if not extinct, presumably waits to be rediscovered in some small area of western Panama. The general type locality "Chiriquí" was a province extending from coast to coast across western Panama, a region that nowadays is divided between the provinces of Bocas del Toro on the Atlantic watershed and Chiriquí on the Pacific side. The former remains largely in lowland and montane rain forest, whereas the less extensive evergreen seasonal forests have long been extensively disturbed on the Pacific side. Some areas of Pacific forest seem to have been cleared completely within the last half century, and we cannot know what endemic species may have been lost.

E. R. Dunn (1931, p. 393; 1941), who is thought to have examined the holotype in Berlin, placed *maculatus* in the synonymy of *Dendrobates auratus*, where it was maintained by Savage (1968, p. 759) and Silverstone (1975, p. 40), although the latter obviously thought that there must be an error either in the original description of *maculatus* or in Dunn's assignment. Indeed, confusion between actual specimens of the small *maculatus* and the large *auratus*, which have very differently proportioned hands, would be unexpected. Dunn, however, was familiar with central Panamanian populations of *auratus* characterized by rounded green spots (vs. the more usual bands or blotches) on a dark ground. If he examined the faded holotype of *D. maculatus* only casually through a bottle, he might have mistaken it for a spotted juvenile *auratus*.

#### DESCRIPTIONS OF THREE NEW SPECIES FROM AMAZONIA

##### *Dendrobates vanzolinii*, new species Figures 4B, 5-7A

*Dendrobates quinquevittatus*, not of Steindachner. Part: Silverstone, 1975, pp. 33-35 ("pat-

tern 3'" [part], TNHC specimens from Dept. Huánuco, Peru, and USNM 166756 from Dept. Pasco, Peru), figs. 12D (ventral body pattern of TNHC 36488), 14E (dorsal body pattern of TNHC 36499).

**HOLOTYPE:** Museu de Zoologia Universidade de São Paulo (MZUSP) 51597, an adult male obtained by Paulo E. Vanzolini and Miguel Petrere, Jr., January 15-20, 1979, at Pôrto Walter on the Rio Juruá, Territory of Acre, Brazil (8°16' S, 72°46' W).

**PARATYPES:** A total of 11 specimens. **BRAZIL:** *Acre:* MZUSP 51595, 51596 (now = AMNH 108332), 51598-51600, with same data as holotype. **PERU:** *Huánuco:* TNHC 36485, 36488, 36499 from Río Pachitea, Bosque Nacional de Iparia (J. P. and J. E. Bogart, Dec. 1967 and Jan. 1968). *Loreto:* AMNH 43597-43598, from mouth of Río Sepahua, a tributary of the Río Urubama, 11°12' S, 72°58' W (Harvey Bassler, Feb. 3, 1929). *Pasco:* USNM 166756 from Tsioventeni, 4200 ft. [about 1280 m. on divide between Río Ucayali and headwaters Río Pachitea, about 10°35' S, 74°23' W] (Asa C. Thoresen, June 20, 1968).

**ETYMOLOGY:** The species is named after Dr. Paulo E. Vanzolini, seasoned traveler on the rivers of Amazonia and one of the collectors of the holotype and paratopotypes.

**DEFINITION AND DIAGNOSIS:** A small dendrobatid having an adult snout to vent length of about 16-19 mm. Body black, dorsally with pale rounded or elongated spots with diameters smaller than eye (spots yellow in life, at least in some populations); ventrally with larger irregular pale areas; limbs with fine, pale reticulum. Teeth absent. Appressed first finger much shorter than second; finger discs very conspicuous, enlarged in adults to at least twice finger width.

The spotted dorsum distinguishes *Dendrobates vanzolinii* from other small dendrobatids having similar hand structure and reticulated limbs. Such species presently recognized (*D. quinquevittatus*, *D. fantasticus*, *D. reticulatus*) have lineate, reticulate, or cross-lined dorsa, or head and upper back uniformly colored.

**MEASUREMENTS (IN MM.) OF HOLOTYPE:** The undissected holotype (fig. 5) is an adult

male as determined by the presence of vocal slits. Length from snout to vent 17.5; tibia length from heel to fold of skin on knee 7.3; greatest width of body 8.1; greatest head width (between angles of jaws) 6.0; head width between edges upper eyelids 5.8; approximate width of interorbital area 2.5; head length from tip of snout to angle of jaw 5.0; tip of snout to center of naris 0.6; center of naris to anterior corner of eye 1.7; distance between centers of nares 2.3; eye length from anterior to posterior corner 2.2; horizontal diameter of tympanum (posteriorly indistinct) about 0.8; corner of mouth to lower edge tympanic ring 0.7; length from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger 5.4; width of disc of third finger 1.2; width of third finger (penultimate phalanx) below disc 0.6; width of disc of third toe 0.7; width of third toe (penultimate phalanx) below disc 0.5; width of disc of fourth toe 1.0; width of fourth toe below disc 0.6.

#### DESCRIPTION

Size small, snout-vent length (SVL) of adults 16.7–19.0 mm. (three males 16.7–18.8 mm.; six females 16.8–19.0 mm.). Widest part of head between jaw articulations, but distance between outer edges upper eyelids nearly as great (to <0.5 mm.) in some individuals. Head narrower than body, with greatest head width 70–88 percent of greatest body width in five well-preserved adults from type locality (96% in one paratopotypic juvenile 11.7 mm. SVL). Greatest head width 30–36 percent of SVL in adults (39–40% in three juveniles 11.3–15 mm. SVL). Adult males with well-developed vocal slits, but little or no external indication of the shallow subgular vocal sac. Teeth absent.

Skin in preservative varying from nearly smooth to weakly granular, especially on lower back and thighs; usually strongly and coarsely granular on belly and undersides of thighs. Snout sloping, rounded or obtuse in lateral profile, bluntly rounded to truncate in dorsal or ventral aspect. Naris situated near tip of snout and directed laterally; both nares visible from front and from below but not

from above. Canthus rostralis rounded; loreal region vertical and flat or slightly concave. Interorbital area wider than upper eyelid. Snout more or less equal to eye length; center of naris–edge of eye/eye length = 0.70–0.78 in five adults from type locality (0.61 in one juvenile). Tympanum seemingly either circular or vertically elliptical, but concealed posterodorsally; its area less than 50 percent that of eye.

Hand relatively large (fig. 4B), its length (proximal edge metacarpal tubercle to tip longest finger) in adults being 76–90 percent of greatest head width (hand length/head width:  $\bar{X}$  = 0.848 in three males, 0.834 in six females); smaller in juveniles (Hand/HW = 0.69, 0.74 in juveniles 11.3 and 11.7 mm. SVL). Relative length of appressed fingers  $3 > 4 > 2 > 1$ ; appressed first finger roughly three-fourths the length of second finger. Discs conspicuously expanded on all but first finger. In adults, disc of third finger 2.00–2.50 times wider than distal end of adjacent phalanx, without apparent sexual dimorphism in the type series (expanded 2.00–2.50 times finger,  $\bar{X}$  = 2.300, in three males; 2.17–2.33,  $\bar{X}$  = 2.260 in six females). Discs relatively less expanded in one juvenile (11.7 mm. SVL), whose third finger disc is only 1.75 times wider than end of adjacent phalanx, but two other juveniles (11.3, 15.0 mm. SVL) have discs expanded 2.33–2.50 times finger width. A large circular outer metacarpal tubercle on median base of palm, a smaller inner metacarpal tubercle on base of first finger, and one or two usually prominent subarticular tubercles on fingers (one each on fingers 1, 2, one or two on finger 4, two on finger 3). Distal subarticular tubercles on fingers 3 and especially 4 may be small and inconspicuous, but all other tubercles on hand prominently raised albeit with rounded surfaces; lack of pigment contributes to prominent appearance of tubercles (fig. 4B).

Hind limbs of moderate length, with heel of appressed limb reaching tympanum or eye. Tibia 38–47 percent of SVL, averaging slightly longer in males (42–47%,  $\bar{X}$  = 43.7% in three males; 38–43%,  $\bar{X}$  = 41.0% in six females). Relative lengths of appressed toes  $4 > 3 > 5 > 2 > 1$ ; first toe short, reaching

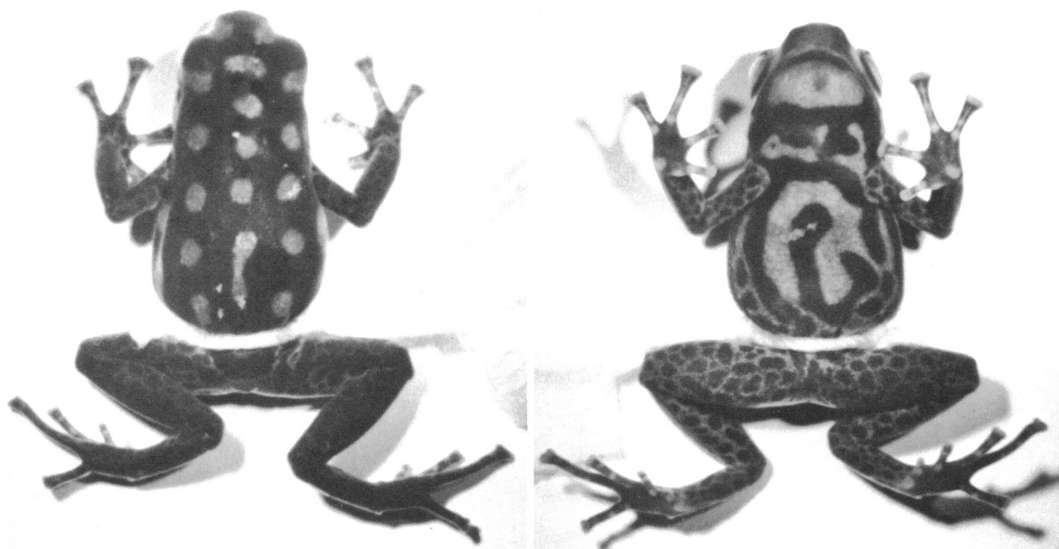


FIG. 5. *Dendrobates vanzolinii*, new species. Dorsal and ventral views of holotype (MZUSP 51597),  $\times 2.9$ .

bottom of subarticular tubercle on base of second toe, and with unexpanded disc; other toes with discs distinctly expanded (but noticeably smaller than finger discs). Moderate-sized inner and small outer metatarsal tubercles, somewhat protuberant but with rounded surfaces. One to three slightly protuberant subarticular tubercles (one each on toes 1, 2, two each on 3 and 5, three on 4), these being small but usually prominent (especially prominent on toes 1, 2, and 5). An obliquely aligned, uniformly low but usually prominent tarsal ridge, extending along the distal one-half to one-third of tarsus to the inner metatarsal tubercle. Hands and feet lacking webbing, supernumerary tubercles, or lateral fringe (fig. 4B).

In life, paratypes of *Dendrobates vanzolinii* from Río Sepahua, Peru, had "lemon yellow spots on black field" (H. Bassler's note for AMNH 43597–43598). The paratype from Tsioventeni, Peru, similarly had golden yellow spots on a deep black body (A. C. Thoresen's color transparency of USNM 166756, shown here in fig. 7A). In preservative, these and a few other specimens have

a brown color, but more recently collected specimens (from type locality) retain an overall black ground color on the body and limbs. There are about 15–24 pale spots atop the head and back plus several additional spots along each side; one (TNHC 36488) has several interconnected pale lines on the sides, in place of spots. Most of the pale spots are as large as or larger than the tympanum but smaller than the eye; most specimens have a few pairs of spots that are bridged by pale lines, forming short, randomly placed stripes which may be aligned in any direction (fig. 6).

The arms and legs are encircled by a network of pale bluish gray or very pale brown, giving an appearance of round black or brown spots on a pale ground. Thoresen's color transparency of the paratype from Tsioventeni (fig. 7A) shows that in life its limb spots were black in a reticulum of pale blue.<sup>5</sup> The pale network, or reticulum, ex-

<sup>5</sup> In life, there is interpopulational variation in the color of the limb reticulation of the related *Dendrobates quinquevittatus*, for which I have recorded blue, yellow,

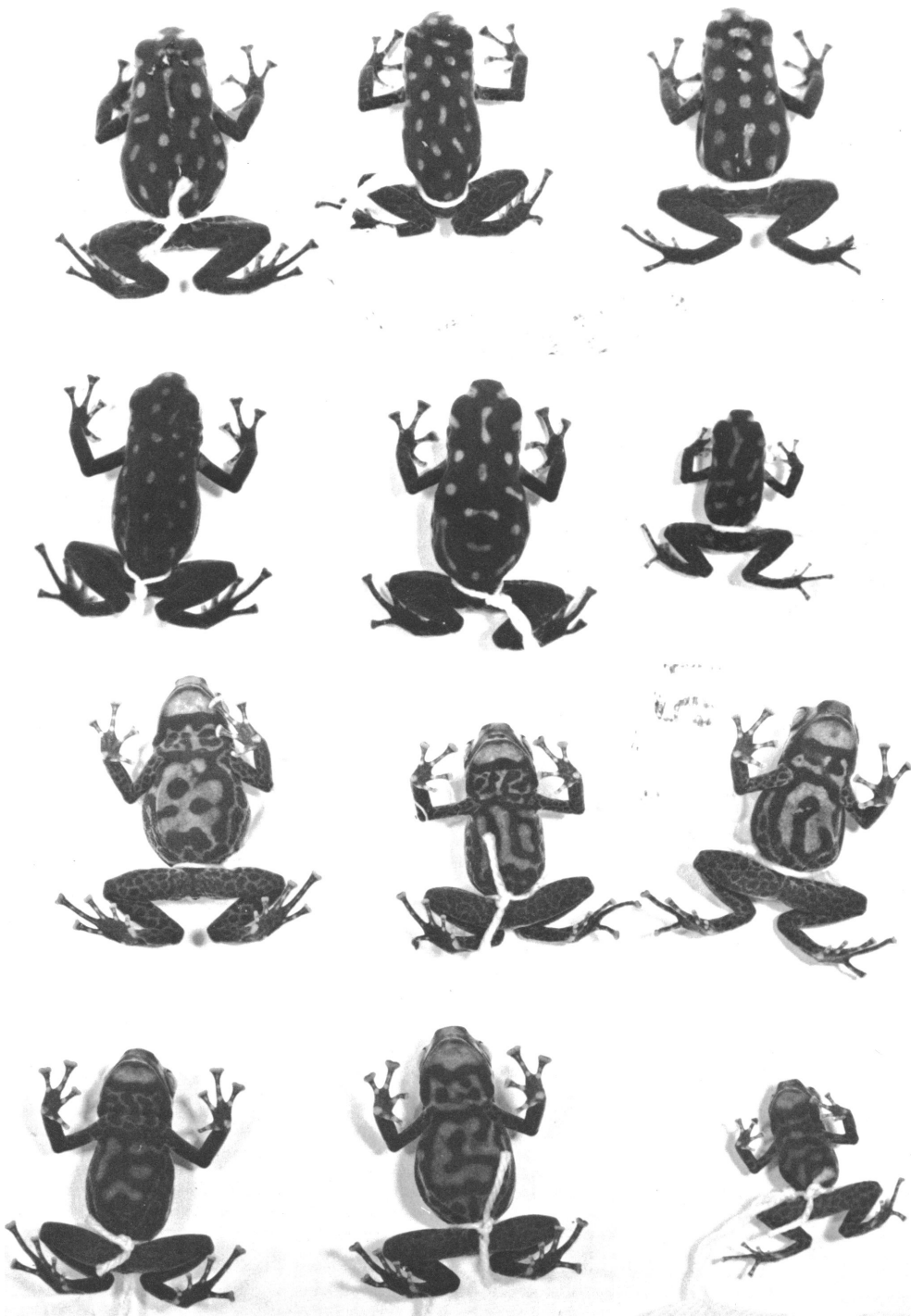


FIG. 6. *Dendrobates vanzolinii*, new species. Variation in color pattern of specimens from type locality (Pôrto Walter, Rio Juruá, Brazil). Dorsal and ventral views of same specimens: Top rows, left to right, MZUSP 51595, 51596 (now AMNH 108332), 51597. Bottom rows, MZUSP 51598–51600.

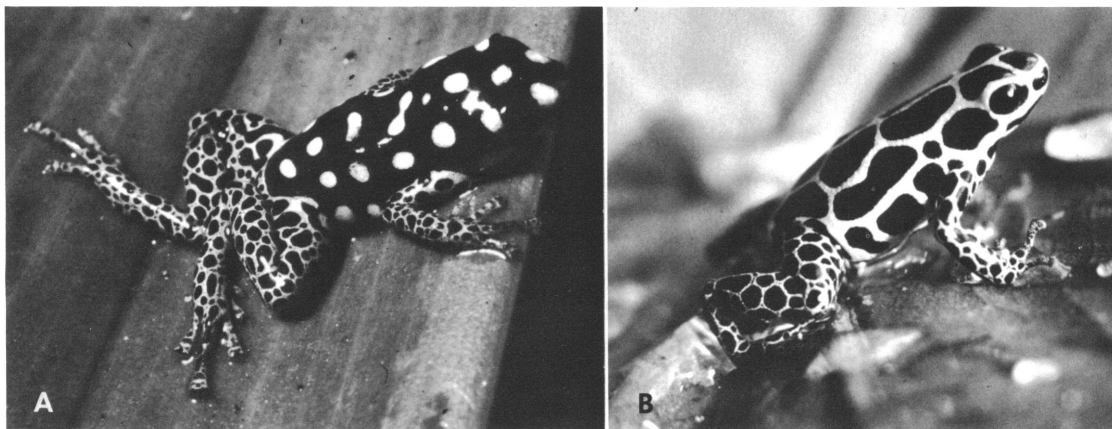


FIG. 7. A. *Dendrobates vanzolinii*, new species (USNM 166756, juvenile ♂ 15.0 mm. SVL) from Tsioventeni, 1280 m. elev., Peru. B. *Dendrobates quinquevittatus* (USNM 166767, adult ♀ 18.9 mm. SVL) from Santa Isabella, about 370 m., upper Río Neguachi (Nevati) below Tsioventeni. Not to scale. From color transparencies made in June–July 1968, courtesy of Asa C. Thoresen.

tends even onto the tops of the digits and onto the palms and soles of some individuals. Proximally, the reticulum may encroach slightly onto the body in the groin region.

Ventrally, the head and body are black or brown with pale bluish white (in preservative) markings: All specimens have a large pale marking across the chin.<sup>6</sup> Some specimens have a pale reticulum across the chest and base of the throat, whereas others have a few pale lines or blotches in this area. The belly is highly variable, with either interconnected or discrete pale blotches.

#### DISCUSSION

*Dendrobates vanzolinii* occurs in east-central Peru and adjacent Brazil, in the upper drainages of the Ucayali and Juruá rivers. The several known localities in Peru and one

green, and bronze. The color appears to have been pale bronze in a specimen found geographically close to the Tsioventeni paratype (Thoresen's transparency of *D. quinquevittatus* from Sta. Isabella, fig. 7B).

<sup>6</sup> Extrapolating from *Dendrobates quinquevittatus* and *D. reticulatus*, the pale chin marking of *D. vanzolinii* in life may be expected to match the bright dorsal markings, yellow in this case and in *quinquevittatus* (red in *reticulatus*), whereas the pale areas of the belly seem likely to be pale blue (as in both *quinquevittatus* and *reticulatus*).

in Brazil are scattered over a north-south distance of about 320 km., in an area bounded by parallels 8° and 12° South, and meridians 72° and 75° West. This is a lowland forest distribution, except for one record of nearly 1300 m. elevation at Tsioventeni on the divide between the upper Río Ucayali and the headwaters (Río Neguachi) of its tributary, the Río Pachitea, to the west.

*Dendrobates vanzolinii* seems to be broadly sympatric with *D. quinquevittatus*, at least in the Río Pachitea drainage, but they have yet to be found at the same locality. Figure 7 shows specimens that were taken within 50 km. of each other. The similarly patterned limbs are an indication of close relationship, and I predict that *vanzolinii* will be found to have a "buzz call" (Myers and Daly, 1976, p. 226) as do its presumed relatives *quinquevittatus* and *reticulatus* (fig. 2). I also would expect that the skin alkaloids of *D. vanzolinii* will prove to be a mixture mainly of pumiliotoxins (A and C classes) and histrionicotoxins (Daly et al., 1978), as in recently analyzed samples from *D. quinquevittatus* and *D. reticulatus* (unpubl. data).

*Dendrobates vanzolinii* seems to be generally larger than *quinquevittatus*, and to have a somewhat larger hand, but adequate

comparisons cannot be made without first analyzing geographic variation in the latter species. Silverstone's (1975) data are useless because he included at least five species under the name *D. quinquevittatus*.

Although the total sample is small, *Dendrobates vanzolinii* maintains its characteristic dorsal pattern at localities hundreds of kilometers apart, in an elevational range of about 1200 meters. This is Silverstone's (1975) *quinquevittatus* "pattern 3," in part. There is no real approach to the lineate or reticulate dorsal patterns of *quinquevittatus*, despite Silverstone's (1975, p. 34) mention of "transitional patterns." His perception of a transition was based on specimens of *Dendrobates captivus*, named herein (see fig. 9), and on specimens of a mainly cross-lined frog that occurs in the Huallaga and upper Marañón drainages of Andean Peru. I have not reached a conclusion on the status of the last group of frogs, except that they are quite distinct from *vanzolinii* (cf., figs. 14I–G in Silverstone, 1975).

With one exception, the several specimens that formed the basis of Silverstone's *quinquevittatus* "pattern 3" are included herein as paratypes of *D. vanzolinii*. That exception is Museum of Comparative Zoology no. 28061, a *quinquevittatus*-group frog from the Río Apaporis, Colombia; it is illustrated as figure 14F in Silverstone. This figure does look a little like his adjacent figure 14E, of a *vanzolinii* paratype, but the Colombian frog is inaccurately drawn. The artist unfortunately omitted a pale vertebral line that was still conspicuous on the specimen when I saw it in 1980.

#### ***Dendrobates captivus*, new species**

Figures 4C, 8–10

*Dendrobates quinquevittatus*, not of Steindachner. Part: Silverstone, 1975, p. 35 (only AMNH 42963 [cited in error under Dept. San Martín, Peru], 42970, 43491).

**HOLOTYPE:** AMNH 42963, an adult male obtained by Harvey Bassler (no. 316) in August, 1929, at the mouth of the Río Santiago, 580 feet (177 m.) elevation, Department of Amazonas, Peru. The Río Santiago

flows into the Río Marañón at about 4°26' S, 77°38' W.

**PARATYPES:** Two adult specimens from the type locality, as follows: AMNH 42970 (H. Bassler no. 426, August 1929, male), AMNH 43491 (H. Bassler no. 902, October 14, 1924,<sup>7</sup> female).

**ETYMOLOGY:** *Captivus* is a Latin adjective meaning captured, especially in the sense of having been taken in war (see fn. 9).

**DEFINITION AND DIAGNOSIS:** A very small dendrobatid, with at least some adults of both sexes maturing at less than 16 mm. SVL. Brown, with pale (yellow or red?) spots, some larger than eye; body spots above tending to be elongated and dorsolaterally aligned (like pair of broken stripes), ventral spots tending to be few and irregular; also a pale "axillary" spot proximally on upper arm, and a pale spot each on upper and underside of thigh, but no flash marks in groin or calf. Teeth absent. Appressed first finger shorter than second; finger discs conspicuous, enlarged about twice finger width.

A spotted dorsum, lack of pale reticulation on hind limbs and venter, and a smaller hand serve to distinguish *Dendrobates captivus* from *D. quinquevittatus*, which occurs sympatrically. *Dendrobates captivus* differs from *D. mysteriosus* and *D. vanzolinii* in having the pale body spots dorsolaterally aligned, and in having a smaller hand and apparently smaller body size; it also differs greatly from *vanzolinii* (but not from *mysteriosus*) in ventral and hind-limb color pattern.

**MEASUREMENTS (IN MM.) OF HOLOTYPE:** The undissected holotype (fig. 8) is an adult male as determined by the presence of well-developed vocal slits. Length from snout to vent 15.4; tibia length from heel to fold of skin on knee 7.0; greatest width of body 5.7; greatest head width (between angles of jaws) 5.1; head width between center edges upper

<sup>7</sup> Bassler assigned his own numbers to about 1700 Peruvian amphibians sometime before the collection was catalogued at the American Museum. Possibly his numbers were simply to facilitate the formal cataloguing, but in any case they were not assigned chronologically and are not original field numbers.

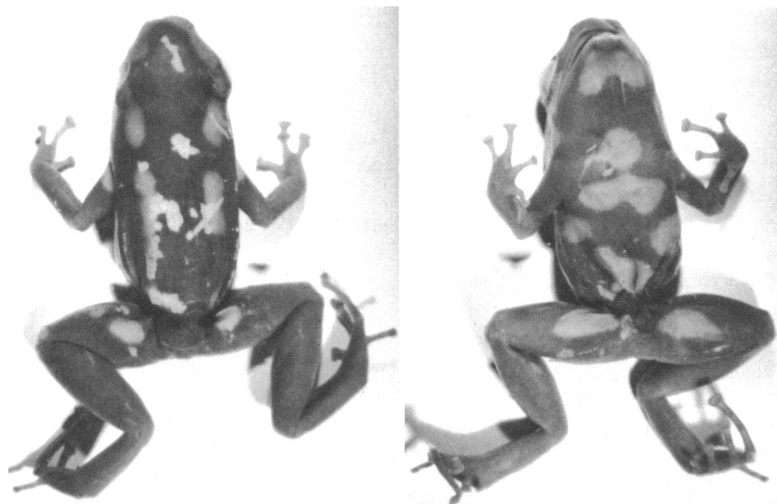


FIG. 8. *Dendrobates captivus*, new species. Dorsal and ventral views of holotype (AMNH 42963),  $\times 2.9$ . There are several abrasions, especially on the dorsum; see also figure 9 (left) for color pattern.

eyelids 4.7; approximate width of interorbital area 2.5; head length from tip of snout to angle of jaw 4.8; tip of snout to center of naris 0.4; center of naris to anterior corner of eye 1.5; distance between centers of nares 2.1; eye length from anterior to posterior corner 2.1; horizontal diameter of tympanum (posteriorly indistinct) about 0.9; corner of mouth to lower edge tympanic ring 0.5; length from proximal edge of medial palmar tubercle to tip of longest (3rd) finger 3.5; width of disc on third finger 0.7; width of third finger (penultimate phalanx) below disc 0.3; width of disc of third toe 0.6; width of toe (penultimate phalanx) below disc 0.3; width of disc of fourth toe 0.8; width of fourth toe below disc 0.4.

#### DESCRIPTION

Size very small ( $< 16$  mm.): two adult males (vocal slits open) 14.6 and 15.4 mm. SVL, one adult female (large ova present) 15.8 mm. SVL. Width of head between jaw articulations greater than (holotype), or equal (female paratype) to, distance between outer edges upper eyelids. Head narrower than body (90–97% of greatest body width). Greatest head width 33–35 percent of SVL. Adult males with large vocal slits, but no ex-

ternal indication of the shallow, subgular vocal sac. Teeth absent.

Skin essentially smooth in preservative. Snout sloping, rounded in lateral profile, truncate or slightly rounded in dorsal and ventral aspect. Naris situated near tip of snout, directed ventrolaterally; both nares visible from front and from below but not from above. Canthus rostralis rounded; loreal region nearly flat and nearly vertical, sloping slightly inward toward lip. Interorbital area more or less twice width of an upper eyelid. Snout shorter than eye length; center of naris–edge of eye/eye length = 0.65 in female, 0.71–0.75 in two males. Tympanum circular, concealed posterodorsally, no more than one-half size of eye.

Hand relatively small (fig. 4C), its length (from proximal edge metacarpal tubercle to tip of longest finger) being 65 percent of greatest head width in one adult female, 71–75 percent in two males. Relative lengths of appressed fingers  $3 > 4 \geq 2 > 1$ ; appressed first finger roughly three-fourths the length of second finger. Discs conspicuously expanded on all but first finger (slightly expanded). Disc of third finger 2.33 times wider than distal end of adjacent phalanx in male holotype (hands of paratypes desiccated). A circular outer metacarpal tubercle on median

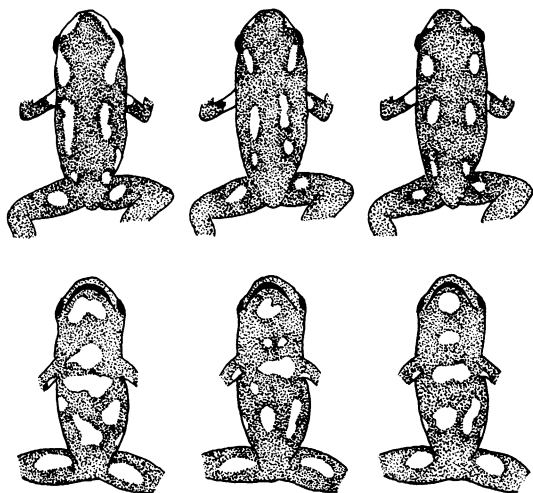


FIG. 9. *Dendrobates captivus*, new species. Variation in color pattern in the type series. From left to right, dorsal and ventral views of AMNH 42963♂ (holotype), 42970♂, 43491♀.

base of palm, a smaller inner metacarpal tubercle on base of first finger, and one or two subarticular tubercles on fingers (one each on fingers 1, 2, 4, two on finger 3); the tubercles are slightly to moderately raised swellings with rounded surfaces.

Hind limbs of moderate length, with heel of appressed limb reaching eye. Tibia 41 percent of SVL in female, 43–45 percent in two males. Relative lengths of appressed toes  $4 > 3 > 5 > 2 > 1$ ; first toe well defined, reaching middle or top of subarticular tubercle on base of second toe, but with barely expanded disc. Discs of toes 2–4 distinctly expanded (nearly as wide as those on figures). Small inner and outer metatarsal tubercles, rounded and slightly protuberant. One to three low subarticular tubercles (one each on toes 1, 2, two on 3, 5, three on 4), these being poorly developed. Tarsal ridge absent (or at least not clearly discernible on types). Hands and feet lacking webbing, supernumerary tubercles, or lateral fringe (fig. 4C).

The ground color in preservative is medium-dark brown, with white spots that tend to be regularly placed, at least in the three specimens at hand (fig. 9). Starting on the canthus rostralis and continuing down the body behind each eye is a series of rounded

to elongated spots (which might be perceived as a pair of very broken dorsolateral stripes). There is a pale spot atop each thigh. Laterally, there is a pale marking between the lip and posterior half of the eye, a spot below and slightly behind the tympanum (this spot may be absent or poorly defined on one side), and a small to fairly large, rounded or elongated spot on the flanks. Also, there is an axillary “flash marking” that is positioned proximally on the posterodorsal part of the arm. Ventrally (bottom fig. 9), there is a chin spot, several spots on the venter, and one on the underside of each thigh. The limbs turn lighter brown distally, without evident markings.

#### DISCUSSION

*Dendrobates captivus* is known only from three specimens obtained by Harvey Bassler at the mouth of the Río Santiago, in 1924 and 1929. In each year, Bassler had established a base camp on the west bank of the Santiago at its junction with the Río Marañón; the elevation of that camp, as marked on one of his 1924 survey maps, is 580 feet (177 m.).

The Río Santiago lies immediately behind (west of) the Cerros de Campanquis (or Campanquiz), the Andean front range that sharply delimits this part of the western edge of the Amazonian basin. These mountains, according to Bassler’s reckoning (MSa, MSb) rise somewhat abruptly to a height of 700 to 800 m. above the Amazonian plain. The Río Marañón at this point cuts a deep, narrow canyon known as the Pongo de Manseriche. Bassler noted that, although water depth may exceed 30 m., the “Pongo is so narrow and has so many rapids and whirlpools that it is passable only during the dry season, and for this reason . . . the lower entrance is usually shown upon maps as the head of navigation on the Río Marañón.” Although the Río Santiago is navigable to small steamers for a considerable distance, the Marañón is not navigable by launches above the mouth of the Santiago because of shallow rapids.<sup>8</sup>

<sup>8</sup> This point marked the beginning of the “Alto Marañón” to Bassler, although his localities so qualified mostly lie still farther upriver, especially in the long stretch between the tributaries Cenipe and Chinchipe.



Bassler (MSa, MSb) described the lower valley of the Río Santiago as a level plain interrupted by occasional isolated hills rising 150 to 250 m. above the plain. He concluded that this valley had peneplained owing to the resistance of rocks comprising the "Manse-riche" (Campanquis) Range, which restricts the torrential Santiago-Alto Marañón drainage to a narrow canyon. The lower Santiago Valley was extensively forested and essentially uninhabited in the 1920s, although the rivers served as highways for Indians traveling on their own affairs.<sup>9</sup>

Silverstone (1975) included the three type specimens of *Dendrobates captivus* in his account of *D. quinquevittatus*, believing them to be transitional between his *quinquevittatus* "patterns 1 and 3" (see discussion under *D. vanzolinii*). However, the specimens do represent a species different from *quinquevittatus*; I can find no evidence even of close relationship between these species in the material at hand. *Dendrobates captivus* lacks the distinctive limb reticulation that I view as a synapomorphy uniting *D. quinquevittatus*, *D. fantasticus*, *D. reticulatus*, and *D. vanzolinii*.

The linear spotted pattern of the type specimens seems to separate *D. captivus* from other dendrobatids characterized by small size and a short first finger. It occurs sympatrically with *D. quinquevittatus* as shown by a specimen of the latter taken by Bassler at the mouth of the Río Santiago (AMNH 43482); this individual, a small adult or subadult female (15.5 mm. SVL, ova enlarging), has characteristically patterned limbs and venter and a reticulate dorsal pattern somewhat similar to the frog shown in figure 7B.

*Dendrobates quinquevittatus* shows strong

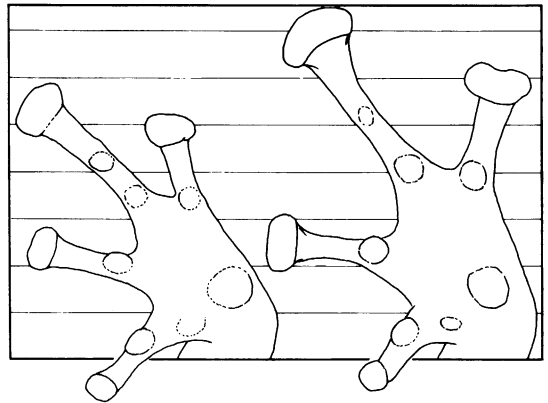


FIG. 10. Hands of similar-sized specimens of *Dendrobates captivus* (left) and *Dendrobates quinquevittatus* (right), both adult males. Notice that although *D. captivus* has a smaller hand, its first finger is actually longer. (Left, AMNH 42963♂ 15.4 mm. SVL, [holotype]. Right, AMNH 94107♂ 15.5 mm. SVL, from Cusuime, Ecuador.)

arboreal tendencies, at least in some populations. *D. captivus* probably is more terrestrial, judging from its relatively smaller hand and longer first finger. This can be seen by direct comparison of the hands of similar-sized specimens (fig. 10). It also is reflected in the ratio hand length (from proximal edge of palmar tubercle to tip of longest finger)/greatest head width, as follows:

#### HAND LENGTH/HEAD WIDTH (ADULTS ONLY)

*Dendrobates captivus* (mouth Río Santiago)

1♂, 0.69; 1♀, 0.58

*Dendrobates quinquevittatus* (Cusuime, Ecuador)

9♂, 0.76–0.90,  $\bar{X} = 0.824 \pm 0.015$ ;

16♀, 0.74–0.96,  $\bar{X} = 0.823 \pm 0.014$

The above sample of *quinquevittatus* (from the series AMNH 94089–94115) is from a locality about 200 km. north of the mouth of the Río Santiago. The single specimen of *quinquevittatus* from the Río Santiago locality has the ratio of hand length/head width = 0.83, which is close to the means of the more northern sample.

Based on the meager evidence of spotted patterns, and relatively well-defined first dig-

<sup>9</sup> Such affairs still included ritualistic but nonetheless bloody raids staged upon one another by Jivaro subgroups of the region. At the mouth of the Santiago in 1924, Bassler's party witnessed "a half dozen large canoes with a war party of Aguarunas passing the Base Camp returning from a raid upon the Huambisas." One of the dugouts contained two prisoners laid out in the bottom and covered over with a mat of palm leaf. These unfortunate souls are commemorated in the name *Dendrobates captivus*.

its on both hand and foot (compared with *quinquevittatus*), I suggest that *Dendrobates captivus* be considered as the probable sister species of *D. mysteriosus* (*q.v.*), a larger frog from higher in the Marañón drainage. The large pale spots on either the dorsal or especially the ventral surface of the thigh may provide a necessary synapomorphy in support of such a relationship, but it is difficult to make much of such characters without knowledge of their variation or appearance in life.

***Dendrobates mysteriosus*, new species**

Figures 4D, 11

**HOLOTYPE:** AMNH 55349, a subadult female obtained by Harvey Bassler in July 1929, in the vicinity of Santa Rosa, 3000 feet (~900 m.) elevation, upper Río Marañón drainage, Department of Cajamarca, Peru. The type locality lies in the hills northwest of the confluence of the Río Chinchipe with the Río Marañón, at about 5°22' S, 78°41' W (see Discussion and fig. 12).

**ETYMOLOGY:** The specific epithet is fabricated from the Latin *mysterium* (mystery) + the adjective-forming suffix *-osus* (abounding in or full of). The intended meaning of the name ("the mysterious *Dendrobates*") alludes to many unanswered questions about the very nature of this species.

**DEFINITION AND DIAGNOSIS:** Adult size probably small to moderate (i.e., <25 mm. SVL; one immature female = 17.6 mm. SVL). Body and limbs dorsally and ventrally with irregularly arranged pale spots, some larger than eye. Teeth absent. Appressed first finger shorter than second; finger discs at least moderately expanded (third finger disc 1.6× finger width in one immature female, probably greater in adults).

Only two other spotted *Dendrobates* are known in western Amazonia. The larger spots and lack of pale reticulation on the limbs distinguish this species from the smaller *D. vanzolinii*. Larger body size, relatively larger hand, and somewhat larger, more randomly placed spots seem sufficient to separate *Dendrobates mysteriosus* from *D. captivus*, which occurs lower in the same drainage system.

**MEASUREMENTS (IN MM.) OF HOLOTYPE:**

It is an immature female as revealed by uniformly tiny ovarian ova. Length from snout to vent 17.6; tibia length from heel to fold of skin on knee 7.5; greatest width of body 7.0; greatest head width (between angles of jaws) 5.8; head width between edges upper eyelids 5.6; approximate width of interorbital area 2.5; head length from tip of snout to angle of jaw 5.2; tip of snout to center of naris 0.5; center of naris to anterior edge of eye 1.7; distance between centers of nares 2.4; eye length from anterior to posterior corner 2.1; horizontal diameter of tympanum (posteriorly indistinct) about 1.1; corner of mouth to lower edge tympanic ring 0.6; length from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger 4.7; width of disc on third finger 0.8; width of third finger (penultimate phalanx) below disc 0.5; width of disc of third toe 0.6; width of third toe (penultimate phalanx) below disc 0.5; width of disc of fourth toe 0.7; width of fourth toe below disc 0.5.

**DESCRIPTION OF HOLOTYPE**

The unique specimen is a small frog (17.6 mm. SVL) in a fair state of preservation, although the color pattern is considerably faded after half a century in alcohol (fig. 11). I first noticed the specimen in the early 1970s while going through miscellaneous amphibians and reptiles that had been set aside years before for the use of Emmett Reid Dunn.<sup>10</sup> Prior to my examination, incisions had been made along both sides in an evident attempt to determine the sex; I found it necessary to open the specimen further and to remove most of the already shredded intestinal tract and the many food items filling the body cavity. The damaged gonads were then seen to be immature ovaries with undifferentiated ova. Nonetheless, the specimen seems to have the general habitus of an adult dendrobatid and might not have been far from mature size; in my judgment, it probably will prove to represent a rather small species of less than 25 mm. SVL. Teeth are lacking.

<sup>10</sup> Dunn died in 1956, before completing his revisionary studies of Central and South American dendrobatids.

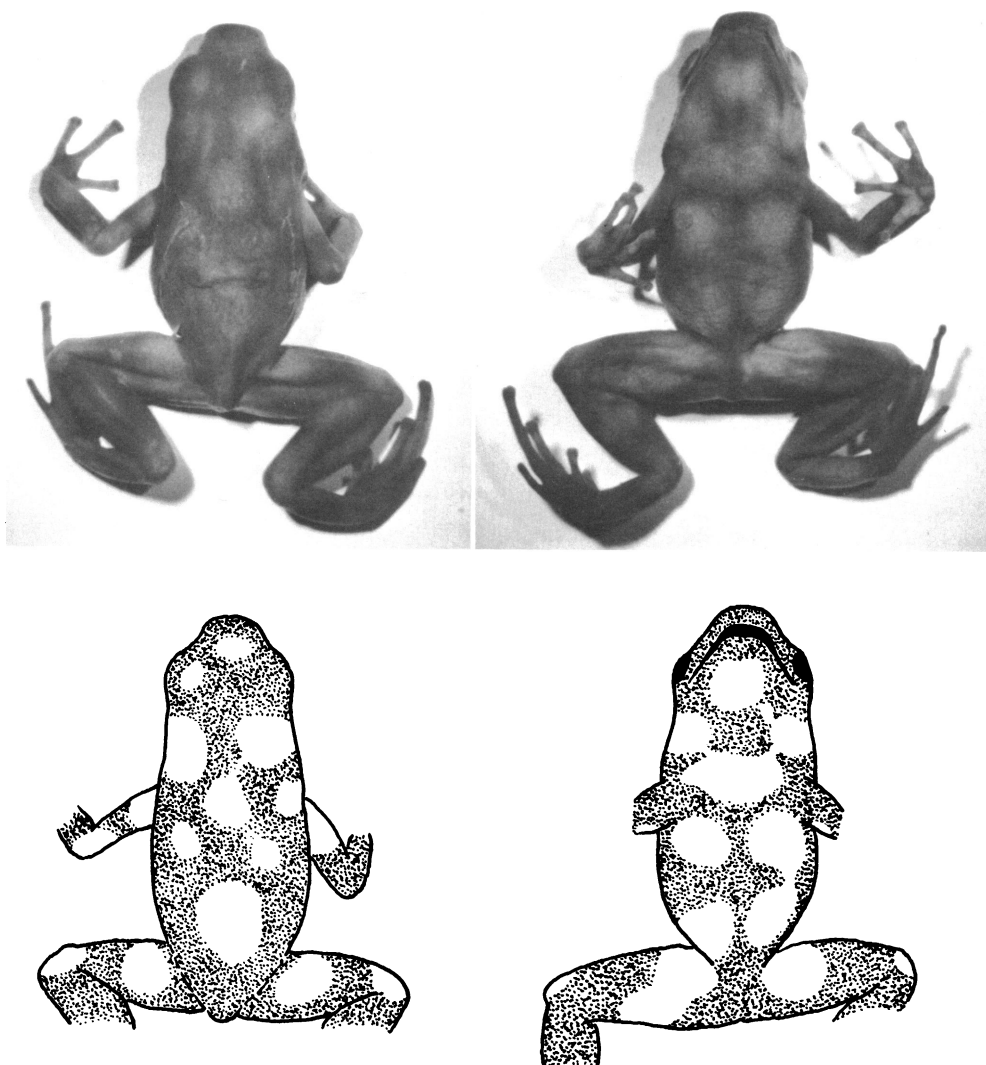


FIG. 11. *Dendrobates mysteriosus*, new species. Dorsal and ventral views of holotype (AMNH 55349), including drawings that emphasize the now-faded color pattern,  $\times 2.9$ .

The skin is nongranular on the dorsum and limbs but retains coarse granulation on the sides and venter. Body wider than head. Head width greatest between angles of jaws, but distance between outer edges of upper eyelids nearly as great (see Measurements). Greatest head width 83 percent of greatest body width and 33 percent of SVL. Snout sloping, obtuse in lateral profile, truncate in dorsal or ventral aspect. Nares situated near

tip of snout and directed ventrolaterally; both nares visible from front and below but not from above. Canthus rostralis rounded; loreal region vertical and slightly concave. Interorbital area wider than upper eyelid. Snout slightly longer than eye (eye/snout = 0.95; center naris–edge eye/eye = 0.81). Tympanum nearly circular, its area greater than 50 percent of eye, concealed postero-dorsally.

Hand relatively large (fig. 4D), its length (proximal edge metacarpal tubercle to tip longest finger) being 81 percent of greatest head width. Relative lengths of appressed fingers  $3 > 4 > 2 > 1$ ; appressed first finger about three-fourths the length of second finger, its disc not approaching that of second. Finger discs moderately expanded, with disc of third finger being 1.60 times wider than distal end of adjacent phalanx. A large, nearly circular outer metacarpal tubercle on median base of palm, a small inner metacarpal tubercle on base of first finger, and one or two prominent subarticular tubercles (one each on fingers 1, 2, and two each on fingers 3, 4); all the tubercles are well defined, moderately raised swellings with rounded surfaces.

Hind limbs of moderate length, with heel of appressed limb reaching tympanum; tibia 43 percent of SVL. Relative lengths of appressed toes  $4 > 3 > 5 > 2 > 1$ ; first toe well defined, reaching subarticular tubercle of second toe, and with slightly expanded disc. Discs of toes 2–4 also slightly expanded (smaller than finger discs), those on toes 3 and 4 being 1.20 and 1.40 times wider than adjacent phalanges. Small inner and outer metatarsal tubercles, rounded and slightly protuberant. One to three nonprotuberant subarticular tubercles (one each on toes 1, 2, two each on 3, 5, and three on 4), all rather poorly defined. Tarsal ridge and/or tubercle not definitely present (nor definitely absent—an originally weak tarsal keel might have been obliterated due to slight desiccation of the skin). Hands and feet lacking webbing, supernumerary tubercles, or lateral fringe (fig. 4D).

Although the holotype of *Dendrobates mysteriosus* is faded after some 50 years in alcohol, the color pattern is still discernible and can be reconstructed with reasonable assurance (fig. 11). Body and limbs are dull brown with a dorsal and ventral pattern of variable-sized, irregularly arranged, pale yellowish spots or blotches. Several of these pale markings are interconnected, particularly on the venter; most markings are much larger than the eye, but the smallest dorsal spot is about the size of the tympanum. The

pattern is obscure distally on the limbs (but the hind legs do lack the pale reticulum characterizing the *D. quinquevittatus* complex).

Based on the common warning colors of other species in the genus, *Dendrobates mysteriosus* might be expected to have spots of some shade of yellow, red, or green on either a brown or black field, or less likely some other combination such as yellow spots on a red field. The pale ventral markings might well be a different color from those above, possibly blue or yellow.

#### DISCUSSION

*Dendrobates mysteriosus* is known only from the one specimen obtained by Harvey Bassler at "Santa Rosa, 3000 ft., Alto Marañón," in July 1929. There are quite a few places with the name Santa Rosa in Peru, including several in the upper Marañón drainage, but examination of an unpublished report and survey maps (Bassler, MSc) allows the type locality to be placed with some confidence.

The unique specimen was obtained by Bassler during a memorable trek in which he and a few assistants covered 650 km. (404 miles) of rugged country on foot in 39 days, all the while mapping their trail and making geological examinations along the way—and somehow finding time to collect fossils and to preserve a few frogs and snakes! After a thousand kilometers of river travel, Bassler arrived on June 24 at Yupicusa (Yupicúz on recent maps), the head of canoe navigation on the upper Marañón, at 900 feet above sea level.<sup>11</sup> From here he took an existing trail that placed him several days later at Pomará (1150 ft.), higher on the Marañón. From Pomará the trail led inland to high country west

<sup>11</sup> Elevations are as given on Bassler's geological survey maps. Willard (1966) also had access to Bassler's reports and maps, but unfortunately he made a few errors in transcribing some localities to his own "sketch map." Of localities immediately pertinent, Willard placed Santa Rosa on the wrong side of, and too close to, the Río Marañón, and he mislabelled the Río Chinchipe as "Cenepe R." (the latter being the Río Cenipe, a lower tributary of the Marañón, where Bassler also worked).



FIG. 12. The approach to the village of Santa Rosa, 3860 ft. elev. ( $\sim 1175$  m.), on the west flank of the Cordillera Oriental, as photographed by Harvey Bassler in late June 1929. Bassler's specimen of *Dendrobates mysteriosus* evidently was found beyond the village, at about 900 m. elev. on the trail down to the Río Chinchipe. "The lower hills in the distance upon the left and [those] just beyond Río Chinchipe consist of the Tertiary sediments which occupy the synclinal valley between the Cordillera Oriental and the Cordillera Occidental. The photo looks out over this syncline toward the Cordillera Occidental." Copy of an original photograph in Bassler (MSc), courtesy of Exxon Corporation.

of the main river. On June 29, he camped near the Quebrada La Yunga at an elevation of 2650 ft. On June 30, the last day of the month, he passed through the small village of Santa Rosa at 3860 ft., and made camp 5.5 km. airline west-southwest of Santa Rosa at 3500 ft., with the trail crossing the 3000-foot contour both to the east and west of camp (fig. 12).

Assuming that the specimen was actually caught at the stated elevation of 3000 ft. in "July" as catalogued (rather than June 29 or 30), it must have been found on July 1, in the forested hills within 5–10 km. west of Santa Rosa. By the same night, Bassler had descended westward into the dry valley of the Río Chinchipe, to camp near the river at Pueblo Sapotal Viejo, at an elevation of only

1490 ft. He seems not to have returned to the vicinity of Santa Rosa. He explored far up the Chinchipe Valley, returning southward along its western slope to Jaen, then crossing to the eastern bank of the Río Marañón near Bella Vista. He traveled eastward through areas of cactus desert to Bagua Grande and ascended the Utcumbamba Valley to the mountain towns of Chachapoyas and Yurumarca, thence returning to Bella Vista on the Río Marañón. Balsa rafts were used to navigate nearly 100 km. of the Río Marañón from Bella Vista back down to Yupicusa, where he arrived on August 2 and where he retrieved the dugouts that had been left there.

On the way back to his headquarters at Iquitos, Bassler paused at the Río Santiago

where he obtained two more specimens of *Dendrobates captivus* (having taken the first specimen there in 1924). For reasons already discussed under that species, I suggest that *captivus* and *mysteriosus* may be sister species. Unless I have overlooked some available character of importance, a test of this relationship probably must await the acquisition of new material. Any data on colors in life, vocalizations, tadpoles, or skin toxins might prove especially valuable for additional comparisons. Before naming these species, it was hoped that my colleague John Daly and I would have occasion for obtaining such data, a pastime that has occupied us on some 20 trips in the last dozen years. But we are gradually realizing that there always will be another poison frog to be sought on the next mountain or across the next river. So, the new names are offered in hope of encouraging others who find it interesting to pursue small frogs in obscure places.

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