A REVISION OF THE POISON-ARROW FROGS OF THE GENUS *DENDROBATES* WAGLER

By PHILIP A. SILVERSTONE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY
SCIENCE BULLETIN 21 • JUNE 30, 1975

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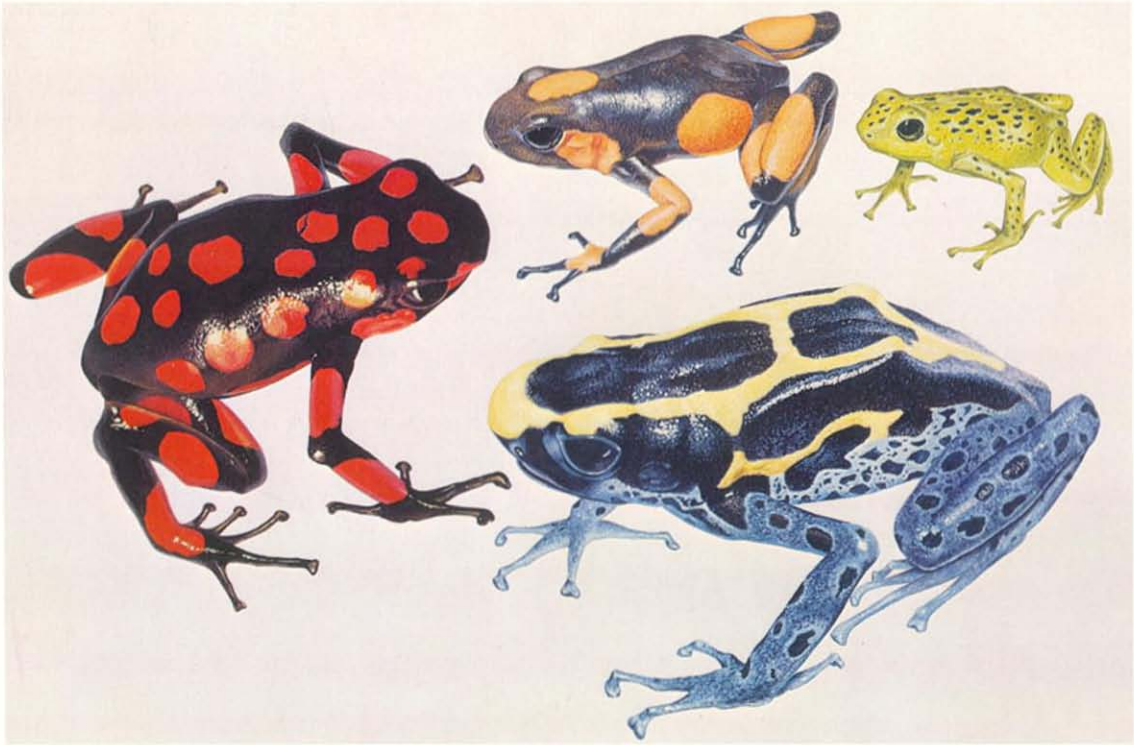

FRONTISPIECE I. Clockwise, starting with largest frog: Dyeing Poison-arrow Frog (*Dendrobates tinctorius*), Saut Tortue, French Guiana; Kôkoê-pá (*D. histrionicus*), upper Río Napipí, Colombia; Kôkoê-pá (*D. histrionicus*), Finca Chibiguí, Río Arquía, Colombia; Golden Poison-arrow Frog (*D. altobueyensis*), holotype, Alto del Buey, Colombia. Not to scale.

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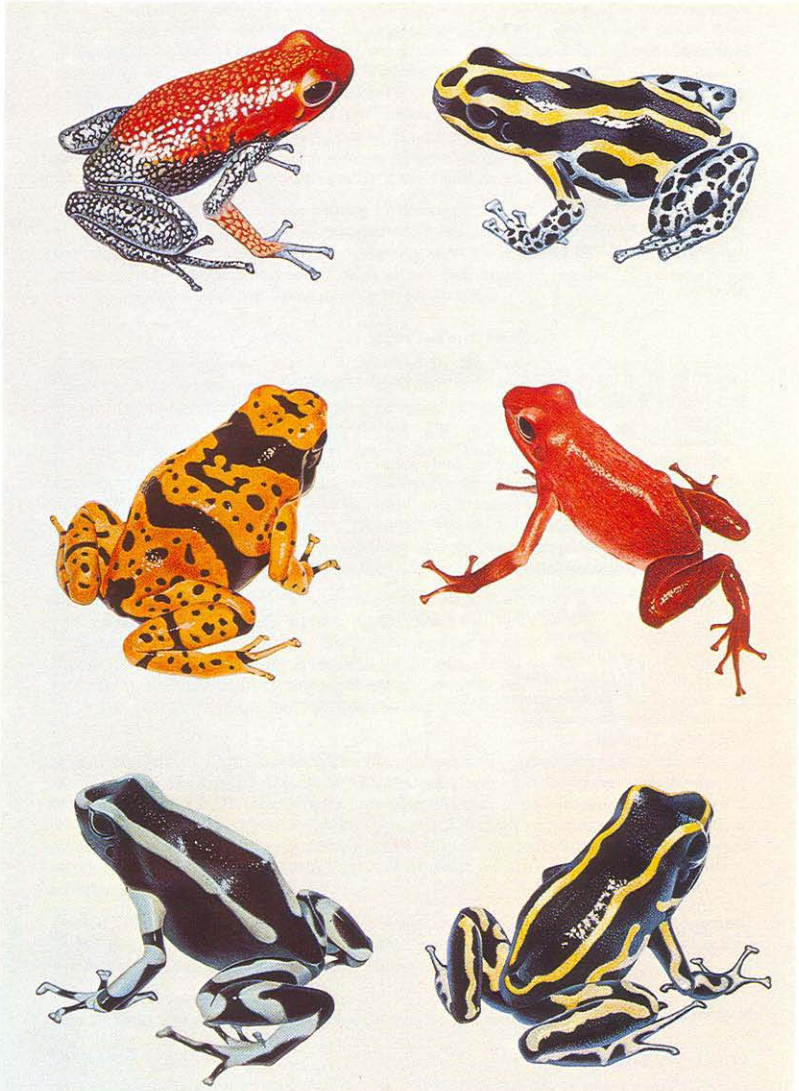

FRONTISPIECE II. Left side, top to bottom: Granular Poison-arrow Frog (*Dendrobates granuliferus*), Rincón de Osa, Costa Rica; Yellow-banded Poison-arrow Frog (*D. leucomelas*), San Félix, Venezuela; Green Poison-arrow Frog (*D. auratus*), Camino de Yupe, Colombia. Right side, top to bottom: Amazonian Poison-arrow Frog (*D. quinquevittatus*), Utinga near Belém, Brasil; Andean Poison-arrow Frog (*D. opisthomelas*), Santa Rita, Colombia; Yellow-striped Poison-arrow Frog (*D. truncatus*), Mariquita, Colombia. Not to scale.

A REVISION OF THE POISON-ARROW FROGS OF THE GENUS *DENDROBATES* WAGLER[1]

By PHILIP A. SILVERSTONE[2] [3]

ABSTRACT: The bones and thigh and jaw muscles of 14 of the 16 known species of *Dendrobates*, 15 of the 20 known species of *Phyllobates*, and 12 of the more than 40 known species of *Colostethus* were examined. All species examined (including *C. bocagei*, which has been reported to have a "ranid" thigh muscle pattern) have a "dendrobatid" thigh muscle pattern (the distal tendon of insertion of the *semitendinosus* muscle pierces that of the *gracilis major* muscle). Dendrobatids also differ from ranids in lacking the *adductor mandibularis externus superficialis* (one of the jaw muscles). Only two species of dendrobatids (*D. histrionicus* and *D. leucomelas*) lack an omosternum. Most species of dendrobatids lack palatine bones; of the species examined, only two (*Colostethus palmatus* and *C. trinitatis*) have palatine bones. Most specimens of *Dendrobates* examined have some of their vertebrae fused. Most specimens of the other two genera lack such fusion.

The genus *Dendrobates* consists of 16 species, including two new species from the Chocoan region of Colombia (*D. altobueyensis* and *D. fulguritus*). Species of *Dendrobates* are placed into four groups: (1) *histrionicus* group (*D. histrionicus, D. leucomelas*); (2) *minutus* group (*D. altobueyensis, D. fulguritus, D. minutus, D. opisthomelas, D. quinquevittatus, D. steyermarki*); (3) *pumilio* group (*D. granuliferus, D. pumilio, D. speciosus*); (4) *tinctorius* group (*D. auratus, D. azureus, D. galactonotus, D. tinctorius, D. truncatus*). It is proposed that five species (*D. bassleri, D. ingeri, D. parvulus, D. pictus*, and *D. trivittatus*) be transferred from *Dendrobates* to *Phyllobates*.

Dendrobatids probably arose in South America after the beginning of Eocene and entered Central America in Pliocene. *Dendrobates* probably invaded Central America in three waves. The present distribution of the lowland species of *Dendrobates* is limited principally by rainfall and associated plant formations, and is correlated with Haffer's Pleistocene interglacial humid refuges. Four species of *Dendrobates* probably arose in Central America and 12 in South America. The principal component of the diet of *Dendrobates* is ants. Descriptions, collecting localities, and range maps are given for each species of *Dendrobates*. Illustrations depict 15 species, nine of them in color.

INTRODUCTION

The poison-arrow frogs (Dendrobatidae), totaling over 70 known species (publications in press bring the total to 100 species), occur only in the Neotropics, from Nicaragua south to Perú, Bolivia, and Brasil. Many species of poison-arrow frogs are famous for their bright coloration. Amerindians extract blowgun poison from some species.

The taxonomy of poison-arrow frogs, at the familial and generic levels, has been and remains confused and controversial. Noble (1926), Starrett (1968), and Lynch (1971) considered dendrobatids closely related to elosiine leptodactylids. Griffiths (1959) placed dendrobatids in the family Ranidae. Savage (1968) replaced them in the family Dendrobatidae; he recognized three genera, *Dendrobates* Wagler 1830 (toothless, brightly colored), *Phyllobates* Bibron *in* Sagra 1841 (toothed, brightly colored), and *Colostethus* Cope 1867a (toothed, dully colored). In this paper, I redefine the genus *Dendrobates* and discuss the 16 included species.

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[3]This bulletin is a revised version of my doctoral dissertation submitted to the University of Southern California.

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The figures are by P. Brame (Figs. 14, 20-22), E. Templeton (19, 23), M. Butler (18), J. Clark (15), L. Reynolds (17), and me (1-13, 16, 24). The master body outline for Figures 11-14 is by J.T. Kitasako. I am grateful to B. Shreve for donating Figure 15, and to J. Nakanishi for his beautiful paintings (Frontispieces).

My studies were aided by a NSF Summer Fellowship for Graduate Teaching Assistants (1966), by a NDEA Title IV Fellowship (1966-1969), by Biomedical Sciences Support Grant FR-07012-02 no. 5703 from the National Institutes of Health to the University of Southern California (1969), and by the Natural History Museum of Los Angeles County Foundation (1971).

Materials and Methods

All measurements are to the nearest one-half millimeter.

Tadpole stages are those of Gosner (1960).

Osteological specimens were cleared with glycerin and two percent potassium hydroxide and were stained with alizarin red S.

Patterns and subpatterns in the accounts of *D. histrionicus* and *D. quinquevittatus* are for convenience of description; they are not intended to represent taxa.

Grouped under the heading "doubtful records" are localities that are separated by a major geographic barrier from all other collecting localities for the species, or that lie far outside the known elevational range of the species. I have not included these doubtful records on the range maps; I have included them in the locality lists to bring them to the attention of future collectors, who may be able to verify them.

In the species accounts, under the heading "stomach contents," the museum number of a specimen of dendrobatid is cited first, followed by the names (and numbers of individuals) of the invertebrate taxa found in its stomach.

In the synonymies, a period separates the name of a taxon from the names of all authors except the taxon's original author.

Museum abbreviations

The following abbreviations indicate the location of preserved specimens:

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
BM	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
CAS-SU	Stanford University collection, at CAS
CM	Carnegie Museum, Pittsburgh
CRE	Allan Hancock Foundation, University of Southern California, Los Angeles (Costa Rican Expeditions)
FMNH	Field Museum of Natural History, Chicago
GOV	Gustavo Orcés V. collection, at USNM
ILS	Instituto de La Salle, Bogotá
JAP	James A. Peters collection, at USNM

JMS	Jay M. Savage private osteological collection, at CRE
KM	Kraków Museum, Jagellonian University, Kraków
KU	Museum of Natural History, University of Kansas, Lawrence
LACM	Natural History Museum of Los Angeles County, Los Angeles
LG	Jean Lescure private collection, Paris
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MHNP	Muséum National d'Histoire Naturelle, Paris
MPEG	Museu Paraense Emilio Goeldi, Belém
MRHN	Institut Royal des Sciences Naturelles de Belgique, Brussels
NHMW	Naturhistorisches Museum, Vienna
NMG	Naturhistoriska Museet, Göteborg
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
SCN	Sociedad de Ciencias Naturales La Salle, Caracas
TNHC	University of Texas, Austin
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor
UPR	University of Puerto Rico, Mayagüez
USNM	National Museum of Natural History, Washington
WCAB	W.C.A. Bokermann private collection, São Paulo
ZMA	Zoologisch Museum, Amsterdam
ZSBS	Zoologische Sammlung des Bayerischen Staates, Munich

Dendrobatid Genera

I originally intended to revise only the genus *Dendrobates*, but found it poorly defined. To better define it, I examined the thigh and jaw muscles and the skeletons of 41 species of the three currently recognized dendrobatid genera (14 of the 16 known species of *Dendrobates*, 15 of the 20 known species of *Phyllobates*, and 12 of the more than 40 known species of *Colostethus*), and I examined the external characteristics of most of the described species of the family. From these analyses, I drew two conclusions. First, because of the existence of species intermediate in morphology, one cannot separate dendrobatids into three discrete genera by employing only the morphological characteristics used by previous workers. Second, with the analysis of additional morphological characteristics, there remain some (but fewer) species that cannot be assigned unequivocally to any of the three genera. Thus, any rigidly applied definition of more than one genus for dendrobatid frogs could result in unnatural (= polyphyletic) groups. Despite this, I continue to recognize the three currently accepted genera as categories of convenience, that is, as taxonomic units convenient to study, but not necessarily natural. The alternative would place the over 70 described species of dendrobatids into a single unwieldy genus. Below are definitions of the three genera recognized.

Generic definitions

Definition of Colostethus.—Maxillary and premaxillary teeth present; disks of second, third, and fourth fingers relatively small (Fig. 1); first finger shorter than, equal to, or longer than second; toe webbing present or absent; in life, skin of dorsum usually dully colored; palatine bones present or absent; omosternum present; vertebrae not fused; tadpoles with oral disk laterally indented, number of denticles usually not reduced, and anus dextral.

Definition of Phyllobates.—Maxillary and premaxillary teeth present or absent; disks of second, third, and fourth fingers relatively small (Fig. 1); first finger equal to or longer than second; toe webbing present or absent; in life, skin of dorsum partly or entirely brightly colored; palatine bones absent; omosternum present; vertebrae usually not fused; tadpoles with oral disk laterally indented, number of denticles not reduced, and anus dextral.

Definition of Dendrobates.—Maxillary and premaxillary teeth absent; disks of second, third, and fourth fingers relatively large (Fig. 1); first finger shorter than second; toe webbing absent; in life, skin of dorsum partly or entirely brightly colored; palatine bones absent; omosternum present or absent; some of vertebrae often fused; tadpoles with oral disk laterally indented or not, number of denticles reduced or not, and anus median or dextral.

Problems in defining dendrobatid genera.—Some species of dendrobatids are sufficiently different to warrant maintenance of more than one dendrobatid genus (e. g., *Colostethus palmatus* is semiaquatic and has teeth, palatine bones, extensive toe webbing, and dull dorsal coloration; *Dendrobates tinctorius* is terrestrial, lacks teeth, palatine bones, and toe webbing, and has bright dorsal coloration). Unfortunately, the existence of intermediate species impedes identification of discrete evolutionary lineages. Examples of intermediate species are *Dendrobates pictus* (some specimens of this species have numerous teeth, other specimens have only a few teeth, and most specimens lack teeth), *Phyllobates femoralis* (this species has bright stripes, but also has basally webbed toes), a new species I am currently describing (the ventral pattern and color of this species resemble those of *Dendrobates pictus*, but the dorsal and lateral pattern and color resemble those of many species of *Colostethus;* the species has teeth and basally webbed toes), and an undescribed species of *Colostethus* (this species has extensive toe webbing, but lacks palatine bones).

The current distinction between members of *Phyllobates* and *Colostethus* is based only on color (which presumably coincides with presence or absence of

skin toxins). Using color as a sole generic criterion is unwise, because some nominal species of *Colostethus* (e.g., *C. palmatus)* have bright ventral coloration. Using presence or absence of palatine bones as a criterion might be better, but this would place most nominal species of *Colostethus* with *Phyllobates.*

I am concerned here more with the relationship of *Phyllobates* to *Dendrobates* than with that of *Phyllobates* to *Colostethus.* Using presence or absence of maxillary and premaxillary teeth as a generic criterion does not separate the brightly colored poison-arrow frogs into two natural groups (*Phyllobates* and *Dendrobates*), because this characteristic varies intraspecifically in at least one species. I have, therefore, used this characteristic only in conjunction with finger disk size and finger length. The distinction between *Phyllobates* and *Dendrobates* can be made more consistent, and the resulting units more natural, by shifting five brightly colored species currently considered *Dendrobates* to the genus *Phyllobates.* Three of these species, *Dendrobates bassleri* Melin 1941, *D. ingeri* Cochran and Goin 1970, and *D. parvulus* Boulenger 1882a, have teeth, small finger disks, and the first finger longer than the second. The concurrence of these characteristics unequivocally assigns these species to the genus *Phyllobates,* as defined above. After shifting these three toothed species to *Phyllobates,* there remain two nominal species of *Dendrobates, D. pictus* (Bibron *in* Tschudi 1838) and *D. trivittatus* (Spix 1824), that resemble *Phyllobates* in certain respects. In both of these species, the finger disks are relatively small, and the first finger is equal to (in many specimens of *D. pictus*) or longer than the second finger. All specimens of *D. trivittatus* and most specimens of *D. pictus* lack teeth. I propose that these two species also be transferred to the genus *Phyllobates* for the following reasons: (1) In all toothed species of brightly colored poison-arrow frogs (*Phyllobates*), the disks of the second, third, and fourth fingers are relatively small (less than 1.5 times the width of the fingers); whereas in all toothless species presently allocated to *Dendrobates,* except *D. pictus* and *D. trivittatus,* the disks of the second, third, and fourth fingers are relatively large (usually two or more times the width of the fingers). (2) In all toothed species of brightly colored poison-arrow frogs (*Phyllobates*), the first finger is equal to or longer than the second; whereas in all toothless species presently allocated to *Dendrobates,* except *D. pictus* and *D. trivittatus,* the first finger is shorter than the second. (3) Although most specimens of *D. pictus* lack teeth, some specimens of this species from Bolivia and Perú have teeth; thus the tooth characteristic does not place *D. pictus* unequivocally in the genus *Dendrobates.* (4) J.P. Bogart (personal communication) concluded that *D. pictus* and *D. trivittatus* are chromosomally more similar to the toothed dendrobatids than to the toothless dendrobatids.

Unfortunately, transfer of *D. trivittatus* to *Phyllobates* causes a nomenclatural problem. According to W. Peters (1873), who saw Spix's type specimens, which were destroyed in World War II (U. Gruber, personal communication), *Hyla nigerrima* Spix, designated by Fitzinger (1843) as the type species of *Dendrobates,* is conspecific with *D. trivittatus* (= *Hyla trivittata* Spix). Strict application of the rules of zoological nomenclature would result in using the generic name *Dendrobates* for the species now referred to *Phyllobates;* a new generic name would be required for the species now referred to *Dendrobates.* To obviate this problem, I requested (Silverstone 1971b) the International Commission on Zoological Nomenclature to use its plenary powers to change the type-species designation for the genus *Dendrobates* from *Hyla nigerrima* Spix to the third species included in Wagler's (1830) original concept of *Dendrobates, Calamita tinctorius* Schneider. The name *D. tinctorius* has been applied in the literature to several species; in this paper, I designate a neotype to objectively fix the name.

In my opinion, the definition of *Dendrobates* employed in this paper makes this genus more natural. Better definition of dendrobatid genera must await the gathering of additional data by other workers. I hope this revision will be a useful starting point for these workers.

Anatomy

This section summarizes the results of an anatomical study of 41 species of dendrobatid frogs; further details and a list of specimens examined are in my dissertation (Silverstone 1971a).

Dendrobatid frogs differ externally from all other New World frogs in the following triple combination of characteristics: paired dorsolateral raised areas (called "scutes" in the literature) occur on the skin of the digital disks (Fig. 1), vomerine teeth are absent, and the tarsal fold usually extends less than the full length of the tarsus.

Variation in the surface color of the muscles of dendrobatid frogs forms a continuum, with the species of the genus *Colostethus* at the light-colored extreme of the continuum and most species of *Dendrobates* at the dark-colored extreme.

All dendrobatids examined (including *C. trinitatis,* contrary to Dunlap [1960]) have a *gracilis minor* muscle. Unlike ranids, all (including *C. bocagei,* contrary to Griffiths [1959], who said that *C. bocagei* has a ranid thigh muscle pattern) have the distal tendon of the *semitendinosus* muscle piercing that

of the *gracilis major* muscle. All have a *depressor mandibulae* muscle formula of DFSQ$_4$AT (formula after Starrett [1968]). Unlike ranids, all dendrobatids examined have a jaw *adductor* muscle formula of s (i.e., the *adductor mandibularis externus superficialis* muscle is absent).

Vertebral fusion is absent in the 17 specimens of *Colostethus* examined, present in only two of the 29 specimens of *Phyllobates* examined, and present in 28 of the 46 specimens of *Dendrobates* examined (in *Dendrobates*, presence and extent of vertebral fusion vary intraspecifically; see Table 1). The apparent absence of vertebral fusion in four species of *Dendrobates* may be an artifact of small sample size.

The pectoral girdle is always firmisternal. *D. histrionicus* and *D. leucomelas* lack an omosternum; all other dendrobatids examined have an omosternum (Fig. 2).

Variation in the dendrobatid hyoid apparatus is minor (Fig. 3).

Most variation in shape and size of skull bones is intraspecific. Palatine bones are absent in all dendrobatids examined except *C. palmatus* and *C. trinitatis*. In the adult specimens examined, the orbitosphenoid region is usually completely ossified in *Dendrobates*, completely ossified in half the specimens of *Phyllobates* and partially ossified in the rest, and usually unossified or partially ossified in *Colostethus*. In adult specimens of *Phyllobates* and *Colostethus*, presence and degree of orbitosphenoid ossification vary intraspecifically. In *D. tinctorius* and some specimens of *D. auratus* and *D. histrionicus*, the frontoparietals, nasals, and sphenethmoid are fused together (Fig. 4). In *D. auratus*, *D. azureus*, *D. leucomelas*, *D. tinctorius*, *D. truncatus*, and some specimens of *D. histrionicus* and *D. pumilio*, the dorsal surfaces of the frontoparietals and nasals are sculptured (Fig. 4).

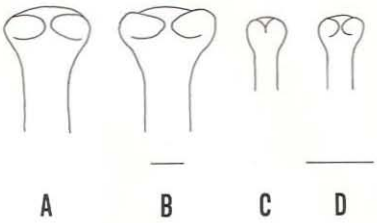


FIGURE 1. Disks of third finger of dendrobatid frogs, dorsal aspect, showing family characteristic of paired "scutes," generic difference between small disks of *Phyllobates* and *Colostethus* and large disks of *Dendrobates*, and sexual dimorphism in finger disk size occurring in some species of *Dendrobates*. (A) *Dendrobates tinctorius* (LACM 43927), neotype, female, 49 mm snout-vent length; (B) *D. tinctorius* (LACM 43914), male, 43 mm; (C) *Phyllobates bicolor* (USNM 137366), male, 37 mm; (D) *Colostethus talamancae* (CRE 7195), male. Lines equal one millimeter. Line at B is scale for A-C; line at D is scale for D only.

FOOD

R.R. Snelling (LACM) identified the stomach contents of 25 specimens of 12 species of *Dendrobates* (see Table 2 and the species accounts). Most of the 2075 food items are small invertebrates that

TABLE 1
Vertebral fusion in 14 species of *Dendrobates*.

Species	n	no fusion	Fusion between vertebrae			
			1+2	2+3	2+3 and 8+9	1+2+3 and 8+9
D. auratus	11	8	1	2		
D. azureus	1	1				
D. fulguritus	1			1		
D. galactonotus	1	1				
D. granuliferus	1				1	
D. histrionicus	11			2	8	1
D. leucomelas	2	2				
D. minutus	2			2		
D. opisthomelas	1	1				
D. pumilio	6				4	2
D. quinquevittatus	4	3	1			
D. speciosus	1				1	
D. tinctorius	2	1	1			
D. truncatus	2	1		1		
	46	18	3	8	14	3

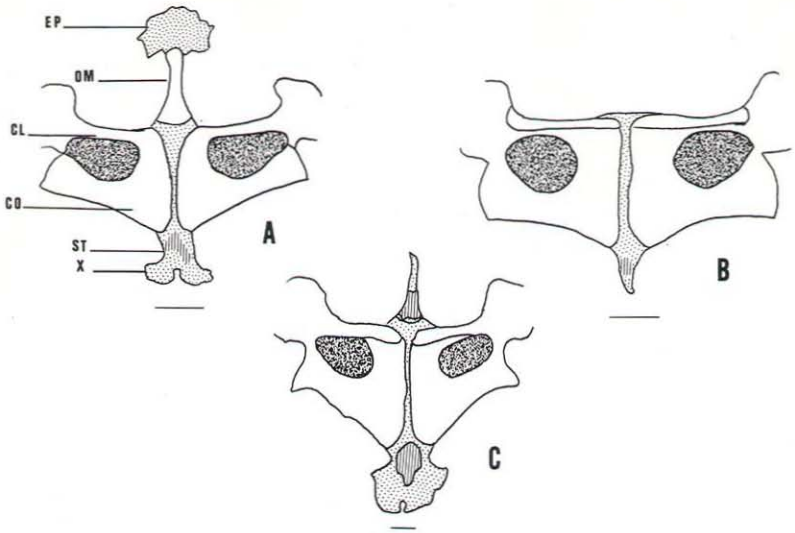


FIGURE 2. Pectoral girdles of dendrobatid frogs, ventral aspect. (A) *Phyllobates vittatus* (JMS 1682); (B) *Dendrobates histrionicus* (LACM 60985); (C) *D. tinctorius* (LACM 43923). CL: clavicle; CO: coracoid; EP: episternum; OM: omosternum; ST: sternum proper; X: xiphisternum. Nomenclature after Ecker (1889). Stippling indicates cartilage, vertical lines indicate calcified cartilage, white indicates bone, heavy mottling indicates opening or foramen. Lines equal one millimeter.

inhabit litter on the forest floor. Small terrestrial ants are the principal prey. Of 1067 ants in the stomachs, only four are arboreal. The predominance of ants agrees with Noble's (1918) report on the stomach contents of Nicaraguan *D. auratus* and *D. pumilio*.

LIFE HISTORY, HABITS, HABITAT, AND APOSEMATIC COLORATION

Frogs of the genus *Dendrobates* have aggressive intraspecific behavior (probably territorial defense),

TABLE 2

Stomach contents of 25 specimens of 12 species of *Dendrobates*. Column A: percentage of total number of prey individuals. Column B: percentage of total number of stomachs. R. Snelling identified the stomach contents.

Food Category	A (%)	B (%)
Ants	51.4	100.0
Mites	26.7	56.0
Springtails	9.7	8.0
Termites	6.4	20.0
Beetles	2.6	60.0
Insect larvae	2.6[1]	20.0
Aphids and true bugs	0.2	8.0
Wasps	0.2	8.0
Thrips	0.1	8.0
Centipedes	0.1	4.0

[1]Includes moth larvae 1.4, beetle larvae 1.0, fly larvae 0.2

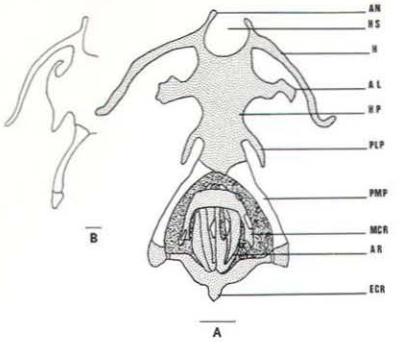


FIGURE 3. (A) Hyoid apparatus and larynx of *Dendrobates histrionicus* (JMS 1663), ventral aspect. AL: alary process of hyoid plate; AN: anterior process of hyale; AR: arytenoid cartilage; ECR: esophageal process of cricoid cartilage; H: hyale; HP: hyoid plate; HS: hyoglossal sinus; MCR: muscular process of cricoid cartilage; PLP: posterolateral process of hyoid plate; PMP: posteromedial process of hyoid plate. Nomenclature after Trewavas (1933). Stippling indicates cartilage, white indicates bone, heavy mottling indicates opening or foramen. (B) Outline of right side of hyoid apparatus of *D. tinctorius* (LACM 43923), ventral aspect, showing expansion of alary process and its fusion with posterolateral process. Lines equal one millimeter.

complex courtship behavior, and parental care (Senfft 1936; Dunn 1941; Duellman 1966; Goodman 1971; Crump 1972; Bunnell 1973; Silverstone 1973). At least some species (and probably all species) of *Dendrobates* lack amplexus (Senfft 1936; Crump 1972; W.N. Polder, personal communication). The female lays eggs on the ground or on vegetation. The male parent (or perhaps both parents; see Mudrack [1969] on a species of *Colostethus*) guards the eggs; when the tadpoles hatch, they wriggle onto the back of a parent, who carries them to water and releases them therein (Senfft 1936). The parent does not carry the entire brood in one trip; it carries from one to three tadpoles at a time (Senfft 1936; also collectors' reports and museum records cited in the species accounts). The carrier is usually reported to be male, but at least in some species, females do carry tadpoles (*Dendrobates azureus:* Hoogmoed 1972; *D. pumilio:* Kitasako 1967; also in other dendrobatids: *Colostethus* species: Mudrack 1969; *C. talamancae:* CRE 901; *Phyllobates* new species: MCZ 24443; *P. femoralis:* Hoogmoed field number 389 at RMNH, and KU 111515). Tadpole-carrying adults of the genus *Dendrobates* use small, still bodies of water, such as the water in bromeliad leaf axils and in holes in fallen logs, as tadpole deposition sites (Savage 1968; also museum records and my field observations). The tadpoles complete their development in the water.

Clutch size is relatively small in *Dendrobates* (two to 16: Oeser 1932; Oertter 1953; Crump 1972; Silverstone 1973). Females (at least in *D. auratus*) oviposit more than once during the breeding season. For example, two captive female *D. auratus* laid eggs 21 times between 5 June and 21 November 1933 (Senfft 1936). The clutch size was seven to 12. If

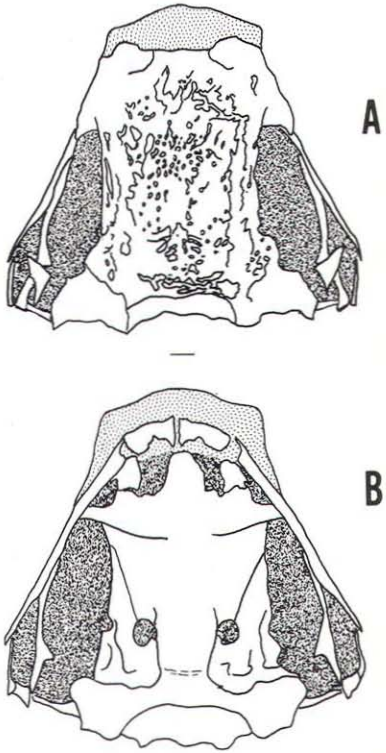


FIGURE 4. Skull of *Dendrobates tinctorius* (LACM 43923), showing sculpturing and fusion of dorsal bones. (A) dorsal aspect; (B) ventral aspect. Stippling indicates cartilage, white indicates bone, heavy mottling indicates opening or foramen. Line equals one millimeter.

one assumes an average clutch size of 10 and an equal number of layings (about 10) by each female, then the total number of eggs laid by each female during the breeding season was about 100, far fewer than the thousands of eggs produced per female in many water-ovipositing anurans (Wright and Wright 1949). Largely because of parental care, the offspring of *Dendrobates* must have a higher survival rate than that of the offspring of water-ovipositing anurans.

The species of *Dendrobates* are diurnal. Their diet indicates that they usually remain on the forest floor, although they can climb to over 12 meters (Dunn 1941). They rarely enter flowing water, but sometimes enter and sit in small, still bodies of water (e.g., a wild specimen of *D. auratus* sat for several minutes in a water-filled pan at our camp on the Camino de Yupe, Colombia).

The species of *Dendrobates* occur from Nicaragua to Brasil, primarily in wet lowland tropical forest, but two species occur in wet subtropical forest at higher elevations; elevation range is sea level to at least 2200 m (Figs. 5–9).

Amerindians extract blowgun poison from at least three species of dendrobatids (*Dendrobates auratus, Phyllobates aurotaenia,* and *P. bicolor*). The powerful skin toxins of the brightly colored species of poison-arrow frogs are lethal when injected experimentally into birds and mammals (Tokuyama, Daly and Witkop 1969), but the frogs lack a delivery system. The unpleasant taste of the unpurified skin toxins, combined with the color vision (Walls 1942) and learning abilities (Brower 1958) of diurnal birds, suggest that the bright coloration of poison-arrow frogs has an aposematic function.

Dendrobates Wagler 1830

1788. *Hyla* (part). Lacépède: 566–567.
1799. *Calamita* (part). Schneider: 175.
1802. *Rana* (part). Shaw: 135.
1803. *Hyla* (part). Daudin: 25–26.
1826. *Hylaplesia* (part). Boie *in* Schlegel: 239.
1830. *Dendrobates* Wagler: 202. No type-species designated. Included species: *Hyla nigerrima, Hyla trivittata, Calamita tinctorius.*
1841. *Dendrobates* (part). Duméril and Bibron: 649–656.
1843. *Dendrobates.* Fitzinger: 32. Designated *Hyla nigerrima* as type-species.
1882a. *Dendrobates* (part). Boulenger: 142–146.
1968. *Dendrobates.* Savage: 759–763.

Diagnosis.—*Dendrobates* differs from *Phyllobates* in having the first finger shorter than the second and in having relatively large finger disks; the disks of the second, third, and fourth fingers are usually at least twice the width of the fingers. (In *Phyllobates,* the first finger is longer than, or rarely equal to, the second; the disks of the second, third, and fourth fingers are usually no wider than 1.5 times the width of the fingers.) *Dendrobates* differs from *Colostethus* in having relatively large finger disks, bright coloration in life, and skin toxins.

Description.—The snout-vent length of adults is 12 to 50 mm (Fig. 10 and Table 3); in most species, females average longer than males. The skin is smooth or granular. Teeth are absent. Adult males have vocal slits; females lack vocal slits. The tip of the snout is truncate to slightly rounded in dorsal aspect. The interorbital distance is wider than the upper eyelid. The diameter of the eye is greater than the distance from the eye to the nostril. The posterodorsal portion of the tympanum is concealed. Each digital disk bears on its dorsal surface a pair of raised "scutes" separated by a median groove (Fig. 1). The disks of the second, third, and fourth fingers are larger than those of *Phyllobates* and *Colostethus* (Fig. 1); in some species, these disks average wider in males than in females. The first finger is shorter than the second (except in some specimens of *D. truncatus,* in which the first finger is equal in length to the second). The fingers lack fringes and webbing. A subarticular tubercle occurs on the ventral surface of each digital joint. An oblong inner and round outer tubercle occur on both the metacarpus and metatarsus. A tarsal fold is present; it does not extend the full length of the tarsus. A tarsal tubercle (at the proximal end of the tarsal fold) is present or absent. The toes lack fringes and webbing.

Sexual dichromatism usually is absent. In life, the iris is black (or rarely dark brown) and is never reticulated. Bright colors (red, orange, yellow, green, blue, and intermediate shades) cover the entire body or occur as spots, bands, stripes, marbling, or reticulation, usually on a black or brown ground color (Figs. 11–15). In preservative, the bright colors become white, gray, brown, or black, and the color pattern may become indistinguishable from the ground color.

The surfaces of the muscles usually are densely flecked with dark pigment. Palatine bones are absent. The orbitosphenoid region is completely ossified. The omosternum is present or absent. In many specimens, some of the vertebrae are fused.

Tadpole measurements are in Table 4. The tadpoles have one or two rows of oral papillae, which border the entire posterior lip (except in *D. opisthomelas*), but border only the lateral portions of the anterior lip. The tadpoles have the oral disk laterally indented or not, a wide median break in the second anterior denticle row, and a denticle formula of $\frac{1\text{–}1}{3}$, sometimes reduced to $\frac{1\text{–}1}{1}$ or fewer. The anus of the tadpoles is median or dextral.

New combinations, new synonyms, and species of uncertain status.—Table 5 shows all names proposed for or referred to the genus *Dendrobates.* Twenty-three of these names are new combinations or new synonyms: *Dendrobates bassleri, D. braccatus, Phyllobates chocoensis, D. eucnemis, D. fantasticus, Hylaplesia flavopicta, D. hahneli, D. ingeri, D. labialis, D. lateralis, D. machadoi, D. minutus ventrimaculatus, Hyla nigerrima, D. paraensis, D. parvulus, Hylaplesia picta, D. pictus guayanensis, D. reticulatus, D. tetravittatus, D. tinctorius cocteaui, D. tinctorius igneus, D. tinctorius wittei,* and *Hyla trivittata.*

Above, I stated my reasons for transferring *D. bassleri, D. ingeri, D. parvulus, D. pictus* (described as *Hylaplesia picta,* and including *D. braccatus, D. eucnemis, Hylaplesia flavopicta, D. hahneli,* and *D. pictus guayanensis*), and *D. trivittatus* (described as *Hyla trivittata,* and including *D. tetravittatus* and perhaps *Hyla nigerrima*) to the genus *Phyllobates.* I have examined the type specimens of *D. bassleri, D. braccatus, D. eucnemis, D. hahneli, D. ingeri, D. parvulus,* and *Hylaplesia picta.* Because of the color patterns reported in their original descriptions and possessed by their types, I consider *D. braccatus, D. eucnemis, Hylaplesia flavopicta, D. hahneli,* and *D. pictus guayanensis* synonyms of *D. pictus.* Bokermann (1966) considered *D. tetravittatus* a synonym of *D. trivittatus.* I have not seen the types of *D. tetravittatus;* I accept Bokermann's opinion, which agrees with my interpretation of the original description of *D. tetravittatus.* W. Peters (1873) considered *Hyla nigerrima* a synonym of *D. trivittatus.* I have not seen the types of *Hyla nigerrima,* which were destroyed in World War II; I provisionally accept Peters' opinion. Thus the following new combinations are formed (without making judgments on subspecific status of the synonyms): *Phyllobates bassleri, P. ingeri, P. parvulus, P. pictus,* and *P. trivittatus.*

I have examined the type specimens of *D. fantasticus, D. galactonotus, D. minutus ventrimaculatus, D. paraensis, D. quinquevittatus, D. reticulatus, D. tinctorius igneus,* and *D. tinctorius wittei.* Because of the color patterns reported in their original descriptions, I consider *D. tinctorius cocteaui* and *D. t. wittei* synonyms of *D. histrionicus,* and *D. machadoi* a synonym of *D. tinctorius.* Some specimens (not type material) have color patterns intermediate between that of the holotype of *D. quinquevittatus* and those of the types of *D. fantasticus, D. minutus ventrimaculatus, D. reticulatus,* and *D. tinctorius igneus;* therefore, I consider the latter four names synonyms of *D. quinquevittatus.* The types of *D. paraensis* and *D. galactonotus* have similar color patterns and well-developed tarsal tubercles; therefore, I consider *D. paraensis* a synonym of *D. galactonotus.*

Dendrobates lateralis Guichénot 1848 is a syno-

TABLE 3

Snout-vent length of 1658 adult specimens of 15 species of *Dendrobates,* including sample size (n), range, mean and standard error (x̄±SE), and standard deviation (SD).

Species	All Specimens				Males				Females			
	n	Range	x̄±SE	SD	n	Range	x̄±SE	SD	n	Range	x̄±SE	SD
alboguevensis	2	15.5–17.0	16.3	—	1	15.5	15.5	—	1	17.0	17.0	—
auratus	296	25.0–42.0	32.8±0.19	3.34	106	25.0–39.5	30.7±0.29	3.04	190	27.0–42.0	33.9±0.21	2.94
azureus	10	38.5–45.0	41.6±0.77	2.45	3	38.5–39.5	39.0±0.28	0.50	7	39.0–45.0	42.7±0.76	2.04
fulguritus	17	13.5–16.5	14.8±0.17	0.73	10	13.5–15.0	14.5±0.15	0.49	7	14.0–16.5	15.2±0.30	0.80
galactonotus	18	30.5–40.5	34.7±0.54	2.29	7	30.5–36.5	33.2±0.69	1.84	11	33.0–40.5	35.7±0.62	2.07
granuliferus	30	19.0–22.0	20.7±0.15	0.83	13	19.0–22.0	20.7±0.24	0.87	17	19.0–22.0	20.8±0.20	0.83
histrionicus	319	24.0–38.0	33.2±0.13	2.46	206	24.0–38.0	33.2±0.18	2.64	113	28.0–38.0	33.1±0.19	2.09
leucomelas	31	30.5–37.5	33.8±0.32	1.83	15	30.5–35.0	32.8±0.36	1.39	16	32.5–37.5	34.8±0.41	1.66
minutus	114	12.0–15.5	13.4±0.06	0.69	50	12.0–15.0	13.2±0.10	0.73	64	12.0–15.5	13.5±0.08	0.65
opisthomelas	49	14.5–19.5	17.0±0.18	1.29	26	14.5–18.5	16.8±0.24	1.24	23	14.5–19.5	17.3±0.27	1.31
pumilio	486	17.5–24.0	20.8±0.06	1.38	169	18.0–24.0	20.9±0.11	1.43	317	17.5–24.0	20.7±0.07	1.34
quinquevittatus	114	14.5–21.5	17.1±0.14	1.53	32	14.5–20.0	16.6±0.24	1.38	82	15.0–21.5	17.3±0.17	1.55
speciosus	20	27.5–30.0	28.8±0.15	0.67	8	27.5–29.0	28.4±0.18	0.51	12	28.5–30.0	29.1±0.17	0.60
tinctorius	118	34.0–50.0	44.4±0.33	3.60	45	34.0–46.5	41.0±0.40	2.68	73	39.0–50.0	46.5±0.27	2.30
truncatus	37	23.5–31.0	27.2±0.33	2.03	18	23.5–28.0	25.6±0.32	1.38	19	27.0–31.0	28.7±0.28	1.22

TABLE 4
Measurements (mm) of tadpoles of six species of *Dendrobates*. HB = head-body length; TL = total length. The column headings are the stages of Gosner (1960).

Species		25	26	27	28	29	30	31	32	33	34	35	36	37	38	40	41	42	43	44	45
auratus	n	4	2		1	1	4				2		1		1	2	6	2	1	1	
	HB	5.5–6.5	5.0–8.0		12.0	9.5	9.0–12.0				11.5–12.5		12.5		14.0	13.5–14.0	13.5–16.0	14.5–15.5	15.0	14.5	
	TL	13.5–16.5	12.0–19.0		28.5	23.5	24.0–30.0				29.5–33.5		33.5		35.0	34.0–35.5	32.0–36.5	30.0–39.0	25.0	15.5	
histrionicus	n	1								1		1	2	1	1		2				
	HB	3.0								9.0		10.0	9.0	11.0	12.0		13.0–14.0				
	TL	10.5								22.0		24.0	25.0	27.0	28.0		29.0				
minutus	n	14	1		2	1	2									1					1
	HB	3.5–5.5	6.5		6.5	7.0	7.5–8.5									9.0					8.0
	TL	9.0–15.0	16.5		18.5–20.0	20.0	20.5–23.5									24.5					8.0+
opisthomelas	n		4	3	2	2	2	1	1			2	2	1		4	1				
	HB		6.0–8.0	5.0–9.0	6.0–9.0	8.0	7.5–8.0	7.0	9.0			7.5	8.0–9.0	8.5		9.0–10.0	9.0				
	TL		18.5–21.0	15.0–19.0	18.5–23.5	19.0	19.0–23.0	17.5	20.0			21.5–22.5	23.0–25.5	23.5		23.0–27.0	25.0				
pumilio	n	1	2		4												2	1			
	HB	3.0	3.0–3.5		3.0–4.5												8.5–9.0	10.0			
	TL	8.0	9.0–9.5		8.5–12.5												20.0–22.0	21.0			
tinctorius	n	9	3	5	2	1								2	1		2			1	
	HB	5.5–9.0	9.5–10.5	11.0–12.0	13.0–13.5	13.5								14.0–16.0	14.0		15.5–16.0			15.5	
	TL	13.5–19.0	22.0–26.0	26.0–30.5	31.5–34.5	34.5								35.5	34.0		35.5–39.5			27.5	

TABLE 5

Species and subspecies described as or referred to *Dendrobates*. All names in first column were described as *Dendrobates* unless otherwise indicated. Subspecies are listed under their species.

NAME	AUTHOR AND DATE	OPINION ON STATUS
altobueyensis	new species	*Dendrobates altobueyensis*
amoenus	Werner 1901	*Dendrobates auratus*
aurata (Hyla)	Wied 1821	not *Dendrobates;* status uncertain
auratus (Phyllobates)	Girard 1855	*Dendrobates auratus*
aurotaenia	Boulenger 1913	*Phyllobates aurotaenia*
azureus	Hoogmoed 1969	*Dendrobates azureus*
bassleri	Melin 1941	*Phyllobates bassleri*
betsileo	Grandidier 1872	*Mantella betsileo*
braccatus	Fitzinger *in* Steindachner 1864	*Phyllobates pictus*
braccatus	Cope 1887	*Phyllobates pictus*
chocoensis (Phyllobates)	Posada Arango 1869	*Phyllobates bicolor*
ebenaui	Boettger 1880	*Mantella betsileo*
eucnemis	Fitzinger *in* Steindachner 1864	*Phyllobates pictus*
fantasticus	Boulenger 1883	*Dendrobates quinquevittatus*
flavopicta (Hylaplesia)	A. Lutz 1925	*Phyllobates pictus*
fulguritus	new species	*Dendrobates fulguritus*
galactonotus	Fitzinger *in* Steindachner 1864	*Dendrobates galactonotus*
galindoi	Trapido 1953	*Dendrobates pumilio*
granuliferus	Taylor 1958	*Dendrobates granuliferus*
hahneli	Boulenger 1883	*Phyllobates pictus*
histrionicus	Berthold 1845	*Dendrobates histrionicus*
histrionicus confluens	Funkhouser 1956	*Dendrobates histrionicus*
histrionicus sylvaticus	Funkhouser 1956	*Dendrobates histrionicus*
ignitus	Cope 1874a	*Dendrobates pumilio*
ingeri	Cochran and Goin 1970	*Phyllobates ingeri*
inhambanensis	Bianconi 1849	*Phrynomerus bifasciatus*
labialis	Cope 1874b	*Phyllobates* ?; status uncertain
lateralis	Guichénot 1848	*Eupsophus taeniatus*
latimaculatus	Bibron *in* Günther 1858	*Dendrobates auratus*
leucomelas	Fitzinger *in* Steindachner 1864	*Dendrobates leucomelas*
lugubris	O. Schmidt 1857	*Phyllobates lugubris*
machadoi	Bokermann 1958	*Dendrobates tinctorius*
madagascariensis	Grandidier 1872	*Mantella madagascariensis*
minutus minutus	Shreve 1935	*Dendrobates minutus*
minutus ventrimaculatus	Shreve 1935	*Dendrobates quinquevittatus*
nigerrima (Hyla)	Spix 1824	*Phyllobates trivittatus* ?
nigriventris (Hylaplesia)	A. Lutz 1925	*Eleutherodactylus nigriventris*
obscurus	Duméril and Bibron 1841	*Dendrobates*; status uncertain
opisthomelas	Boulenger 1899	*Dendrobates opisthomelas*
paraensis	Boulenger 1913	*Dendrobates galactonotus*
parvulus	Boulenger 1882a	*Phyllobates parvulus*
phantasticus	Werner 1901	Emendation of *D. fantasticus*
picta (Hylaplesia)	Bibron *in* Tschudi 1838	*Phyllobates pictus*
pictus guayanensis	Heatwole, Solano and Heatwole 1965	*Phyllobates pictus*
pumilio	O. Schmidt 1857	*Dendrobates pumilio*
quinquevittatus	Fitzinger *in* Steindachner 1864	*Dendrobates quinquevittatus*
ranoides	Boulenger 1918	*Colostethus ranoides*
reticulatus	Boulenger 1883	*Dendrobates quinquevittatus*
shrevei	Dunn 1940	*Dendrobates minutus*
speciosus	O. Schmidt 1857	*Dendrobates speciosus*
steyermarki	Rivero 1971	*Dendrobates steyermarki*
talamancae	Cope 1875	*Colostethus talamancae*
tetravittatus	Miranda Ribeiro 1926	*Phyllobates trivittatus*
tinctorius (Calamita)	Schneider 1799	*Dendrobates tinctorius*
tinctorius cocteai	Boulenger 1913	Emendation of *D. t. cocteaui*
tinctorius cocteaui	Steindachner 1864	*Dendrobates histrionicus*
tinctorius daudini	Steindachner 1864	*Dendrobates tinctorius*
tinctorius igneus	Melin 1941	*Dendrobates quinquevittatus*
tinctorius vittatus	Cope 1893	*Phyllobates vittatus*
tinctorius wittei	Laurent 1942	*Dendrobates histrionicus*
tinctorum	Fowler 1916	Emendation of *D. tinctorius*
trivittata (Hyla)	Spix 1824	*Phyllobates trivittatus*
trivittatus maculatus	W. Peters 1874	*Dendrobates auratus* ?
truncatus (Phyllobates)	Cope 1861	*Dendrobates truncatus*
typographicus	Oertter 1951	Emendation of *D. typographus*
typographus	Keferstein 1867	*Dendrobates pumilio*

nym of *Eupsophus taeniatus*, a leptodactylid frog (J.M. Cei personal communication).

Three species are of uncertain status. *Hyla aurata* Wied 1821 has been thought to be a *Dendrobates*. The type specimen had half-webbed toes; thus it was not a *Dendrobates* nor a *Phyllobates*. The type is not at AMNH and probably is lost. *Dendrobates labialis* Cope 1874b probably is a species of *Phyllobates*. The type specimen is lost, and the description is inadequate. *Dendrobates obscurus* Duméril and Bibron 1841, from an unknown locality, was synonymized with *D. trivittatus* (Spix) by W. Peters (1873). The specimen now labeled as the holotype of *D. obscurus* (MHNP 4906) is not *D. trivittatus*. It is a specimen of *Dendrobates* that has lost its color pattern; I cannot identify it to species. It differs from the original description (in the original description, the snout-vent length was 42 mm, the dorsum granular, the finger disks relatively small, and the first finger longer than the second; in MHNP 4906, the snout-vent length is 31.5 mm, the dorsum smooth, the finger disks relatively large, and the first finger shorter than the second). MHNP 4906 may not be the original holotype.

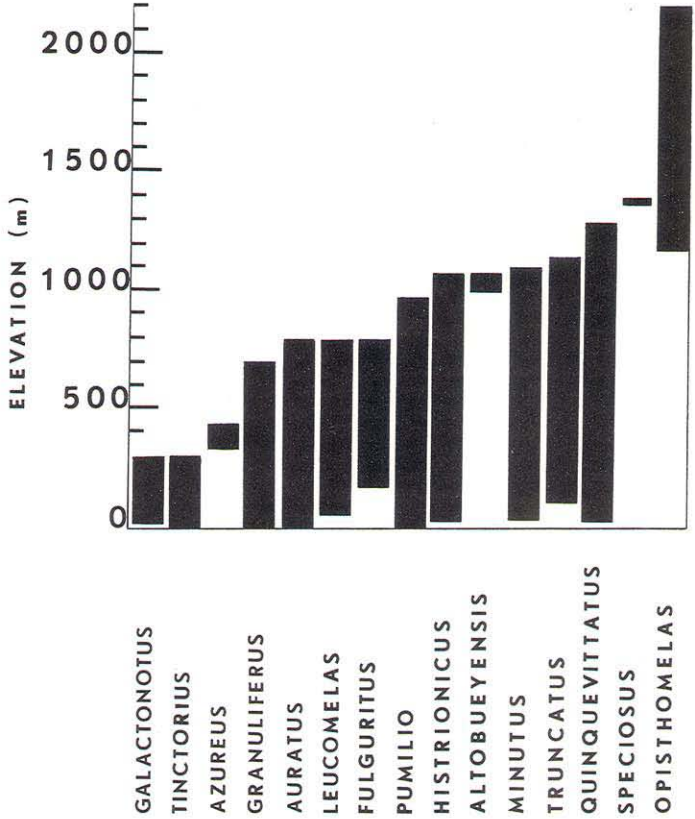


FIGURE 5. Elevation records (in meters) of 15 species of the genus *Dendrobates*.

Content.—As defined here, the genus *Dendrobates* contains 16 species: *Dendrobates altobueyensis* new species, *D. auratus* (Girard 1855), *D. azureus* Hoogmoed 1969, *D. fulguritus* new species, *D. galactonotus* Fitzinger *in* Steindachner 1864, *D. granuliferus* Taylor 1958, *D. histrionicus* Berthold 1845, *D. leucomelas* Fitzinger *in* Steindachner 1864, *D. minutus* Shreve 1935, *D. opisthomelas* Boulenger 1899, *D. pumilio* O. Schmidt 1857, *D. quinquevittatus* Fitzinger *in* Steindachner 1864, *D. speciosus* O. Schmidt 1857, *D. steyermarki* Rivero 1971, *D. tinctorius* (Schneider 1799), and *D. truncatus* (Cope 1861).

Key to the species of Dendrobates

1a. Omosternum present (Fig. 2C) 3
1b. Omosternum absent (Fig. 2B) 2

2a (1b). Wide light (yellow or orange in life) transverse dorsal bands with intrusions and spots of black ground color (Frontispiece II); snout-vent length of adults 30.5–37.5 mm; east of the Andes in the Guianan region of Colombia, Venezuela, and Guyana. . . . . *D. leucomelas* (page 26)

2b. Transverse dorsal bands usually absent (Frontispiece I; Fig. 13); if present, without intrusions and spots of ground color (Figs. 13L–O); snout-vent length of adults 24–38 mm; west of the Andes in the Chocoan region of Colombia and Ecuador . . . . . *D. histrionicus* (page 18)

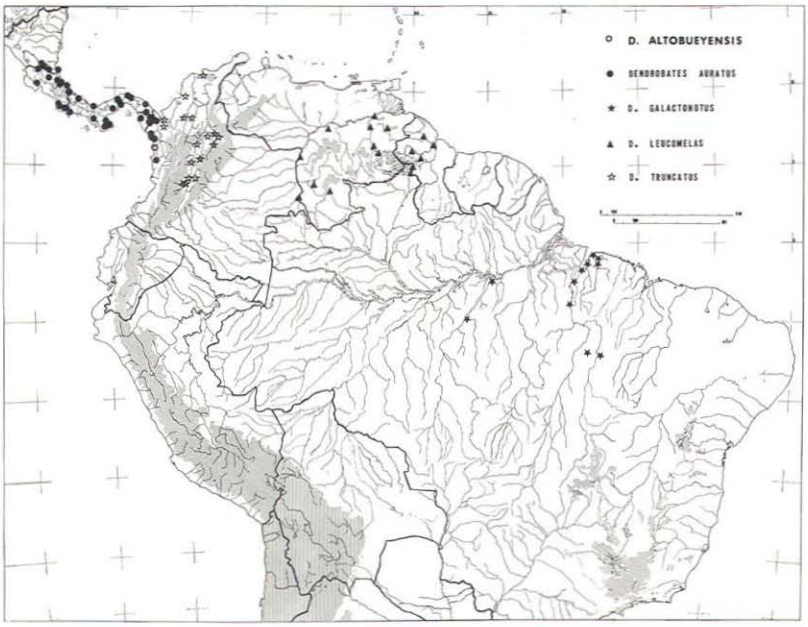


FIGURE 6. Distribution of *Dendrobates altobueyensis*, *D. auratus*, *D. galactonotus*, *D. leucomelas*, and *D. truncatus*. Areas above 1000 m elevation shaded.

3a (1a). Dorsum striped 4
3b. Dorsum not striped 9

4a (3a). Snout-vent length of adults less than 22 mm 5
4b. Snout-vent length of adults greater than 23 mm 7

5a (4a). Venter and limbs usually partly or entirely reticulated in pattern (Figs. 12B–D), rarely spotted (Fig. 12A) or marbled (Fig. 12E); snout-vent length of adults 14.5–21.5 mm; Amazon drainage and Guianas (Frontispiece II; Fig. 14) . . . . . *D. quinquevittatus* (page 33)
5b. Venter and limbs not reticulated in pattern 6

6a (5b). Venter light (gold or yellow in life) with black spots or marbling (Fig. 16, left); incomplete median stripe on anterior portion of dorsum (Fig. 11A); snout-vent length of adults 13.5–16.5 mm; Chocoan region of Colombia . . . . . *D. fulguritus* (page 28)
6b. Venter dark (black or brown in life) with light (blue or white in life) spots or marbling (Fig. 16, right); usually no median stripe on anterior portion of dorsum (Fig. 11B); snout-vent length of adults 12–15.5 mm; Panamá and Chocoan region of Colombia. . . . . *D. minutus* (page 30)

FIGURE 7. Distribution of *Dendrobates steyermarki, D. granuliferus, D. histrionicus,* and *D. pumilio.* Areas above 1000 m elevation shaded.

7a (4b). Venter and limbs usually partly or entirely reticulated in pattern (Figs. 12F–G); snout-vent length of adults 34–50 mm; Guianas and adjacent Brasil (Frontispiece I; Fig. 15) . *D. tinctorius* (page 45)

7b. Venter and limbs not reticulated in pattern; snout-vent length of adults 23.5–42 mm 8

8a (7b). Skin of dorsum slightly granular; dorsolateral stripes relatively narrow and yellow in life (Frontispiece II); snout-vent length of adults 23.5–31 mm; Magdalena Valley and Caribbean coastal plain of Colombia, west to Golfo de Urabá (Figs. 12K–L) . . . . . *D. truncatus* (page 49)

8b. Skin of dorsum smooth; dorsolateral stripes relatively broad and blue, blue-green, green, or yellow-green in life (Frontispiece II); snout-vent length of adults 25–42 mm; Caribbean lowlands from Nicaragua to Golfo de Urabá (Colombia), and Pacific lowlands from Costa Rica to Chocoan region of Colombia (Figs. 12I–J) . . . . . *D. auratus* (page 40)

9a (3b). Snout-vent length of adults 24 mm or less 10

9b. Snout-vent length of adults 25 mm or more 15

10a (9a). Venter and limbs usually partly or entirely reticulated in pattern (Figs. 12B–D), rarely spotted (Fig. 12A) or marbled (Fig. 12E); snout-vent length of adults 14.5–21.5 mm; Amazon drainage and Guianas (Fig. 14) . . . . . *D. quinquevittatus* (page 33)

10b. Venter and limbs not reticulated in pattern 11

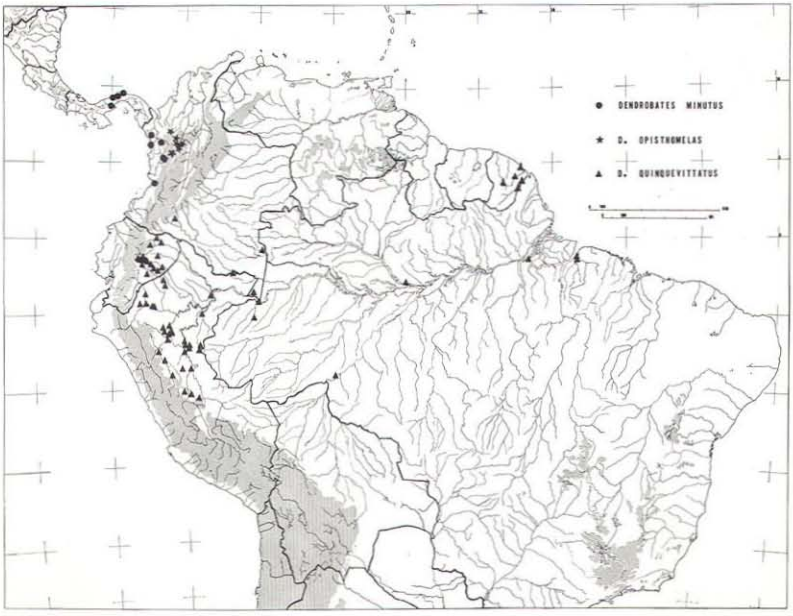


FIGURE 8. Distribution of *Dendrobates minutus*, *D. opisthomelas*, and *D. quinquevittatus*. Areas above 1000 m elevation shaded.

11a (10b). Tarsal tubercle usually well developed (this tubercle occurs at the proximal end of the tarsal fold, at about the midpoint of the tarsus) 12

11b. Tarsal tubercle absent or slightly developed 13

12a (11a). Skin of belly slightly to moderately, but distinctly, granular; snout-vent length of adults 14.5–19.5 mm; 1160–2200 m or higher in Andes of Colombia (Frontispiece II; Figs. 12N–O) . . . . . *D. opisthomelas* (page 31)

12b. Skin of belly smooth; snout-vent length of only known specimen 16 mm; 1200 m on Cerro Yapacana in Guianan region of Venezuela. . . . . *D. steyermarki* (page 36)

13a (11b). Dorsum strongly granular; dorsum lacks black dots or spots; snout-vent length of adults 19–22 mm; Golfo Dulce region of Pacific lowlands of Costa Rica (Frontispiece II) *D. granuliferus* (page 36)

13b. Dorsum smooth or slightly granular; dorsum often has black dots or spots 14

14a (13b). Color usually red (in life; color variable in western Panamá); venter and limbs sometimes different color than dorsum; snout-vent length of adults 17.5–24 mm; Caribbean lowlands of Central America from Nicaragua to western Panamá (Figs. 11H–K, 12M) . . . . . *D. pumilio* (page 37)

14b. Color yellow or gold (in life); venter and limbs same color as dorsum; snout-vent length of two known adults 15.5–17 mm; Alto del Buey in Chocoan region of Colombia (Frontispiece I) . . . . . *D. altobueyensis* (page 27)

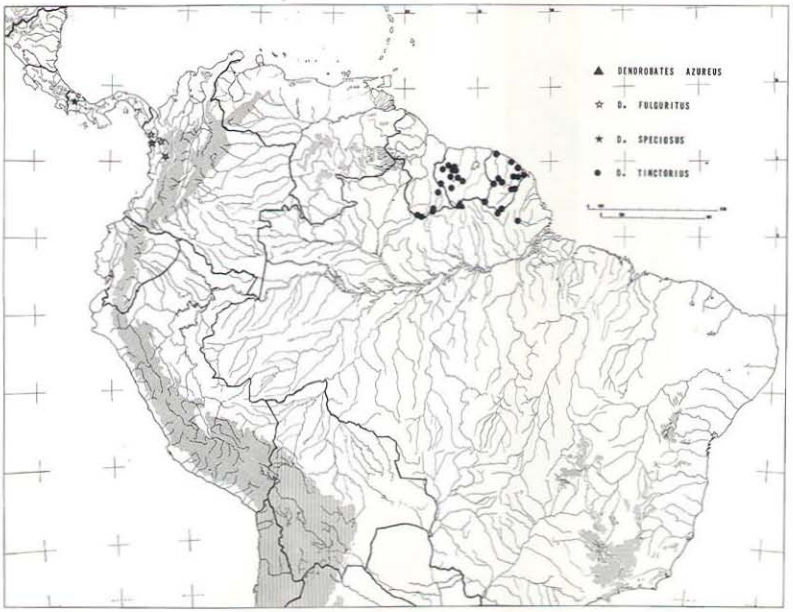


FIGURE 9. Distribution of *Dendrobates azureus*, *D. fulguritus*, *D. speciosus*, and *D. tinctorius*. Areas above 1000 m elevation shaded.

15a (9b). Tarsal tubercle well developed (this tubercle occurs at the proximal end of the tarsal fold, at about the midpoint of the tarsus); snout-vent length of adults 30.5–40.5 mm; lowlands of lower Amazon drainage (Figs. 11F–G). . . . . *D. galactonotus* (page 44)

15b. Tarsal tubercle absent or slightly developed 16

16a (15b). Body usually partly or entirely reticulated in pattern (Figs. 11E, 12F–G), rarely spotted (Fig. 12H); Guianan region of South America (east of the Andes) 17

16b. Body not reticulated in pattern; Central America and Chocoan region of South America (west of the Andes) 18

17a (16a). Tympanum equals one-third diameter of eye; posture hunch-backed (in life); snout-vent length of adults 38.5–45 mm; Suriname-Brasil border (Figs. 11E, 12H) . . . . . *D. azureus* (page 43)

17b. Tympanum equals one-half diameter of eye; posture not hunch-backed (in life); snout-vent length of adults 34–50 mm; Guianas and adjacent northern Brasil (Figs. 11C–D, 12F–G, 15) . . . . . *D. tinctorius* (page 45)

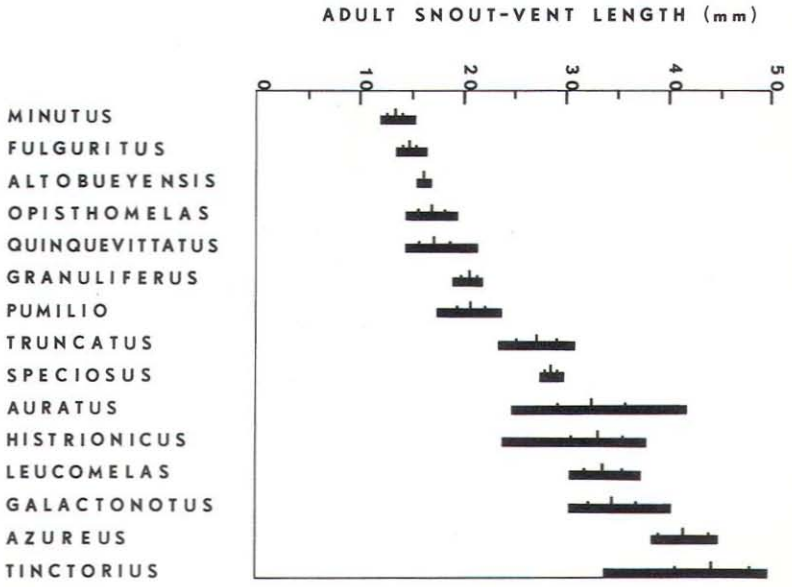


FIGURE 10. Snout-vent length (in millimeters) of 1658 adult specimens of 15 species of the genus *Dendrobates*, arranged by mean snout-vent length, showing range, mean, and one standard deviation on each side of mean. Sexes are combined.

18a (16b). Dorsum unicolor (red or red-orange in life); snout-vent length of adults 27.5–30 mm; mountains of western Panamá (has been collected at 1372 m) (Fig. 17) . . . . . *D. speciosus* (page 39)

18b. Dorsum not unicolor (never red or red-orange in life); dorsum dark (black or brown in life) with light (blue, blue-green, green, or yellow-green in life) spots or curving bands; snout-vent length of adults 25–42 mm; Caribbean lowlands from Nicaragua to Golfo de Urabá (Colombia), and Pacific lowlands from Costa Rica to Chocoan region of Colombia (Figs. 11L–P, 12I–J) . . . . . *D. auratus* (page 40)

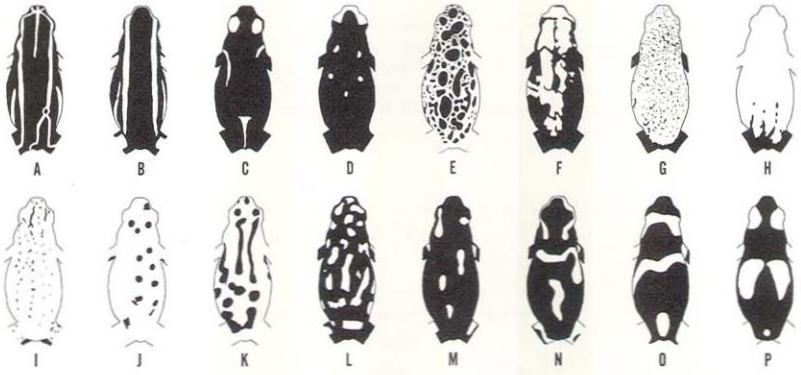


FIGURE 11. Dorsal pattern variations in *Dendrobates*. (A) *D. fulguritus*, holotype, Playa de Oro, Colombia (LACM 42319); (B) *D. minutus*, Finca Chibiguí, Colombia (from series LACM 43838–43); (C) *D. tinctorius*, Tafelberg, Suriname (RMNH 13853); (D) *D. tinctorius*, Linker Coppename Rivier, Suriname (ZMA 157k); (E) *D. azureus*, paratype, Sipaliwini, Suriname (RMNH 13843f); (F) *D. galactonotus*, holotype, Rio do Muria, Brasil (NHMW 19189); (G) *D. galactonotus*, Cachoeira Cahy, Brasil (ZSBS 14/1914); (H) *D. pumilio*, Finca La Selva, Costa Rica (from photo by J.T. Kitasako); (I) *D. pumilio*, Finca La Lola, Costa Rica (from photo by J.T. Kitasako); (J-K) *D. pumilio (D. galindoi*, paratypes), Isla Bastimentos, Panamá (from series FMNH 71054–87); (L) *D. auratus*, Nicuesa, Panamá (MCZ 16015); (M) *D. auratus*, confluence Ríos Truandó and Nercua, Colombia (from series LACM 60983, 61052–55); (N) *D. auratus*, Camino de Yupe, Colombia (from series LACM 44230–55); (O-P) *D. auratus*, Cerro Los Hermanos, Colombia (from series LACM 44224–28). Body outlines diagrammatic and not to scale.

histrionicus group

This group contains two species (*D. histrionicus* and *D. leucomelas*).

Definition: snout-vent length of adults moderate (24–38 mm); stripes absent; color in life sometimes red; dorsal skull bones often fused together and sculptured; omosternum absent; tadpoles (known only in *D. histrionicus*) have oral disk unindented, denticles reduced in number, and anus median.

Dendrobates histrionicus Berthold 1845
Kôkoé-pá

Frontispiece I and Figure 13

1841. *Dendrobates tinctorius* (part, var B). Duméril and Bibron: 652–654.

1845. *Dendrobates histrionicus* Berthold: 43–44, type locality: Popayán, Colombia.

1858. *Hylaplesia tinctoria* (part, var C, F). Günther: 125.

1864. *Dendrobates tinctorius* (part, var *cocteaui)*. Steindachner: 260–262.

1913. *Dendrobates tinctorius* (part, var *coctaei* and *chocoensis*; the name *chocoensis* is misapplied [I consider *P. chocoensis* Posada a synonym of *P. bicolor* Bibron *in* Sagra]). Boulenger: 1026-1028, plate 104, figs. 2-6.

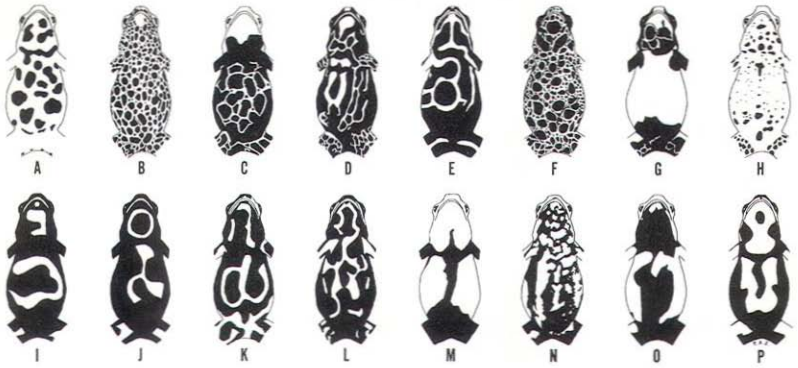


FIGURE 12. Ventral pattern variations in *Dendrobates*. (A) *D. quinquevittatus*, holotype, Salto do Girao, Brasil (NHMW 16517); (B) *D. quinquevittatus* (syntype, *D. reticulatus*), Yurimaguas, Perú (BM 1947.2.15.10); (C) *D. quinquevittatus* (syntype, *D. fantasticus*), Yurimaguas, Perú (BM 1947.2.15.3); (D) *D. quinquevittatus*, Río Pachitea, Perú (TNHC 36488); (E) *D. quinquevittatus*, Achinamisa, Perú (UMMZ 89980); (F) *D. tinctorius*, New River, Guyana (BM 1939.1.1.16); (G) *D. tinctorius*, Rivière Matarony, French Guiana (from series LACM 43922–31); (H) *D. azureus*, holotype, Sipaliwini, Suriname (RMNH 13837a); (I-J) *D. auratus*, Camino de Yupe, Colombia (from series LACM 44230–55); (K) *D. truncatus*, syntype, "New Grenada" (ANSP 2251); (L) *D. truncatus*, Mariquita, Colombia (from series LACM 44269–76); (M) *D. pumilio*, Finca La Selva, Costa Rica (from photo by J.T. Kitasako); (N) *D. opisthomelas*, syntype, Santa Inés, Colombia (BM 1947.2.15.29); (O) *D. opisthomelas*, Santa Rita, Colombia (from series LACM 43881–97); (P) *D. fulguritus*, paratype, Camino de Yupe, Colombia (from series LACM 42314–18). Body outlines diagrammatic and not to scale.

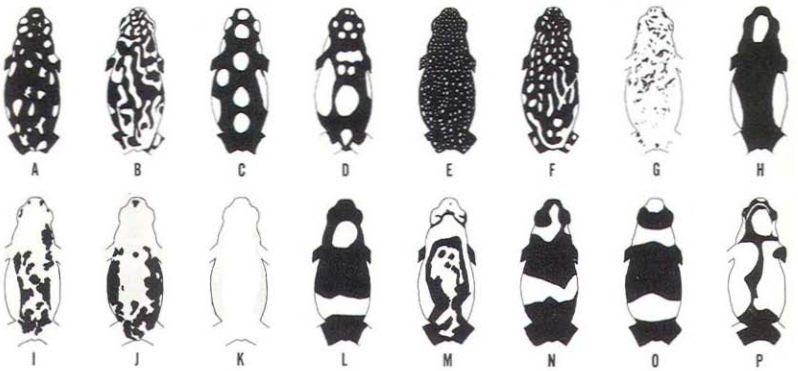


FIGURE 13. Pattern variations in *Dendrobates histrionicus*, dorsal aspect (A-O) and ventral aspect (P). Subpattern 1a (A-D); Subpattern 1b (E); Subpattern 1c (F); Pattern 2 (G); Subpattern 3a (H); Subpattern 3b (I-J); Subpattern 3c (K); Pattern 4 (O). Transitions to Pattern 4: from Subpattern 3a (L); from Subpattern 3b (M); from Subpattern 1a (N). (A) *D. h. wittei*, holotype, Los Mangos (=Los Cisneros), Colombia (MRHN 1038); (B) Jiménez, Colombia (from series BM 1908.5.29.55–62); (C-D) upper Río Napipí, Colombia (from series LACM 42784–43027); (E) Quebrada Pangala, Colombia (AMNH uncat); (F) *D. h. sylvaticus*, paratype, Hacienda Espinosa, Ecuador (CAS-SU 10576); (G) *D. h. confluens*, paratype, Madrigar, Colombia (USNM 145801); (H) Río Arquía, Colombia (from series LACM 42552–653); (I) trail between Quebrada Bochoramá and Río Tadocito, Colombia (from series LACM 43716–41); (J) trail between Playa de Oro and Quebrada Bochoramá, Colombia (LACM 43710); (K) Peña Lisa, Colombia (BM 1913.11.12.82); (L) same series as H; (M) same series as I; (N) Alto del Buey, Colombia (LACM 71817); (O) purchased in Cali, Colombia, probably from west of the Andes (from series LACM 43900–03); (P) same series as C-D. Body outlines diagrammatic and not to scale.

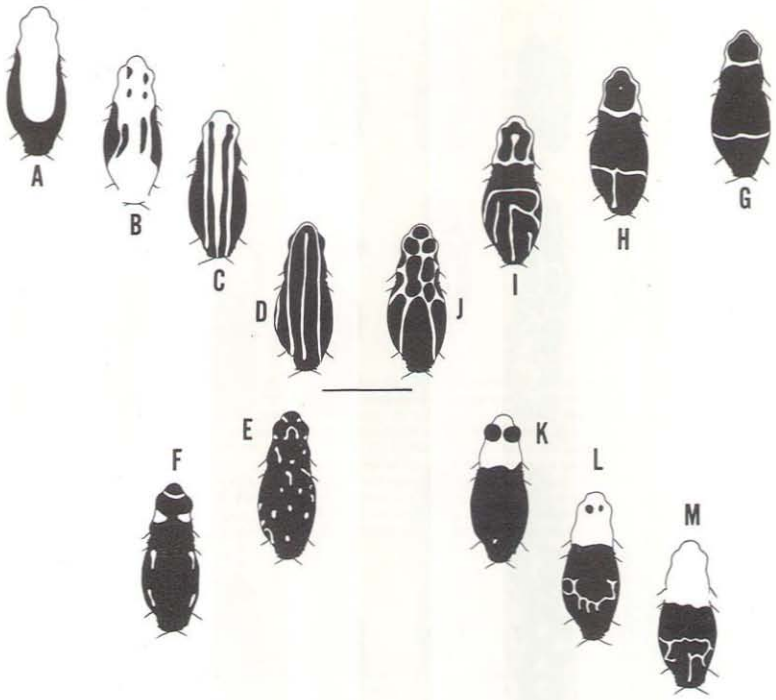


FIGURE 14. Dorsal pattern variations in *Dendrobates quinquevittatus*. Subpattern 1a (D); Subpattern 1b (J); Pattern 2 (G); Pattern 3 (E-F); Subpattern 4a (M); Subpattern 4b (A). Transitions are shown as follows: from Pattern 1 to Pattern 4b: center to upper left (D-A); from Pattern 1 to Pattern 4a: center to lower right (J-M); from Pattern 1 to Pattern 3: center to lower left (J-F); from Pattern 1 to Pattern 2: center to upper right (J-G). (A) *reticulatus* pattern, Iquitos, Perú (AMNH 43612); (B-C) Río Itaya near Iquitos, Perú (AMNH 43600, 43469); (D) *D. quinquevittatus*, holotype, Salto do Girao, Brasil (NHMW 16517); (E) Río Pachitea, Perú (TNHC 36499); (F) Río Apaporis, Colombia (MCZ 28061); (G) Sausi, Perú (AMNH 43056); (H) Chazuta, Perú (AMNH 42792); (I) Achinamisa, Perú (AMNH 42514); (J) Gallenazo, Perú (LACM 72063); (K) Domo Santa Clara, Perú (USNM 127933); (L) northern Perú (NHMW 3828:1); (M) *fantasticus* pattern (*D. fantasticus*, syntype), Yurimaguas, Perú, (BM RR.1947.2.15.4) Line equals one centimeter.

1942. *Dendrobates tinctorius* (part, *D. t. chocoensis, D. t. histrionicus, D. t. wittei*); *Dendrobates tinctorius wittei* Laurent: 12-14, figs. 13-14, 17-20, holotype: MRHN 1038, Los Mangos, Colombia.

1956. *Dendrobates histrionicus sylvaticus* Funkhouser: 73-74, plate 1, fig. 1, holotype: CAS-SU 10568, Hacienda Espinosa, 9 km W Santo Domingo de los Colorados, Pichincha, Ecuador.

1956. *Dendrobates histrionicus confluens* Funkhouser: 75-76, holotype: CAS-SU 13151, La Ciudad de Madrigar, 1°46'N, 77°30'W, Nariño, Colombia.

1970. *Dendrobates lugubris* (part). Cochran and Goin: 19-21 (not the plate).

1970. *Phyllobates bicolor* (part). Cochran and Goin: 35-37 (BM 1910.7.11.53 only).

1970. *Dendrobates tinctorius wittei, D. t. histrionicus, D. t. chocoensis, D. t. confluens*. Cochran and Goin: 26-28, plate 5A-C; 28-31, plate 4G-I; 31-32, plate 4A-C; 32-34, plate 4D-F.

1971. *Dendrobates histrionicus*. Daly et al.: plate 1A-G (color photos).

Definition.—Snout-vent length of adults 24-38 mm; skin of back smooth; tarsal tubercle absent; color in life: spots (or rarely bands) of red, red-

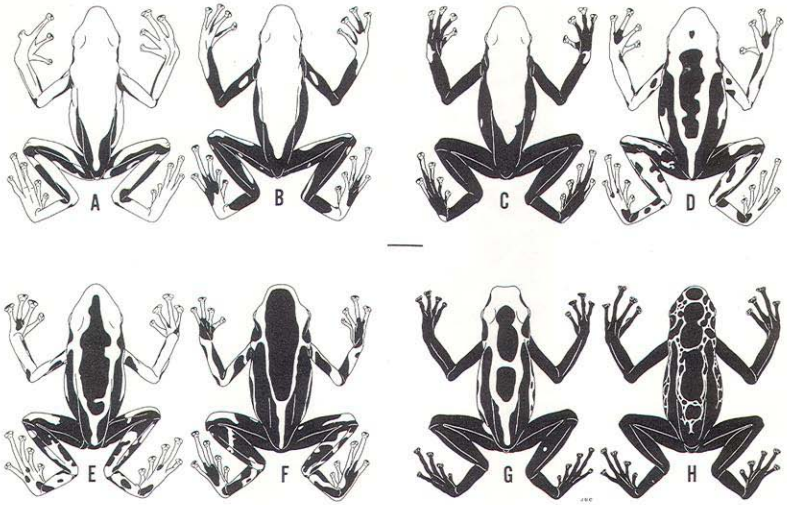


FIGURE 15. Dorsal pattern variations in *Dendrobates tinctorius*. (A-B, D-G) Oyapock drainage, French Guiana (MHNP); (C) between Dorlin and Sophie, French Guiana (MCZ 43509); (H) New River, Guyana (BM). Line equals one centimeter. B. Shreve donated this figure.

orange, orange, yellow-orange, yellow, or white on ground color of black, dark brown, light brown, tan, white, or orange; rarely, dorsum unicolor orange; no stripes or reticulation, no green or blue; omosternum absent.

Diagnosis.—*D. histrionicus* is a member of the *histrionicus* group, differing from *D. leucomelas* in usually lacking light transverse dorsal bands; when present, the bands lack intrusions of ground color (*D. leucomelas* always has light transverse dorsal bands containing numerous spots and intrusions of ground color). *D. histrionicus* differs from *D. speciosus* in lacking an omosternum.

Description.—Measurements are in Tables 3 and 6; the smallest specimens are from the northern and southern extremes of the range. The skin is smooth, except the posterior belly and ventral surface of the thighs, which are granular or rugose. The tympanum is round, and its diameter equals one-half of the diameter of the eye. The finger disks are not sexually dimorphic. The tarsal tubercle is absent.

Variation in color and color pattern is mostly interpopulational, and is greatest on the upper San Juan drainage, and relatively minor on the western Atrato drainage. The main color patterns in life are as follows: Pattern 1: This pattern is black with small to medium-sized red dorsal spots, and may be divided into three subpatterns: Subpattern 1a (Frontispiece I; Figs. 13A-D, P; includes *D. h. wittei* Laurent 1942; variety *coctaei* Boulenger 1913, part): This subpattern is known from the western Atrato drainage, the Baudó drainage, the Alto del Buey, and the middle and lower San Juan drainage. The ground color is black, with spots of red, red-orange, or orange in different individuals from the same populations. The dorsum has four to 20 small to medium-sized spots, sometimes in a median row (Fig. 13C). The upper arms, lower arms, thighs, calves, and feet have wide bracelets (often incomplete ventrally) of the same color as the dorsal spots. The venter usually has large, often confluent spots (Fig. 13P).

Subpattern 1b (Fig. 13E): This subpattern is known from the lower San Juan drainage. The markings are small, close-set red or orange spots or tiny dots on a black ground color.

Subpattern 1c (Fig. 13F; includes *D. h. sylvaticus* Funkhouser 1956): This subpattern is known from

FIGURE 16. Ventral patterns of *Dendrobates fulguritus* (left: paratype, Camino de Yupe, Colombia, from series LACM 42314-18) and *D. minutus* (right: Belén, Colombia, LACM 43802). Line equals one millimeter.

FIGURE 17. *Dendrobates speciosus*, 28.5 mm female, Gutiérrez, Panamá (LACM 60998), dorsal aspect.

northwestern Ecuador (Provincia Pichincha). The dorsum and venter have very close-set red or red-orange spots, sometimes reducing the ground color to black marbling. The limbs have fewer spots or are mostly black, and lack bracelets.

Pattern 2 (Fig. 13G; includes *D. h. confluens* Funkhouser 1956): This pattern is known from extreme southwestern Colombia (Departamento Nariño) and northwestern Ecuador (Provincia Esmeraldas); one specimen with this pattern was also taken at Andagoya, Colombia (Departamento Chocó). The dorsum is nearly unicolor orange with black scratchings; the venter is the same or with more extensive black, and the limbs are yellowish.

Pattern 3: This pattern has large spots of variable color, and may be divided into three subpatterns: Subpattern 3a (Frontispiece I; Fig. 13H, L; includes *D. h. histrionicus* Berthold 1845): This subpattern is known from the eastern Atrato drainage (Río Arquía) and the upper Río San Juan. The spots and the ground color vary within the same populations (in an individual, the ground color of the dorsum may differ from that of the venter). The spots are red, red-orange, or orange, and are outlined with dark brown when the ground color is light brown. The ground color is black, chocolate brown, or light brown with a yellowish tinge. The head has a large, oblong dorsal spot, sometimes broken in two, and usually a pair of lateral spots, extending onto the throat. The sacral region sometimes has a small or large spot. Each side of the body has a large spot, which sometimes extends onto the venter and sometimes is confluent with the sacral spot, forming a transverse band (Fig. 13L). The limbs have bracelets as in Subpattern 1a.

Subpattern 3b (Figs. 13I–J, M; includes variety *coctaei* Boulenger 1913, part): This subpattern is known from the upper San Juan drainage and the Río Condoto. The dorsum is heavily mottled with chocolate brown on a tan, orange, or light brown ground color. The limbs have bracelets, and the dorsum and sides have large spots of orange, yellow-orange, yellow, or pale yellow (nearly white); the spots sometimes have intrusions of ground color. One specimen, from the upper San Juan drainage, has a small orange spot in the middle of a large pale yellow lateral spot; another specimen, from the same locality, has the lateral spots and head-spot confluent, forming a transverse neck-band (Fig. 13M). Rarely, the spots are absent (Fig. 13J). The venter is chocolate brown or black.

Subpattern 3c (Fig. 13K; includes variety *chocoensis* as used by Boulenger 1913): This subpattern is known from the Ríos San Juan and Condoto. The limbs and sometimes the dorsum have orange spots. The sides of the body and of the belly have large orange spots outlined with brown; these orange spots become brown in preservative. The ground color of

TABLE 6

Snout-vent length of samples of adults from eight populations of *Dendrobates histrionicus*, arranged in order from north to south. COLOMBIA: (1) Camino de Yupe, (2) upper Río Napipí, (3) west of Finca Chibiguí, (4) Quebrada Bochoramá, (5) trail between Quebrada Bochoramá and Río Tadocito, (6) Quebradas Taparal and Docordó, (7) La Guayacana. ECUADOR: (8) Santo Domingo de los Colorados.

Locality	All Specimens			Males			Females		
	n	Range	$\bar{x} \pm SE$	n	Range	$\bar{x}$	n	Range	$\bar{x}$
(1) Yupe	49	28.5–35.5	32.4±0.23	29	28.5–35.5	32.7	20	30.5–34.0	32.0
(2) Napipí	48	30.0–37.0	34.2±0.15	39	30.0–37.0	34.2	9	33.0–35.5	34.2
(3) Chibiguí	49	33.0–38.0	35.7±0.15	32	33.0–38.0	36.0	17	33.5–36.5	35.3
(4) Bochoramá	35	31.0–37.0	33.7±0.23	21	31.0–37.0	33.7	14	32.0–36.0	33.6
(5) Tadocito	26	30.5–37.0	35.0±0.29	17	30.5–37.0	34.9	9	33.0–36.5	35.1
(6) Taparal	15	33.0–38.0	35.1±0.40	9	34.0–35.5	34.7	6	33.0–38.0	35.8
(7) Guayacana	52	29.0–33.5	31.1±0.16	30	29.0–33.0	31.1	22	30.0–33.5	31.1
(8) Domingo	10	25.0–29.5	28.2±0.42	7	25.0–29.5	27.9	3	28.0–29.0	28.7

the dorsum and sides is tan or yellow, and that of the venter is chocolate brown and tan.

Pattern 4 (Fig. 13O): This pattern is known from specimens sold as pets (Cali, Colombia, is the shipping point, but the specimens probably come from west of the Andes); some specimens from the upper San Juan drainage (Fig. 13M), the Alto del Buey (Fig. 13N), and the Río Arquía (Fig. 13L) are transitional toward this pattern. This pattern is banded; the limb bracelets, the tip of the snout, and two transverse bands (one on the nape and one on the sacral region, the latter completely encircling the body) are red, red-orange, or orange. The ground color of the dorsum and venter is black.

Breeding call—The breeding call resembles the sound of a small saw on wood. It is a hoarse, rasping note, repeated regularly at about three notes per second, and emitted in an unbroken series for as long as four minutes and 40 seconds; given singly, the note resembles the quack of a duck. Calling sites are fallen logs and branches, standing trunks and buttresses, and herb and palm leaves. The mean height above ground for 71 observations of calling males on the Camino de Yupe, Colombia, was 56 cm (maximum 163 cm); calling rarely occurred on the ground, except during courtship pursuit (Silverstone 1973).

Tadpoles (Fig. 18).—Measurements are in Table 4. The oral papillae are few, large, in one row, and border the entire posterior lip, but border only the lateral portions of the anterior lip. The oral disk is not laterally indented. The denticle formula is $\frac{1-1}{1}$, $\frac{1-0}{1}$, or $\frac{0-1}{1}$. The denticles in the anterior row usually are reduced in number (the number of denticles on each side varies from zero to eight); the posterior denticle row is complete. The beaks are massive and serrate, and the lower beak is not indented. The eyes are dorsal. The spiracle is sinistral, very low, and difficult to discern. The dorsal fin does not reach the body. The anus is median. The tip of the tail is narrowly rounded. In preservative, the head–body is uniform dark gray, and the tail is uniform light tan.

I found tadpoles (LACM 71904: Stage 36, on 17 August on the Alto del Buey; LACM 71908: Stages 25, 33, 35–38, 41, on 11–14 June on the Camino de Yupe) and eggs (a clutch of three, on 13 June on the Camino de Yupe) on bromeliads (Silverstone 1973). The oldest tadpoles were acquiring the adult pattern (black with red spots).

Relationships.—Specimens representing all color patterns, including banded specimens purchased from a street vendor in Cali, Colombia, lack an omosternum and have the same breeding call; thus only one species is involved. This species and *D. leucomelas* are the only dendrobatids that lack an omosternum; they probably are closely related. The tadpole of *D. histrionicus* resembles that of *D. pumilio* in its reduced number of denticles and papillae. This suggests that the *histrionicus* group is more closely related to the *pumilio* group than to the other two groups of *Dendrobates*.

Life history—I saw aggressive behavior (wrestling and calling) between males on the Camino de Yupe, Colombia, and courtship behavior at several localities in the Chocoan region of Colombia. Both female pursuit of males and male pursuit of females occurred. The courtship behavior included calling, pursuing, touching, sitting, hugging, shaking, bowing, crouching, and circling (Silverstone 1973).

Three observations not mentioned in the paper cited above were as follows: In April, 1968, in forest

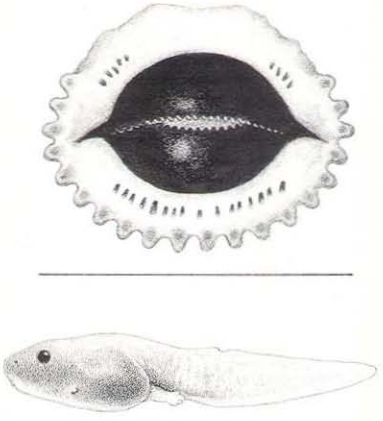


FIGURE 18. Tadpole of *Dendrobates histrionicus*, Camino de Yupe, Colombia (LACM 71908), from bromeliad leaf axil; mouth parts (Stage 33) and lateral aspect (Stage 35). Lines equal one millimeter.

near Finca Chibigui, Río Arquia, males were well spaced and called individually (not in chorus). Often a silent female was concealed beside an exposed calling male.

On 31 May 1968, on the Loma de Encarnación, a hill beside the Quebrada Bochoramá (upper San Juan drainage), a pair courted on the ground from 1025 to 1055 hrs. The male repeatedly uttered a single, quacklike note. The female turned in several tight half-circles, and sat beside the male, facing in the opposite direction. She shook her legs. The male shook his legs and his head. The female went under the fallen leaf on which the male sat. The male descended, faced the female, and shook his arms.

On 20 August 1971, on the Alto del Buey, Serranía de Baudó, a pair (sex determined by dissection) courted on the ground. The female (LACM 71867) crouched flat while the male (LACM 71868) sat behind her, facing her, and touching her back with his hands. The female turned in a half-circle in stages, and then crouched motionless. Then the male turned in a full circle in stages, ending by sitting on the posterior half of the female's back, facing away from her, but too far forward on her back for cloacal approximation to have occurred. The female did not oviposit.

Stomach contents (eight specimens).–From LACM 43246: HYMENOPTERA: Formicidae: *Gnamptogenys* sp (2), *Strumigenys* sp (1), *Pheidole* spp (14), *Solenopsis (Diplorhoptrum)* sp (4), *Smithistruma* sp (2), *Apterostigma* sp (1), Myrmecinae (21); ACARINA: mites of six families (50).

From LACM 43253: HYMENOPTERA: Formicidae: *Gnamptogenys mecotyle* Brown (1), *Strumigenys biolleyi* Forel (5), *Smithistruma* sp (1), *Wasmannia* sp (1), *Apterostigma sp (1), Solenopsis (Diplorhoptrum)* sp (14), *Pheidole* sp (6), *Hypoponera* sp (1); COLEOPTERA: Cisidae sp (4), Ptiliidae sp (1), Languriidae: *Crotchia* ? sp (larvae); THYSANOPTERA: Phlaeothripidae (1); ACARINA: mites of six families (50).

From LACM 43064: HYMENOPTERA: Formicidae: *Octostruma balzani* (Emery) (3), *Strumigenys subedentata* Mayr (1), *Strumigenys* sp (1), *Smithistruma* sp (5), *Cyphomyrmex rimosus* (Spinola) (5), *Pachycondyla* sp (1), *Rogeria* sp (1), *Trachymyrmex* sp (5), *Acromyrmex* sp (1), *Apterostigma* sp (1), *Hypoponera* sp (1), *Pseudomyrmex* sp (1), *Wasmannia auropunctata* (Roger) (14), *Irogera* spp (15), *Pheidole* spp (7), *Crematogaster* sp (1), *Paratrechina* sp (1), *Camponotus* sp (1), *Solenopsis (Diplorhoptrum)* sp (6), fragments (30); COLEOPTERA: Staphylinidae (1), Pselaphidae (1), Curculionidae (2); THYSANOPTERA: Phlaeothripidae (1); ACARINA: mites of five families (50).

From LACM 43732: HYMENOPTERA: Formicidae: *Pheidole* sp (3), *Hypoponera* sp (1), *Cyphomyrmex longiscapus* Weber (1), *Sericomyrmex* sp (1), *Octostruma* sp (1), *Paratrechina (Nylanderia)* spp (2); COLEOPTERA: Staphylinidae (1); ISOPTERA: (1).

From LACM 60985: HYMENOPTERA: Formicidae: *Hypoponera* sp (1), *Pheidole*, three spp (50), *Octostruma balzani* (Emery) (2), *Tapinoma* sp (1), *Azteca* sp (1), *Solenopsis (Diplorhoptrum)* sp (22), *Stenomma* sp (4); ACARINA: mites of four to six families (50).

From LACM 60986: HYMENOPTERA: Formicidae: *Solenopsis geminata* (Fabr.) (5), *Solenopsis (Diplorhoptrum)* sp. (11), *Pheidole* sp (2), *Wasmannia auropunctata* (Roger) (2), *Myrmicocrypta* sp (6), *Hypoponera* sp (1), *Gnamptogenys acuminata* Emery ? (1), *Strumigenys denticulata* Mayr (3), Braconidae (1), Bethylidae (1); COLEOPTERA: Pselaphidae (2), Chrysomelidae (1), Staphylinidae (4), Ptiliidae (4); LEPIDOPTERA: Microlepidoptera: larvae (4); HETEROPTERA: Aphididae (3), Miridae (1); DIPTERA: larvae (3); ACARINA: mites of several families (50).

From LACM 60987: HYMENOPTERA: Formicidae: fragments of *Wasmannia, Anochetus, Cyphomyrmex, Strumigenys, Smithistruma,* and *Rogeria.*

From JMS 1677: HYMENOPTERA: Formicidae: *Acanthognathus ocellatus* Mayr (2), *Octostruma stenognatha* Br. and Kempf (2), *Solenopsis geminata*

(Fabr.) (3), *Solenopsis*, two spp (6), *Crematogaster* sp (3), *Pheidole* spp (23); COLEOPTERA: Pselaphidae ? (2), Scolytidae (1); ISOPTERA: Termitidae: *Nasutitermes* sp (4); HETEROPTERA: Aphididae (1); DIPTERA: Syrphidae: larvae (2); ACARINA: mites of three families (100).

Predators.—At Peña Lisa, Río Condoto, Colombia, an unidentified snake that started to eat a live specimen of *D. histrionicus* quickly rejected the frog (Boulenger 1913).

Parasites.—I found larval nematodes encysted in the thigh and abdominal muscles of *D. histrionicus.*

Toxins.—The skin toxins (histrionicotoxins) of this species have been investigated by Daly et al. (1971). When I captured two living specimens of *D. histrionicus* on the Camino de Yupe, Colombia, they released a white skin toxin; this was unusual, since frogs of the genus *Dendrobates* usually release toxin only under extreme stress, not when seized by a human captor. The toxin tasted like capsicum pepper, and caused a burning sensation when applied to the tongue, to the lips, and to a small wound.

Ethnozoology.—The common name used by the Embená Chocó Indians on the Río Napipí (Atrato drainage) is chicororó, which may be a combination of the Spanish word *chico* (=small) and the Chocó word *bocorró* (=frog). *D. histrionicus* is called kōkoé-pá (in phonetic English: kohng-KWAY PAH) by the Chocó Indians of the Quebrada Bochoramá (upper San Juan drainage), who told me that, unlike the kōkoé *(Phyllobates aurotaenia)*, the species is not sufficiently poisonous to serve as a source of blowgun poison.

Nomenclature.—This species has long been called a subspecies of *D. tinctorius*. It is not conspecific with the large, striped Guianan species to which the name *D. tinctorius* is restricted herein.

Distribution and habitat (Fig. 7).—Elevation records are from 18 to 1070 m. *D. histrionicus* is known from the Chocoan region of western Colombia and northwestern Ecuador, west to the Pacific coast and east to the Andean foothills, in Holdridge's (1967) lowland tropical rain forest and lowland tropical wet forest zones. The wettest parts of the range lack a dry season. *D. histrionicus* is adapted to areas having high precipitation, and drops out in western Ecuador and extreme northwestern Colombia, where the annual precipitation is less, and the dry season is longer. It usually is found on the shady forest floor, but also occurs in low, bushy second growth in disturbed areas.

Localities.—COLOMBIA. ***Chocó:*** Ríosucio (USNM 144947); Serranía de Baudó (ANSP 25618–22, 25624–25); Alto del Buey (LACM 71673–904); Camino de Yupe, Serranía de Baudó, between upper Opogadó and Domingodó drainages (LACM 43183–708, 71908–27); upper Río Napipí near junction Río Merendó (LACM 42700–43182); Bahía de Utría (FMNH 81870; USNM 144991; ILS 188); upper Río Buey (LACM 61056–58; JMS 1662); Finca La Victoria, junction Ríos Pepé and Baudó (USNM 144986–90); road between Las Ánimas and Istmina (LACM 43709); Andagoya (LACM 42531–32, ILS 187; BM 1915.10.21.51–61, 1915.10.21.63–65, 1916.4.25.23; USNM 144941–44, 145791–92, 146839; FMNH 81850–53); 1 km W Andagoya (USNM 124218–32); Andagoya–Opogodó road, 4.8 km from Andagoya (USNM 124262–64); 120 km S Andagoya (USNM 139778); Finca La Granja, 30 km from Quibdó, upper Río Atrato (USNM 144945); Quibdó (ILS 145, 145a); Río San Pablo (AMNH 13695–701, 13703–05, 13707–09, 13712, 13716–19; USNM 147508–10); Quebrada Taparal, 20 km N Palestina, San Juan drainage (AMNH uncat; CAS 119886); Quebrada Pangala, San Juan drainage (AMNH uncat); Caño Docordó, between Cucurrupí and Noanamá, San Juan drainage (AMNH uncat; MCZ uncat); Noanamá (BM 1909.10.30.40); Juntas de Tamaná, Río Tamaná (BM 1910.7.11.53); Río Ingará, Tamaná drainage (BM 1915.10.21.48–50, 1915.10.21.50A); Peña Lisa, Río Condoto (BM 1913.11.12.81–88, 1914.5.21.78–80); Río Condoto (BM 1913.11.12.90–93, 1915.10.21.82–87); Tadó (BM 1910.7.11.51–52); Playa de Oro (LACM 43774–80; USNM 150626–30; FMNH 54226, 54229, 54248–74); 16–24 km W Playa de Oro (USNM 147164–203); trail between Playa de Oro and Quebrada Bochoramá (LACM 43710); Loma de Encarnación, Quebrada Bochoramá, upper San Juan drainage (LACM 43711–15, 43742–73); trail between Quebrada Bochoramá and Río Tadocito (LACM 43716–41); Río Tadocito (UMMZ 121424); junction Ríos San Juan and Llorandó (KU 98523–29); Río San Juan (USNM 144946; FMNH 15643). ***Antioquia:*** Finca Los Llanos, Río Arquía, below junction Río Ocaidó (LACM 42533–40, 42698–99); Finca Chibiguí, Río Arquía, above junction Río Ocaidó (LACM 42541–43, 42654–97); 5 km W Finca Chibiguí (LACM 42544–653). ***Risaralda:*** Santa Cecilia (FMNH 54184, 54186, 54188, 54190, 54197, 54200–02, 54206, 54208–09, 54211, 54213–20, 54222, 54224–25, 54228, 54231–32, 54234–47); 25 km W Pueblorrico (HT 9056 at Universidad del Valle, Cali, Colombia). ***Valle:*** Jiménez, Río Dagua (BM 1908.5.29.55–62; AMNH 3139, 10613–15); Los Mangos [=Juntas =Los Cisneros, Río Dagua] (MRHN 1038); near Buenaventura (BM 95.11.16.32–42). ***Nariño:*** Río Mataje (USNM 147317–19); Imbilí, Río Mira (USNM 147401–29); Madrigar, pass of Río Patía through Cordillera Occidental (CAS-SU 13151, 13246–49, 13251–66; USNM 145800–01); La Guayacana (ANSP 25349–52; FMNH 61772–73, 61775; LACM 60984–87, 61059–64 + uncatalogued).

ECUADOR. ***Esmeraldas:*** Cachabí (WCAB 37113–14; BM 98.3.1.25–28; GOV 9351–59); Río Cupa (JAP 3914); Hacienda Equinox, 38 km NW Santo Domingo de los Colorados (JAP 1766–67, 1788, 1790–92, 1874, 1890, 3107, 3513–14); Tambo Alto (GOV 8475); 1–4 km W El Placer (JAP 2831–35, 2858–61, 2871, 2932–34); 1 km SW Cachui (JAP 3029–30); Río Durango (AMNH 10597–99); Pambelar (AMNH 10600, 10609–10, 10612); Río Sapayo (BM 1902.7.29.21); Playa de Oro (USNM 20603–04); San Javier (AMNH 10605–08; BM 1901.3.29.45–50; GOV 8819); Salidero (AMNH 10601–04). ***Pichincha:*** Santo Domingo de los Colorados (KU 109247–56; CAS-SU 10383; FMNH 172659); 10 km W Santo Domingo de los Colorados on road to Chone (CAS-SU 10382); Hacienda Espinosa, 9 km W Santo Domingo de los Colorados (CAS-SU 10566–76; USNM 145802–03); Ríos Pupusá and Quila near Santo Domingo de los Colorados (CAS-SU 10380–81); Hacienda Lelia, 35 km E Santo Domingo de los Colorados on road to Quito (CAS-SU 10615); 18 km W Santo Domingo de los Colorados,

km 19 on Chone road (JAP 4037, 4097, 4149–52); Dyott Farm, 6 km E Santo Domingo de los Colorados, km 121 (JAP 3949–53, 3955, 4088–89, 4111, 4398–4404, 4440–43); Puerto de Ila (JAP 3837; GOV 9244); Río Mulante, Esmeraldas drainage (CAS-SU 10360–61); Río Blanco at equator (JAP 1856–57); Tanti (Boulenger 1882b: 463).

DOUBTFUL RECORDS. COLOMBIA. ***Antioquia:*** Andes (AMNH 14030); western slope of Cordillera Central (MRHN 484B); ***Risaralda:*** Finca La Selva, Cerro Tatamá, 1700 m (FMNH 54227); ***Cauca:*** Popayán. 1700 m (FMNH 61774).

Cleared and stained material.—Subpattern 1a: LACM 43064; JMS 1662; Pattern 2: LACM 60984-87; JMS 1663-64, 1677; Subpattern 3b: LACM 43732; Pattern 4: LACM 60991.

Dendrobates leucomelas Fitzinger *in* Steindachner 1864
Yellow-banded Poison-arrow Frog
Frontispiece II

1864. *Dendrobates leucomelas* Fitzinger. Steindachner: 260–261, plate 13, figs. 1, 1a–d, holotype: NHMW 19188, Colombia. Steindachner considered *D. leucomelas* conspecific with *Phyllobates auratus* Girard and synonymized both names with *D. tinctorius* (Schneider).
1952. *Dendrobates leucomelas.* Lutz and Kloss: 668–669.
1959. *Dendrobates leucomelas.* Ginés: 129 (text-fig.), 132, color painting on cover.
1961. *Dendrobates leucomelas.* Rivero: 168–169.

Definition. —Snout-vent length of adults 30.5–37.5 mm; skin of back smooth; tarsal tubercle absent or slightly developed; color in life: black with three yellow, yellow-orange, or orange transverse dorsal bands containing black intrusions and spots; omosternum absent.

Diagnosis. —*D. leucomelas* is a member of the *histrionicus* group, differing from *D. histrionicus* in having light transverse dorsal bands containing numerous spots and intrusions of ground color (*D. histrionicus* usually lacks light transverse dorsal bands; when present, the bands lack intrusions of ground color).

Description. —Measurements are in Table 3. The skin is smooth, except the posterior belly and ventral surface of the thighs, which are rugose. The tympanum is round, and its diameter is slightly less than one-half of the diameter of the eye. The finger disks are not sexually dimorphic. The tarsal tubercle is absent or slightly developed.

In life, most Venezuelan specimens are black with three broad yellow transverse dorsal bands containing black intrusions, bands, or spots. The limbs are yellow, spotted with black. The venter is black, sometimes with a yellow spot (Rivero 1961).

Specimens from Hacienda San Felipe, Venezuela, are similar to the above, but the bands are orange (Heatwole et al. 1965).

Relationships. —See the relationships section under *D. histrionicus.*

Stomach contents (one specimen). —From USNM 83940: HYMENOPTERA: Formicidae: *Crematogaster* sp (51), *Trachymyrmex* sp (1), *Strumigenys* sp (1), *Myrmicocrypta* sp (12), *Gnamptogenys exarata* Em.? (1), *Gnamptogenys* sp (1), Myrmecinae (39), *Iridomyrmex* sp (2); ISOPTERA: *Nasutitermes* sp (72).

Ethnozoology. —The Maquiritare Indians of Venezuela consider *D. leucomelas* sacred. They use it as a test animal to assay curare (Rivero 1961).

Nomenclature. —*D. leucomelas* is a Fitzinger label name first published by Steindachner as a synonym of *D. tinctorius* (Schneider). According to Article 11d of the International Code of Zoological Nomenclature (International Trust for Zoological Nomenclature 1964), *D. leucomelas* is an available name, because it was used again before 1961 (by Lutz and Kloss in 1952 and by Ginés in 1959). The same rule makes available the names *D. galactonotus* and *D. quinquevittatus.*

Distribution and habitat (Fig. 6). —Elevation records are from 50 to 800 m. *D. leucomelas* is known from the Guianan Orinoco drainage of Venezuela north to the Río Orinoco, east into Guyana to the Essequibo River, south into extreme northern Brasil, and probably west into extreme eastern Colombia, in Holdridge's (1967) lowland tropical moist forest and lowland tropical wet forest zones. It inhabits shady forest, on the ground and on moist stones and trunks (Rivero 1961).

Localities.—COLOMBIA. Type locality, exact location not stated (NHMW 19188).

BRASIL. ***Roraima:*** Rio Socó (Lutz and Kloss 1952); Uranduique, Rio Ireng (KU 93144).

VENEZUELA. ***Bolívar:*** San Félix, Río Orinoco (AMNH 75789; 77715); Castillor de Guayana, Río Orinoco (USNM 128899); Canaima (USNM 147865; CAS 94975–76); 3 km E Canaima (KU 117308–10); Hacienda San Felipe near Miamo (Heatwole et al. 1965); Auyantepúi AMNH 46044–47, 46051); Guri Dam (AMNH 81455); Río Cuchivero (CAS 94683). ***Amazonas:*** base Cerro Duida (AMNH 23202, 23206; UPR 205); Río Pescado near Cerro Duida (AMNH 23179, 23235); Tapara, Río Cunucununa (UPR 206–07); Belén, Río Cunucununa (USNM 165012–13); 6 km SE Belén (USNM 165019–21); Alto Cunucununa, La Culebra (UPR 198–204; MCZ 27829, 28571); Cerro Yapacana (USNM 83937–41); Misión Coromota-Atures (USNM 137194–96); Yavita (SCN 773).

GUYANA. ***Mazaruni-Potaro:*** Pacaraima foothills (BM 1933.6.19.1–2); Ireng Valley (BM 1903.5.29.3); Kurupung River (UMMZ 83593–95; AMNH 49942); Kopang River (AMNH 43823–25); 16 km N Kaieteur Falls (USNM 118044); Kartabo (AMNH 70983).

Cleared and stained material.—USNM 83940; AMNH 46044.

minutus group

This group contains six species (*D. altobueyensis, D. fulguritus, D. minutus, D. opisthomelas, D. quinquevittatus,* and *D. steyermarki).*

Definition: snout-vent length of adults small (12–21.5 mm); stripes present or absent; color in life sometimes red; dorsal skull bones not fused together or sculptured; omosternum present; tadpoles (known only in *D. minutus* and *D. opisthomelas*) have oral disk indented, denticles not reduced in number, and anus dextral.

Dendrobates altobueyensis new species
Golden Poison-arrow Frog
Frontispiece I

Holotype.—LACM 71972, collected on summit marker of Alto del Buey, Departamento del Chocó, Colombia, 1070 m, on 20 August 1971, by P.A. Silverstone.

Topoparatypes, same collector. —Field number PAS 580.71 (given to INDERENA), 1070 m, 18 August 1971; LACM 71973–74, 1070 m, 19 August 1971; LACM 71975, 1070 m, 22 August 1971; LACM 71976, 1065 m, 22 August 1971; LACM 71977, 985 m, 22 August 1971.

Definition. —Snout-vent length of adults 15.5–17 mm; skin of back slightly granular; tarsal tubercle absent or slightly developed; color in life: entirely yellow or metallic gold, sometimes with greenish tinge; no red, blue, or white; no stripes; sometimes small black spots on dorsum only or on dorsum and venter; omosternum present.

Diagnosis. —*D. altobueyensis* is a member of the *minutus* group, differing from *D. minutus* and *D. fulguritus* in lacking stripes, from *D. opisthomelas* in lacking a well-developed tarsal tubercle and in lacking red color in life, from *D. quinquevittatus* in lacking reticulation, and from *D. steyermarki* in having a slightly granular belly (smooth in *D. steyermarki*), in lacking a well-developed tarsal tubercle, and in lacking red color in life. *D. altobueyensis* resembles *D. pumilio,* but differs in smaller size, in having the venter and limbs the same color as the dorsum (the venter and limbs sometimes are a different color than the dorsum in *D. pumilio*), and in lacking red color in life (red is present in *D. pumilio,* except in many specimens from western Panamá).

Description of holotype. —The holotype is an adult female, 17 mm snout-vent length. The skin is slightly granular, except the palms and soles, which are smooth. Teeth are absent. The tip of the snout is subtruncate in dorsal aspect and rounded in lateral aspect. The canthus rostralis is rounded. The loreal region is slightly concave. The width of the upper eyelid equals two-thirds of the interorbital distance. The diameter of the eye is slightly greater than the distance from the eye to the nostril. The tympanum is round, its diameter is slightly greater than one-half of the diameter of the eye, and its posterodorsal portion is concealed. The second, third, and fourth finger disks are relatively large. The first finger is shorter than the second. The fingers lack fringes and webbing. The tarsal fold is present, but short and poorly defined. The tarsal tubercle is absent. The toes lack fringes and webbing.

In life, the dorsum was greenish yellow with small black spots; the venter was bright yellow. In preservative, the frog is light silvery gray with small to medium-sized black spots on the head, back, sides of the body, and dorsal surface of the limbs; the venter is immaculate.

Description of paratypes. —The snout-vent length of PAS 580.71 was not measured. One paratype (LACM 71977, a 15.5 mm male with open vocal slits) is an adult. One paratype (LACM 71976, 8 mm) is a tiny juvenile. The other three paratypes (LACM 71975, a 14 mm male with closed vocal slits, and LACM 71973–74, 14.5 and 15 mm females) are large juveniles. The paratypes resemble the holotype, except as noted below. The tip of the snout is truncate to subtruncate in dorsal aspect. The diameter of the tympanum varies from slightly less than to slightly greater than one-half of the diameter of the eye. The finger disks are not sexually dimorphic. In LACM 71974, the tarsal fold is a distinct ridge on one foot and indistinct on the other foot, and a slight tarsal tubercle is present on one foot.

The color in life was as follows: PAS 580.71 was entirely yellow except its soles and palms, which were black; LACM 71973–74: one specimen was entirely yellow, and the other entirely golden-yellow with a slight greenish tinge; LACM 71975 was greenish yellow with small black spots on the dorsum and venter; LACM 71976 was entirely metallic gold; LACM 71977 was entirely bright yellow. In preservative, LACM 71973–74 and 71977 are entirely dark gray; 71975 is dark gray with small black spots on the dorsum and venter (only two spots are on the throat); 71976 is entirely dark brown except the throat, chest, and limbs, which are light brown.

Tadpoles. —See distribution and habitat section.

Etymology. —The species is named after the type locality.

Distribution and habitat (Fig. 6). —Elevation records are from 985 to 1070 m. *D. altobueyensis* is known only from the Alto del Buey, a mountain in the Serranía de Baudó, in the Chocoan region of Colombia, in Holdridge's (1967) lowland tropical rain forest zone.

During my stay, the summit of the Alto del Buey was usually cool, drizzly, and obscured by mist. The summit was cleared of vegetation by an expedition of the Instituto Agustín Codazzi in 1956, and in 1971 was covered by grass and a few ferns. The grassy area was about 15.2 m long and 4.6 m wide; on it was an aluminum summit marker. On the upper slopes below the grass was a dense second growth of small trees and bushes, among which were ferns and low terrestrial aroids, whose leaf axils contained water. Almost every aroid leaf axil on the edge of the second growth contained a tadpole. About one-third of the tadpoles were dead when found; this may have been caused by sub-optimal temperatures. The tadpoles (LACM 71906, numbering 17) are of the *minutus* type, with indented oral disk and dextral anus, but it is uncertain whether they are *D. altobueyensis* or *D. minutus*. Primary forest covered the slopes below the second growth; the trunks and branches bore a lush growth of mosses and bromeliads.

I observed *D. altobueyensis* only on and near the summit, although three other species of *Dendrobates*, *D. histrionicus* and *D. minutus* (both common) and *D. fulguritus* (rare), occurred on the forested lower slopes, and two of these (*D. histrionicus* and *D. minutus*) occurred continuously up to the summit, where they were taken together with *D. altobueyensis*. Two of the seven specimens of *D. altobueyensis* (LACM 71976–77) were taken on the ground, in forest, on a ridge on which the trail continued after passing the summit; the other five were taken on the summit, two in grass (LACM 71973, 71975), one beneath the summit marker (PAS 580.71), and two on the platform of the marker (LACM 71972, 71974). Their preference for the marker is easily explained; it was distinctly warmer than its surroundings. Less easily explained is the apparent restriction of this species to the summit. It must be a forest frog, for the grass and second growth probably did not occur before 1956 (the date of the summit marker). Its apparent absence from most of the forest below the summit may be a collecting artifact, but the species probably is confined to the summit and upper slopes of this mountain. If it occurred on the lower slopes, there would be no apparent obstacle to its spread to other lowland areas, yet it has never been found elsewhere in the Chocó.

Dendrobates fulguritus new species
Yellow-bellied Poison-arrow Frog
Figures 11A, 12P, 16

1968. *Dendrobates minutus* (part). Savage: 760–761 (not the figure).

1970. *Dendrobates minutus ventrimaculatus* (part). Cochran and Goin: 23–25 (not the plate).

1970. *Dendrobates lugubris* (part). Cochran and Goin: 19–21 (not the plate).

Holotype. —LACM 42319, collected at Playa de Oro, Departamento del Chocó, Colombia, 160 m, on 1 June 1968, by P.A. Silverstone and J.E. Ramos.

Paratypes, all from Colombia. —LACM 42320 and USNM 150631, topoparatypes; USNM 147159–63, 10–15 km W Playa de Oro, Chocó; ANSP 25623, Serranía de Baudó, Chocó; LACM 71971, Alto del Buey, Chocó, 300–420 m; LACM 42312–18, Camino de Yupe, Serranía de Baudó between upper Opogadó and Domingodó drainages, Chocó, 510–680 m; LACM 42310–11, near Finca Los Llanos, Río Arquía, below confluence Río Ocaidó, Antioquia; FMNH 54203, 54223, Santa Cecilia, Risaralda, 800 m.

Definition. —Snout-vent length of adults 13.5–16.5 mm; skin of back slightly granular; tarsal tubercle absent or slightly developed; color in life: dorsum black with gold, yellow, or yellow-green complete dorsolateral and incomplete lateral stripes, and an incomplete median stripe on anterior portion of dorsum; venter gold or yellow with black marbling or spots, gold or yellow predominates, no red, blue, or white on venter; omosternum present.

Diagnosis. —*D. fulguritus* is a member of the *minutus* group, differing from *D. altobueyensis* in having stripes, from *D. opisthomelas* in having stripes, in lacking a well-developed tarsal tubercle, and in lacking red color in life, from *D. quinquevittatus* in lacking reticulation, and from *D. steyermarki* in having stripes and a moderately granular belly (smooth in *D. steyermarki*) and in lacking a tarsal tubercle. *D. fulguritus* closely resembles *D. minutus*, but differs in having an incomplete light median stripe on the anterior portion of the dorsum, and in usually having the color of the venter predominantly light in preservative (Fig. 16, left), with a yellow or gold ground color in life, bearing black spots or marbling; the venter lacks blue and white in life (*D. minutus* usually lacks an incomplete light median stripe on the anterior portion of the dorsum, and has the color of the venter predominantly dark in preservative, with a black or brown ground color in life, bearing blue or white spots or marbling).

Description of holotype. —The holotype is an adult female, 15 mm snout-vent length. The skin is slightly granular on the dorsum and moderately granular on the venter, except the palms and soles, which are smooth. Teeth are absent. The tip of the snout is subtruncate in dorsal aspect and rounded in lateral aspect. The canthus rostralis is rounded. The loreal region is vertical. The width of the upper eyelid

equals two-thirds of the interorbital distance. The diameter of the eye is slightly greater than the distance from the eye to the nostril. The tympanum is round, its diameter equals one-half of the diameter of the eye, and its posterodorsal portion is concealed. The second, third, and fourth finger disks are relatively large. The first finger is shorter than the second. The fingers lack fringes and webbing. The tarsal fold is present. The tarsal tubercle is absent. The toes lack fringes and webbing.

In life, the iris was black. The dorsum (Fig. 11A) and sides were black with yellow-green upper lips, complete dorsolateral stripes, incomplete lateral stripes, and an incomplete median stripe (the latter on the anterior third of the dorsum, dividing into three branches on the snout). The dorsolateral stripes were continuous with undulating yellow-green stripes extending dorsally along the entire length of the hind limbs. The right dorsolateral stripe divided into two branches on the posterior fourth of the dorsum, forming a loop at the point of division; the right branch was continuous with the right hind limb stripe, and the left branch ran medially toward the anus. The right hind limb stripe formed a small loop (enclosing the black ground color) on the calf. The dorsal surface of the forelimbs was yellow-green. The anteroventral surface of the upper arms was yellow; the rest of the ventral surface of the forelimbs was black. The throat, chest, belly, and ventral surface of the hind limbs were yellow, except a small median throat spot, a tiny dot on each side of the mid-belly, spots on the hind limbs, and a median stripe on the belly (bending dextrolaterally on the chest), which were black. In preservative, the yellow and yellow-green have faded to gray.

Description of paratypes. —Measurements are in Table 3. The paratypes resemble the holotype, except as noted below. The tip of the snout is truncate to subtruncate in dorsal aspect. The loreal region is vertical to slightly concave. The finger disks are not sexually dimorphic.

In life, the stripes of the paratypes were metallic gold, yellow, or yellow with a greenish tinge. All the paratypes had a pair of dorsolateral stripes, usually not branching posteriorly; in one paratype, the stripes expanded on the mid-back, almost touching each other. All the paratypes had an incomplete median stripe on the anterior portion of the dorsum. In some paratypes, the anterior end of this median stripe split into a Y in front of the eyes (one arm of the Y sometimes was absent); in other paratypes, the snout lacked light markings. One paratype had a short, incomplete median stripe on the posterior portion of the dorsum; this stripe was not connected with the dorsolateral stripes. In all the paratypes, broad yellow or gold longitudinal stripes extended dorsally along the entire length of the forelimbs and hind limbs. On the forelimbs, these stripes covered the entire width of the dorsal surface; on the thighs, the stripes covered only the anterodorsal surface, leaving the posterodorsal surface black; on the calves, the stripes enclosed a few round or oblong black spots. Most paratypes had a black spot on each side of the throat; these spots sometimes joined a black median throat spot. In all but two of the paratypes, the venter was predominantly yellow or gold, with black marbling or round or oblong black spots. In one of the two exceptions, an adult, the yellow ventral color was confined to a throat horseshoe and a pair of paramedian stripes; posteriorly, the stripes joined a pair of broad light ventral thigh stripes, and anteriorly, they ended in bulb-shaped expansions on the chest. In the other paratype, a juvenile (LACM 42311), the venter was black, except for a small square gold spot on the chin. In all paratypes, gold, yellow, and yellow-green have faded to gray in preservative.

Tadpoles. —*D. minutus*like (indented oral disk, dextral anus) tadpoles taken from the leaf axils of epiphytic bromeliads at the Camino de Yupe, Colombia (LACM 71907), may be those of *D. fulguritus* (*D. minutus* has not been found there).

Relationships. —*D. fulguritus* is closely related to *D. minutus*. The two species resemble one another in size and in having a striped dorsum. Most specimens of *D. minutus* lack a median dorsal stripe, but some specimens of *D. minutus* (including the holotype and paratypes) from Panamá (Gatún, 3 km east of Achiote, Isla Barro Colorado, and Nicuesa) have an incomplete median stripe on the anterior portion of the dorsum, and three specimens of *D. minutus* from Cerro Santa Rita, Panamá (FMNH 160057, 160066, 160074) have an incomplete median stripe on both the anterior and posterior portions of the dorsum. I consider *D. fulguritus* a distinct species because I have taken it in sympatry with *D. minutus* at two localities (Finca Los Llanos and the Alto del Buey); at these localities it was extremely rare compared with *D. minutus*.

Stomach contents (one specimen). —From LACM 42315: HYMENOPTERA: Formicidae: Myrmecinae: fragments; ACARINA: mites of four families.

Etymology. —The name *fulguritus* (Latin: struck by lightning) refers to the dorsal color pattern.

Distribution and habitat (Fig. 9). —Elevation records are from 160 to 800 m. *D. fulguritus* is known from the lowland forests of the Chocoan region of Colombia, in the Atrato and San Juan drainages, west of the Andes, in Holdridge's (1967) lowland

tropical wet forest zone. *D. fulguritus* may occur in Panamá; I have seen photographs of this species reportedly taken in Panamá, but there are no museum records from that country.

I took LACM 42310 near Finca Los Llanos, in a forest with many palms (including stilt palms) and heavy leaf litter, in the daytime, among roots at the base of a tree. On 16 June 1971, near the Camino de Yupe in the Serranía de Baudó, at 420 m elevation, two individuals of this species were one meter above the ground in a shallow depression in a fallen log. The depression was filled with moss and dead leaves. The log was surrounded by a natural clearing within virgin forest.

Cleared and stained material. —LACM 42315.

Dendrobates minutus Shreve 1935
Blue-bellied Poison-arrow Frog
Figures 11B, 16

1935. *Dendrobates minutus minutus* Shreve: 212–213, holotype: MCZ 15288, Barro Colorado Island, Canal Zone, Panamá.
1940. *Dendrobates shrevei* Dunn: 109–110, holotype: ANSP 21791, Cerro Campana, east of the Canal Zone, Panamá, Panamá.
1968. *Dendrobates minutus* (part). Savage: 760–761, fig. 5D.

Definition. —Snout-vent length of adults 12–15.5 mm; skin of back slightly granular; tarsal tubercle absent; color in life: black or brown with orange, gold, or yellow complete dorsolateral and incomplete lateral stripes; usually no median dorsal stripe; ventral spots or marbling blue or white, no yellow on venter; omosternum present.

Diagnosis. —*D. minutus* is a member of the *minutus* group, differing from *D. altobueyensis* in having stripes, from *D. opisthomelas* in having stripes and in lacking a tarsal tubercle, from *D. quinquevittatus* in smaller size and in lacking reticulation, and from *D. steyermarki* in having stripes and a moderately granular belly (smooth in *D. steyermarki*) and in lacking a tarsal tubercle. *D. minutus* closely resembles *D. fulguritus*, but differs in usually lacking an incomplete light median stripe on the anterior portion of the dorsum, and in having the color of the venter predominantly dark in preservative (Fig. 16, right), with a black or brown ground color in life, bearing blue or white spots or marbling (*D. fulguritus* has an incomplete light median stripe on the anterior portion of the dorsum, and usually has the color of the venter predominantly light in preservative, with a yellow or gold ground color in life, bearing black spots or marbling; the venter lacks blue and white in life).

Description. —*D. minutus* is the smallest species of dendrobatid, and is one of the smallest species of frogs. Measurements are in Table 3. The skin is slightly granular on the dorsum and moderately granular on the venter, except the palms and soles, which are smooth. The tympanum is round, and its diameter equals one-half of the diameter of the eye. In some Panamanian specimens, the second, third, and fourth finger disks average wider in males than in females, but in most specimens, the finger disks are not sexually dimorphic. The tarsal tubercle is absent.

Colombian and most Panamanian specimens lack a median dorsal stripe, but specimens with an incomplete median stripe on the anterior portion of the dorsum (including the types of *D. minutus*) have been taken in Panamá (see *D. fulguritus* account above).

In life, in specimens from the Atrato drainage, Colombia, the dorsum is chocolate brown with orange dorsolateral stripes and sometimes an orange suffusion between the stripes. The anterodorsal surface of the upper arms, upper lip stripes, and dorsal surface of the thighs are orange. Orange, gold, or blue lateral spots sometimes fuse into a diagonal stripe on each side of the body (this lateral stripe usually is incomplete, but rarely is complete, reaching the dorsolateral stripe behind the tympanum). There are blue spots on the dorsal surface of the hands and feet. The venter is black with medium blue or light blue (sometimes with a greenish tinge) spots or marbling.

Tadpoles (Fig. 19). —Measurements are in Table 4. The oral papillae are in one row, and border the entire posterior lip, but border only the lateral portions of the anterior lip. The oral disk is laterally indented. The denticle formula is $1\frac{1}{3}1$. The beaks are massive and serrate, and the lower beak is not indented. The eyes are dorsal. The spiracle is sinistral and low. The dorsal fin varies from not reaching to barely reaching the body. The anus is dextral. The tip of the tail is broadly rounded. In preservative, the head-body and tail are very pale tan with scattered brown dots in a specimen from an adult's back (LACM 43861), and darker (light brown) dorsally, with brown dots on the entire surface except the posterior half of the venter, in larger specimens.

Adults deposit tadpoles in water in leaf axils of bromeliads (Myers 1969:43). V. Lee took three tadpoles in water in man-made bamboo pots near the Río Raposo, Colombia; they fed on mosquito larvae. One of these tadpoles (taken on 13 February 1964) metamorphosed 47 days later (on 30 March); as an adult, it fed on adult mosquitoes (*Culex*) (V.

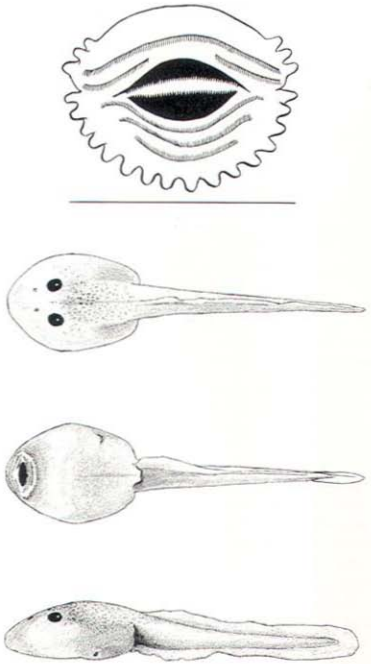


FIGURE 19. Tadpole of *Dendrobates minutus*, Belén, Colombia (LACM 43861), from back of adult; mouthparts, dorsal, ventral, and lateral aspects (Stage 25). Lines equal one millimeter.

Lee, unpublished data). An adult has been taken carrying one tadpole (LACM 43861).

Relationships.—Tadpoles of *D. minutus* and *D. opisthomelas* are the only ones in the genus known to have indented lips and a dextral anus; this and their small size suggest that they belong in the same species group. See the relationships section under *D. fulguritus*.

Life history.—An adult female (LACM 43827), 13.5 mm snout-vent length, contained only two large eggs (3 to 4 mm diameter) in each ovary. The tiny size of the adult, the necessity of laying large terrestrial eggs, and the probable lack of selection pressure in favor of a large clutch size (due to a high offspring survival rate) act together to limit the clutch size in this species.

Distribution and habitat (Fig. 8).—Elevation records are from 25 to 1098 m. *D. minutus* is known from central Panamá to mid-way down the Pacific coast of Colombia (but may extend farther south) in Holdridge's (1967) lowland tropical moist forest, lowland tropical wet forest, and lowland tropical rain forest zones. There is a distributional gap in the Darién region of Panamá, which may be a collecting gap. Specimens from Colombia were taken on heavy leaf litter on the ground in shady forest; specimens from Cerro La Campana, Panamá, were taken on the ground and in leaf axils of bromeliads.

Localities.—PANAMÁ. ***Coclé:*** El Valle de Antón (AMNH 55517). ***Panamá:*** Río Pequení, head of Madden Lake (ANSP 23389; KU 116850); Cerro La Campana (KU 76599–605, 77676, 115496–503, 116742–44; UMMZ 124537–38; AMNH 59660–62; ANSP 21791–93; FMNH 67708–09, 130710, 153666–73). ***Colón:*** Cerro Santa Rita (FMNH 67970, 160057, 160066, 160069, 160073–75); Brazo del Medio, Río Cuango near Palenque (FMNH 153704); trail between Ríos Boquerón and Pequení (H. Trapido field notes HT 7114–15); SW Cerro Bruja (KU 115471–77); 3.5–4 km SE Puerto Pilón (KU 115478–95, 115576, 116738–41); 3 km E Achiote (KU 125025). ***Canal Zone:*** Isla Barro Colorado (MCZ 15288; UMMZ 63580, 63583, 78853; ANSP 23126, 23200; CM 8471, 8483, 8488); Gatún (UMMZ 52719; ANSP 21441–44). ***San Blas:*** Nicuesa (MCZ 16016).

COLOMBIA. ***Chocó:*** trail between upper Ríos Napipí and Opogadó (LACM 43864); upper Río Napipí (LACM 43862–63); Loma de Encarnación, Quebrada Bochoramá, upper San Juan drainage (LACM 43865–75); trail between Tadó and Quebrada Ibordó, on drainage divide between Ríos Atrato and San Juan (seen by me); Alto del Buey (LACM 71905–06, 71928–61). ***Antioquia:*** Belén near Vegaes, Río Arquía (LACM 43802–05, 43861); Finca Los Llanos, Río Arquía, below junction Río Ocaidó (LACM 43806–24, 43849–60); Finca Chibiguí, Río Arquía, above junction Río Ocaidó (LACM 43825–43, 43846–48); 5 km W Finca Chibiguí (LACM 43844–45). ***Valle:*** Rockefeller Foundation virological station, Río Raposo (LACM 60989, 61022–28; USNM 151378, 151380).

Cleared and stained material.—LACM 43827, 60989.

Dendrobates opisthomelas Boulenger 1899
Andean Poison-arrow Frog
Frontispiece II and Figure 12N–O

1899. *Dendrobates opisthomelas* Boulenger: 275, plate 11, fig. 4, 14 syntypes: BM 1947.2.15.21–34, Santa Inés, north of Medellín, Colombia, 1160 m.
1970. *Dendrobates opisthomelas.* Cochran and Goin: 22–23, plate 2G–I.
1970. *Dendrobates minutus minutus.* Cochran and Goin: 25–26, plate 3A–C.
1970. *Dendrobates lugubris* (part). Cochran and Goin: 19–21 (not the plate).

Definition.—Snout-vent length of adults 14.5–19.5 mm; skin of back slightly to moderately granular;

tarsal tubercle well developed; color in life: head and back red; limbs and venter brown, venter sometimes with red spots; no yellow, blue, or white; omosternum present.

Diagnosis.—*D. opisthomelas* is a member of the *minutus* group, differing from *D. minutus* in lacking stripes and in having a well-developed tarsal tubercle, from *D. fulguritus* in lacking stripes and in having red color in life and a well-developed tarsal tubercle, from *D. altobueyensis* in having red color in life and a well-developed tarsal tubercle, from *D. quinquevittatus* in lacking reticulation and in having a well-developed tarsal tubercle, and from *D. steyermarki* in having a slightly to moderately granular belly (smooth in *D. steyermarki*). *D. opisthomelas* differs from the species of the *pumilio* group in smaller size and in having a well-developed tarsal tubercle.

Description.—Measurements are in Table 3. The skin is slightly to moderately granular, except the palms, soles, throat, and part of the forelimbs, which are smooth. The tympanum is round, and its diameter is slightly greater than one-half of the diameter of the eye. The second, third, and fourth finger disks average wider in males than in females. The tarsal tubercle is well developed.

In life, in specimens from Santa Rita, Colombia, the head is red, except for the tympanum, which is brown. The back is dark red with a brown suffusion or bright red. The sides of the body are pinkish or red. The upper arms are red; the lower arms are brown. The dorsal surface of the thighs is red, covered by a brown suffusion posteriorly. The venter is uniform chocolate brown in some specimens, and chocolate brown with irregularly shaped red spots in other specimens.

In preserved specimens of *Dendrobates*, red fades to yellow before becoming white or gray; thus Boulenger, in his original description, stated that the dorsum of the types was yellow. The types (from Santa Inés) have light ventral spots (Fig. 12N); specimens from Quebrada Arriba and some specimens from Santa Rita also have ventral spots (light gray in preservative, red in life).

Tadpoles (Fig. 20).—Measurements are in Table 4. The oral papillae are in one or two rows bordering the posterior lip, but are absent on the median one-fourth of the posterior lip (this gap is unique among known tadpoles of *Dendrobates*); the papillae extend only onto the lateral portions of the anterior lip. The oral disk is laterally indented. The denticle formula is $L\frac{1}{3}$. The beaks are massive and serrate, and the lower beak is slightly indented. The eyes are dorsal. The spiracle is sinistral and low. The dorsal fin does not reach the body. The anus is dextral. The tip of the tail is rounded. In preservative, the head-body

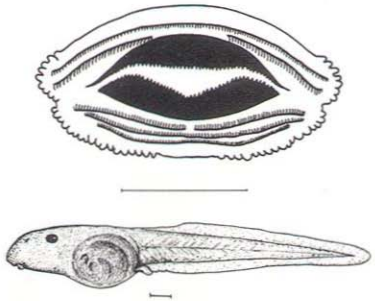


FIGURE 20. Tadpole of *Dendrobates opisthomelas*, Santa Rita, Colombia (LACM 61067), from bromeliad leaf axil; mouthparts (Stage 29) and lateral aspect (Stage 26). Median gap in oral papillae bordering posterior lip is characteristic of this species. Lines equal one millimeter.

is uniform brown dorsally except for tan paramedian areas, and tan with brown mottling laterally and ventrally. The tail is tan with brown dots; the fins are transparent and immaculate.

Adults deposit tadpoles in water in bromeliad leaf axils.

Relationships.—Although *D. opisthomelas* resembles *D. pumilio*, the tadpoles of the two species are different. The resemblance between the tadpoles of *D. opisthomelas* and *D. minutus* suggests that they belong in the same species group.

Stomach contents (one specimen).—From LACM 43885: HYMENOPTERA: Formicidae: Myrmecinae: (fragments); ACARINA: mites of three families.

Parasites.—I found ticks attached to specimens of *D. opisthomelas*.

Nomenclature.—I designate BM 1947.2.15.29, an 18.0 mm male from Santa Inés, north of Medellín, Colombia, 1160 m, collected by A.E. Pratt, as the lectotype of *Dendrobates opisthomelas* Boulenger 1899; this is the specimen illustrated in the original description.

Distribution and habitat (Fig. 8).—*D. opisthomelas* occurs at higher elevations than any other species of *Dendrobates* (1160 to at least 2200 m). One record (Paramillo), at the northern end of the Cordillera Occidental, is 12,500 ft (3813 m). The Paramillo specimens (AMNH 5194–96) were taken by L.E. Miller and H. Boyle, whose base camp was at 12,500 ft, but were collected on 1 February 1915, the day that Miller and Boyle left Paramillo to return to lower elevations (Chapman 1917). Thus the frogs

may have been collected at a lower elevation than that of the camp. The species is known from the Cordilleras Occidental and Central of Colombia, in Holdridge's (1967) premontane moist forest, premontane wet forest, premontane rain forest, and lower montane moist forest zones. At Santa Rita, in the Cordillera Central, I found adults in disturbed, primary forest. They were on the ground and in bromeliads, which were abundant at low levels on trees and on fallen logs. This site has an elevation of 1890–1930 m, a mean annual rainfall of 5000 mm, a mean annual temperature of 20°C, a minimum of 10–12°C, and a maximum of 30°C (data from Empresas Municipales, Medellín). At Quebrada Arriba, in the Cordillera Occidental, I took adults on the ground at 2030 m on fallen leaves on a ridge in open, probably second growth forest, which contained many bromeliads and bamboos and some *Cecropia* trees, but no palms; oak trees (*Quercus humboldtii*) and acorn woodpeckers (*Melanerpes formicivorus*) occurred close to the site of capture. I collected other adults in less-disturbed forest in the same area, on the ground at 2130 m; the ground was covered with a heavy leaf litter, and there were many palms, aroids, and bromeliads.

I found this species only in forest enclaves on the ridges of hills, surrounded by man-made pasture; it was never in open pasture, even in areas where it occurred when forests existed. One cause of its disappearance may be the destruction of sylvan bromeliads, which it needs for tadpole deposition. Extensive habitat destruction probably has reduced its range considerably.

Localities.—COLOMBIA. ***Antioquia:*** Quebrada Arriba, bus stop 10 km by road from town of Andes, mountains near road (LACM 71962–70); Santa Inés, N Medellín (BM RR.1947.2.15.21–29, BM RR.1947.2.15.31–34; USNM 145794); Medellín (USNM 147506–07; AMNH 1364, 1372–74); Llano Grande near Río negro (USNM 63876; FMNH 63874–75; ILS uncatalogued; LACM 43898–99); Santa Rita near Guatapé (LACM 43880–97, 61067); Santuario (USNM 150687–91; ILS 175); Monte del Diablo near La Ceja (USNM 144980–81, 144983–84); Paramillo (AMNH 5194–96).

Cleared and stained material.—LACM 43885.

Dendrobates quinquevittatus
Fitzinger *in* Steindachner 1864
Amazonian Poison-arrow Frog
Frontispiece II and Figures 12A–E, 14

1803. *Hyla tinctoria* (part, fig. 3). Daudin: plate 8, fig. 3.
1864. *Dendrobates quinquevittatus* Fitzinger, Steindachner: 260–262, plate 15, fig. 2, holotype: NHMW 16517, Salto do Girao, Brasil. Steindachner listed *D. quinquevittatus* in the synonymy of *D. tinctorius* (Schneider), and treated the species as *D. tinctorius* var *quinquevittatus*.
1882a. *Dendrobates tinctorius* (part, var Dn-r, Et-u). Boulenger: 143.
1883. *Dendrobates reticulatus* Boulenger: 635–636, plate 57, fig. 2, eight syntypes: BM 1947.2.15.5–12, Yurimaguas, Huallaga River, Perú.
1883. *Dendrobates fantasticus* Boulenger: 636, plate 57, fig. 3, four syntypes: BM 1947.2.15.1–4, Yurimaguas, Huallaga River, Perú.
1935. *Dendrobates minutus ventrimaculatus* Shreve: 213–214, holotype: MCZ 19734, Sarayacu, Ecuador.
1941. *Dendrobates tinctorius igneus* Melin: 66–67, figs. 37a–b, holotype: at NMG, Río Itaya near Iquitos, Perú.
1952. *Dendrobates quinquevittatus.* Lutz and Kloss: 665–668.
1970. *Dendrobates minutus ventrimaculatus* (part). Cochran and Goin: 23–25, plate 3D–F.

Definition.—Snout-vent length of adults 14.5–21.5 mm; skin of back smooth to slightly granular; tarsal tubercle absent; color in life: black with five gold, yellow, orange, or green stripes (one pair dorsolateral, one pair lateral, and one median dorsal), which are sometimes interconnected, or dorsum spotted or banded, or anterior dorsum uniform red; limbs and venter usually reticulated (rarely marbled) with blue, blue-green, orange, or yellow (rarely, reticulation expanded, reducing black ventral ground color to small spots); omosternum present.

Diagnosis.—*D. quinquevittatus* is a member of the *minutus* group, differing from *D. altobueyensis* in having reticulation, from *D. fulguritus* and *D. minutus* in larger size and in having reticulation, from *D. opisthomelas* in having reticulation and in lacking a tarsal tubercle, and from *D. steyermarki* in having reticulation and a slightly granular belly (smooth in *D. steyermarki*) and in lacking a tarsal tubercle.

Description.—Measurements are in Table 3. The skin is smooth to slightly granular on the dorsum and slightly granular on the venter. The tympanum is round, and its diameter equals one-half of the diameter of the eye. The finger disks are not sexually dimorphic. The tarsal tubercle is absent.

There are four basic dorsal color patterns in life (Fig. 14): Pattern 1: This is a striped pattern, known from most of the Amazon drainage and French Guiana, and may be divided into two subpatterns, which usually are present in the same population: Subpattern 1a (Frontispiece II; Figs. 14C–D; includes the holotype of *D. quinquevittatus* and the holotype and some paratypes of *D. minutus ventrimaculatus*): In this subpattern, the stripes are not interconnected. There is a complete stripe on each side of the body, extending onto the upper lip, a pair of complete dorsolateral stripes, and a complete or incomplete median dorsal stripe; the median dorsal stripe may split into a Y on the snout (one arm

of the Y sometimes is absent). The limbs are reticulated.

Subpattern 1b (Fig. 14J; includes some paratypes of *D. minutus ventrimaculatus* and the types of *D. tinctorius igneus*): This subpattern is the same as Subpattern 1a, except that the stripes are interconnected. Specimens from Utinga, Brasil, have five gold stripes on a black ground color. The proximodorsal surface of the upper arm is gold. Reticulation is gold on the throat and pale blue on the belly and limbs. Specimens from Gallenazo, Perú, have five stripes on a black ground color; the stripes are red-orange on the head and anterior back, yellow on the mid-back, and pale green on the posterior back. Reticulation is orange on the throat and blue-green on the belly and limbs (D.B. Wake and R. Etheridge, field notes at CRE). In a specimen from 1.6 km east of Santa Isabel, Perú, the stripes are orange on the dorsum and yellow on the sides; the reticulation is yellow on the limbs (A.C. Thoresen, color slide).

Pattern 2 (Fig. 14G): This pattern is banded, and is known from Igara Paraná, Sausi, and Chazuta, all in Perú. There are two or more light transverse dorsal bands, and sometimes a horseshoe mark on the snout.

Pattern 3 (Fig. 14E–F): This pattern is spotted, and is known from Tsioventeni and Iparia in Perú, and the Río Apaporis in Colombia. There are small light spots on the dorsum. A specimen from Tsioventeni, Perú, has a black ground color with yellow spots on the dorsum and sides, and light blue-green reticulation on the limbs (A.C. Thoresen, color slide).

Pattern 4: In this pattern, the anterior dorsum is uniformly light in color. This pattern may be divided into two subpatterns; specimens bearing these subpatterns were described as two separate species by Boulenger (1883) based on differences in color, pattern (Figs. 12B–C), and size. There is a small but consistent size difference between specimens bearing the two subpatterns; the snout-vent length (in millimeters; mean in parentheses) of the syntypes is: *D. fantasticus:* two males: 17.0–20.0 (18.5); two females: 18.0–19.5 (18.8); four specimens: 17.0–20.0 (18.6); *D. reticulatus:* one male: 15.5; seven females: 15.0–16.5 (16.0); eight specimens: 15.0–16.5 (15.9). The specimens may represent two species; they are included in *D. quinquevittatus* herein because specimens bearing transitional color patterns (Fig. 14) connect both *D. fantasticus* and *D. reticulatus* with *D. quinquevittatus*. Furthermore, the color difference between Boulenger's recently preserved specimens (yellow in *D. fantasticus*, pink in *D. reticulatus*) may have been caused by differential fading (in recently preserved *Dendrobates*, red becomes yellow, and later fades to gray or white); specimens from Campo Santa Clara, Perú, that have a pattern very close to Subpattern 4a (the *fantasticus* pattern) were red in life (G. Rozanski, field notes at USNM), and a specimen lacking locality data, but bearing Subpattern 4b (the *reticulatus* pattern), also was red in life (color slide from R.W. McDiarmid, University of South Florida). Subpattern 4a (Figs. 12C, 14M; includes the syntypes of *D. fantasticus*): This subpattern is known from Yurimaguas, Perú. The light color is confined to the head and shoulders. The posterior back and limbs are broadly reticulated or marbled.

Subpattern 4b (Figs. 12B, 14A; includes the syntypes of *D. reticulatus*): This subpattern is known from Yurimaguas and Iquitos, Perú. The light color extends from the snout to the mid-back or sacral region. The posterior back and limbs are closely reticulated.

In all patterns, the venter (Figs. 12B–E) is closely reticulated, broadly reticulated, or (rarely) marbled. The broadly reticulated condition grades into a dark-spotted appearance (Fig. 12A). There is no consistent correlation between the dorsal and ventral patterns, except that the venter of specimens bearing the *reticulatus* pattern usually is more closely reticulated (i.e., the reticulation has narrower interspaces) than the venter of specimens bearing the *fantasticus* pattern.

Specimens with transitional patterns are known from the following localities: between Patterns 1 and 2 (Figs. 14I–H): Morales, Achinamisa, and Sausi, all in Perú; between Patterns 1 and 3: Achinamisa, Valle, the junction of the Ríos Santiago and Marañón, and the Río Apaga, all in Perú; between Pattern 1 and Subpattern 4a (Figs. 14K–L): Domo Santa Clara and Campo Santa Clara, Perú; between Pattern 1 and Subpattern 4b (Fig. 14B): the Río Itaya near Iquitos, Perú, and the confluence of the Shiona Yacu and Río Conambo in Ecuador.

Tadpoles.—One tadpole (J.P. Bogart field number 87, at TNHC) that may be this species was taken near the Río Pachitea, near the Bosque Nacional de Iparia, Huánuco, Perú, in water in a leaf axil. The tadpole is in Stage 41. The head-body length is 12.5 mm, and the total length is 28.5 mm. Most characteristics are uncertain because of poor condition and advanced stage, but the oral disk appears not laterally indented.

Relationships.—I placed *D. quinquevittatus* in the *minutus* group because of its small size and usually striped dorsal pattern (resembling the pattern of *D. fulguritus*); if its tadpoles differ in oral disk indentation and anal position from those of *D. minutus*, *D. quinquevittatus* should be removed from the *minutus* group.

Stomach contents (five specimens).—From LACM

42307: HYMENOPTERA: Formicidae: *Hypoponera* sp (5), *Crematogaster* sp (2), *Pheidole* sp (4), *Solenopsis* (*Diplorhoptrum*) sp (7), Myrmecinae (22), Laelapidae: *Laelaps* ? sp (2); COLEOPTERA: fragments (2); ACARINA: mites of five families (20).

From LACM 42305: HYMENOPTERA: Formicidae: *Solenopsis* (*Diplorhoptrum*) spp (11), Myrmecinae (4); COLEOPTERA: Bostrichidae (1).

From AMNH 42207: HYMENOPTERA: Formicidae: *Pheidole* sp (2), *Crematogaster* sp (4).

From AMNH 42793: HYMENOPTERA: Formicidae: *Octostruma iheringi* (Em.) (2), *Mycocepurus smithi* (Forel) (10), *Apterostigma* sp (1), *Smithistruma* sp (3), *Crematogaster* sp (4), *Pheidole* spp (25), *Solenopsis (Diplorhoptrum),* two spp (11), Myrmecinae (25).

From AMNH 42552: HYMENOPTERA: Formicidae: *Strumigenys smithi* Forel (1), *Crematogaster* sp (6), *Paratrechina* sp (1), Myrmecinae: three genera.

Nomenclature.—D. quinquevittatus is a Fitzinger label name first published by Steindachner (1864) as a synonym of *D. tinctorius* (Schneider). See the nomenclature section under *D. leucomelas.*

I designate BM RR.1947.2.15.4, an 18.0 mm female from Yurimaguas, Huallaga River, Perú, collected by Dr. Hahnel, as the lectotype of *Dendrobates fantasticus* Boulenger 1883; this is the specimen illustrated in the original description. I designate BM RR.1947.2.15.10, a 15.5 mm female from Yurimaguas, Huallaga River, Perú, collected by Dr. Hahnel, as the lectotype of *Dendrobates reticulatus* Boulenger, 1883.

Distribution and habitat (Fig. 8).—Elevation records are from 14 to 1281 m. *D. quinquevittatus* is known only from east of the Andes, in the Amazon drainage of Colombia, Ecuador, Perú, and Brasil, from the foothills of the Andes east to the mouth of the Amazon, and north into French Guiana, mainly in Holdridge's (1967) lowland tropical moist forest zone, but also in the lowland tropical dry forest, lowland tropical wet forest, and premontane wet forest zones. I took it in lowland forest on a fallen log (Utinga) and a standing tree trunk (Crique Ipoucin); both specimens were one meter above the ground.

Localities.—COLOMBIA. ***Caquetá:*** Aserrío, 20 km from junction Ríos Pescado and Orteguaza, 5 km from right bank Río Pescado (USNM 146843-45). ***Amazonas:*** mouth Río Loretoyacu near Leticia (MCZ 26050); Río Apaporis (MCZ 28061).

ECUADOR. ***Napo:*** Loreto (GOV 9720); Arajuno (JAP 7819); Lago Agrio near junction Ríos Pishino and Aguarico (WED 35765 at KU); Limón Cocha near junction Ríos Jivino and Napo (KU 98822, 98863; LACM 72645). ***Pastaza:*** Sarayacu (MCZ 19734-41; GOV 9165-69; BM 80.12.5.209-10, BM 80.12.5.224-25); Río Pastaza (MCZ 19684-90; FMNH 25956-57, 126488; UMMZ 90368, 90657; CM 10607; BM 1956.1.1.68; LACM44397–98; USNM118705); Pacayacu (GOV 8520, 8939; CAS-SU 10323–25; CAS 94970); Palanda, Río Bobonaza (CAS-SU 10322; GOV 9739–43); Río Shilcayacu, below Puyo (GOV 9737-38); Chichirota (GOV 9729-30); El Pez, between Puyo and Canelos (GOV 9731-34); Don Tomás, 5 km S Montalvo (GOV 9735); Río Villano (JAP 3862; GOV 9721-23, 9725-27); Vera Cruz, 10 km E Puyo (JAP 6107); Río Conambo (GOV 9719); junction Shiona Yacu and Río Conambo (GOV 9009–11); Abitagua (UMMZ 92149); Canelos (AMNH 33886); Andoas (AMNH 49941); 3 km SSE Puyo (JAP 2042); headwaters Río Bobonaza (JAP 2067, 2145–46, 2153–56). ***Morona-Santiago:*** Chiguaza (GOV 8736); Taisha (GOV 7666).

PERÚ. ***Amazonas:*** junction Ríos Santiago and Marañón (AMNH 42970, 43482, 43491); headwaters Río Caterpisa (AMNH 42436); Camaima, Río Cenipa (AMNH 43051). ***Loreto:*** Río Itaya near Iquitos (NMG 513; AMNH 43469, 43600); Iquitos (AMNH 42207, 42441, 42612, 43326, 43335, 43337, 43609, 43611-12; FMNH 45408-10); Pucallpa-Río Aguaytía road, 90-138 km WSW Pucallpa (MCZ 24444); junction Ríos Bombo and Tapiche (AMNH 42015, 42053, 42071-72, 42088, 42418-21, 43291-93); Cachipuerto (AMNH 42611, 42877-78); Cashiboya (AMNH 42050); Pampa Hermosa, Río Cushabatay (AMNH 42587); Río Pisqui (AMNH 60670); Huachi, Río Pastaza (AMNH 49940); Río Apaga (AMNH 42424-25); upper Río Utoquinia and divide between Utoquinia and Tapiche drainages near Brasilian border (AMNH 42906, 43138, 43471, 43578, 43581, 51314); Requena, Monte Carmelo (AMNH 43270); junction Ríos Morona and Marañón (AMNH 42635, 43286); Cerro Azul, 24 km E Contamaná (FMNH 56238, 56247); Igara Paraná, Putumayo drainage (BM 1905.1.31.8); Contamaná (BM 1913.7.28.22); Campo Santa Clara, Quebrada Baños, Quebrada Agua Dulce, and Domo Santa Clara, all near Orellana, Río Ucayali (USNM 127197–200, 127933); Yurimaguas (BM RR.1947.2.15.1-11; LACM 64596); Puesto Shiriara (AMNH 42052). ***San Martin:*** Chazuta (AMNH 42617, 42792-93, 42947, 42949); Morales (AMNH 42062); Tocache (AMNH 42628); Sausi (AMNH 43056-57); Cainarache (AMNH 51315); Valle, Río Huallaga (AMNH 42963); Achinamisa, Río Huallaga (AMNH 42176, 42188-90, 42510-11, 42513-15, 42544, 42547-52, 42554, 42557-58, 42730, 42734, 42737-38, 42740, 43203; UMMZ 89980). ***Huánuco:*** Monte Alegre, Río Pachitea (AMNH 43017, 43033, 43038, 43041); Río Pachitea near Bosque Nacional de Iparia (TNHC 36485, 36488, 36499); Tingo María (CAS 85147, 85150; USNM 166905-06). ***Pasco:*** Tsioventeni, upper Río Nevati, Pichis drainage, in the Gran Pajonal (USNM 166756); 1.6 km E Santa Isabel, Río Nevati, below Tsioventeni (USNM 166767); Gallenazo, Iscozazin Valley, Palcazú drainage (LACM 72062-63).

BRASIL. ***Rondônia:*** Salto do Girao, Rio Madeira, between Manoa and Porto Velho (NHMW 16517). ***Amazonas:*** Benjamin Constant (CAS-SU 11875–78; Lutz and Kloss 1952); Rio Itacoai (Lutz and Kloss 1952); Manaus (CAS 85681). ***Pará:*** Utinga forest preserve near Belém (LACM 42305-08; MPEG 737); Santa Bárbara, Belém-Mosqueiro road (MPEG 749); Gurupá (MRHN 62).

GUYANE FRANÇAISE. Crique Ipoucin, Approuague drainage (LACM 42309); Camopi (MHNP 50–08); Saut Maripa, Fleuve Oyapock (MHNP 50–09; LG 73); Crique Gabrielle, Mahury drainage (LG 701); Mont Galbao (LG 1422).

Cleared and stained material.—Pattern 1a: LACM 42307; AMNH 42552; Pattern 2: AMNH 42793; Pattern 4b: AMNH 42207.

Dendrobates steyermarki Rivero 1971
Demonic Poison-arrow Frog

1971. *Dendrobates steyermarki* Rivero: 389–396, fig. 1, holotype: UPR 3399, Cerro Yapacana, Amazonas, Venezuela, 1200 m.

Definition.—Snout-vent length of only known specimen 16 mm; skin of back smooth; tarsal tubercle well developed; color in life: entirely red, probably with small dark spots [omosternum not examined].

Diagnosis.—*D. steyermarki* is a member of the *minutus* group, differing from all other species of the group in having a smooth belly (slightly to moderately granular in the other species of the group), and from all other species of the group except *D. opisthomelas* in having a well-developed tarsal tubercle. In addition, *D. steyermarki* differs from *D. altobueyensis* in being red (*D. altobueyensis* is yellow), from *D. fulguritus* and *D. minutus* in lacking stripes, and from *D. quinquevittatus* in lacking reticulation. *D. steyermarki* closely resembles *D. opisthomelas* in size, color, and development of the tarsal tubercle, but differs in having a smooth belly. *D. steyermarki* resembles the species of the *pumilio* group in color, but differs in smaller size and in having a well-developed tarsal tubercle.

Description.—The only known preserved specimen (probably an adult, sex unknown) has a snout-vent length of 16 mm. The skin is smooth. The tympanum is round, and its diameter equals one-half of the diameter of the eye. The first finger is very slightly shorter than the second finger when measured along their adjacent surfaces (the original description stated that the first finger is longer than the second, when measured from the external base). The tarsal tubercle is well developed.

In life, the holotype was entirely "dark red, almost scarlet" (Rivero 1971). In preservative, the red has changed to light brown. There are small, scattered, irregularly shaped dark brown spots on the head, back, and dorsal surface of the hind limbs, becoming an ill-defined, close-set, dark brown marbling on the venter and ventral surface of the limbs; light brown predominates on the throat and dark brown on the belly. I suspect that the spots were also present in life, although Steyermark's notes (quoted in Rivero [1971]) do not mention them.

Relationships.—*D. steyermarki* resembles *D. opisthomelas*, and may be more closely related to that species than to any other species of *Dendrobates*.

Distribution and habitat (Fig. 7).—The only record is in the Guianan region of Venezuela, on the summit (1200 m) of Cerro Yapacana, of which Mayr and Phelps (1967) wrote "With an altitude of only 1200 meters, this mountain is not a typical tepui. It rises directly from the densely forested shores of the Orinoco River, about 130 kilometers west of Cerro Duida. Its summit area is approximately 3 square kilometers . . . ." The holotype and other specimens (seen but not collected) were on the ground, "on irregular, mossy terrain, among sandstone crags, in places where the trees reach eight to 10 meters in height" (Rivero 1971).

Localities.—VENEZUELA. ***Amazonas:*** Cerro Yapacana (UPR 3399).

pumilio group

This group contains three species (*D. granuliferus, D. pumilio,* and *D. speciosus*).

Definition: snout-vent length of adults small to moderate (17.5–30 mm); stripes absent; color in life usually red; dorsal skull bones usually not fused together or sculptured; omosternum present; tadpoles (known only in *D. pumilio*) have oral disk unindented, denticles reduced in number, and anus median.

Dendrobates granuliferus Taylor 1958
Granular Poison-arrow Frog
Frontispiece II

1958. *Dendrobates granuliferus* Taylor: 10–13, fig. 5, holotype: KU 43874, north of Río Diquis, 4.8 km north of Palmar, Puntarenas, Costa Rica.
1968. *Dendrobates granuliferus.* Savage: 760, fig. 5B.

Definition.—Snout-vent length of adults 19–22 mm; skin of back strongly granular; tarsal tubercle absent or slightly developed; color in life: dorsum usually red, without black dots or spots; limbs and venter green or blue-green; omosternum present.

Diagnosis.—*D. granuliferus* is a member of the *pumilio* group, differing from *D. pumilio* in having strongly granular skin, without black dots or spots (smooth or slightly granular skin, often with black dots or spots in *D. pumilio*), and from *D. speciosus* in smaller size and in having strongly granular skin. *D. granuliferus* differs from *D. opisthomelas* and *D. steyermarki* in larger size, in having strongly granular skin (slightly to moderately granular in *D. opisthomelas,* smooth in *D. steyermarki*) and green or blue-green hind limbs and venter, and in lacking a tarsal tubercle.

Description.—Measurements are in Table 3. The skin is strongly granular, except the palms, soles, parts of the forelimbs, and throat, which are smooth. The tympanum is round, and its diameter equals

one-half of the diameter of the eye. The finger disks are not sexually dimorphic. The tarsal tubercle is absent or slightly developed.

In life, in most specimens, the head, back, and dorsal surface of the upper arms are red. The dorsal surface of the hind limbs is spotted black and green or blue-green. The lower arms and entire venter are green or blue-green.

Two specimens from the northern limit of the range (Río Dimitis) lacked red; the dorsum and sides were yellow-olive. The dorsal surface of the limbs and most of the venter were blue-green (Savage 1968).

Breeding call.—The breeding call has been described as a non-musical "buzz-buzz-buzz" lasting several seconds, similar to the call of *D. pumilio* and of lower pitch than the call of *D. auratus* (Savage 1968); and as rasping notes like a moving hinge in need of oil, a non-musical series of five to 80 insect-like buzzes, with an average frequency of one note per second; the interval between calls is five to 15 seconds (Goodman 1971).

Relationships.—See the relationships section under *D. pumilio.*

Life history.—Aggressive behavior occurs between males of this species (Goodman 1971; Crump 1972). In courtship, the male leads the female to an oviposition site; vent display by the female triggers oviposition. Amplexus does not occur; the oviposition posture is vent-to-vent (Crump 1972).

Stomach contents (one specimen).—From JMS 1661: HYMENOPTERA: Formicidae: *Pheidole* spp (23), *Solenopsis* (*Diplorhoptrum*) spp (5), *Eurhopalothrix* sp (1), *Lachnomyrmex* sp (1), *Wasmannia auropunctata* (Roger) (4), *Strumigenys* sp (1), *Smithistruma* sp (1), *Sericomyrmex* sp (2), Myrmecinae: three genera (11); COLEOPTERA: (1); ACARINA: mites of six families (19).

Distribution and habitat (Fig. 7).—Elevation records are from sea level to 700 m. *D. granuliferus* is known from the lowland forests of the Golfo Dulce region of the Pacific coast of Costa Rica, mostly in Holdridge's (1967) lowland tropical wet forest zone, but extending into lowland tropical moist forest.

Localities.—COSTA RICA. ***Puntarenas:*** 4.8 km N Palmar Norte, N Río Diquis (KU 43874–80); Río Zapote, 8 km E Palmar Norte (KU 93917–23); Finca Jalaca near Piedras Blancas (H. Trapido field notes H.T. 7999); Rincón de Osa (CRE 3114, 6325, 6391, 7239; UMMZ 125582; LACM 54000); Río Rincón, 4.8 km S bay entrance (CRE 705; JMS 1661; UMMZ 123622); 4.5 km W Rincón de Osa (KU 102152–60); 3.2 km SE Golfito (CRE 2758); Río Dimitis, 14.5 km N Quepos (CRE 2874).

DOUBTFUL RECORD: COSTA RICA. ***San José:*** San Isidro del General (KU 43875).

Cleared and stained material.—JMS 1661.

Dendrobates pumilio O. Schmidt 1857
Flaming Poison-arrow Frog
Figures 11H–K, 12M

1857. *Dendrobates pumilio* O. Schmidt: 12, holotype: KM 1018/1346 (now lost), road between Bocas del Toro and Volcán Chiriquí, Panamá, 5000-7000 ft.
1858. *Dendrobates pumilio* O. Schmidt: 250, plate 2, fig. 13.
1858. *Hylaplesia pumilio.* Günther: 126.
1867. *Dendrobates typographus* Keferstein: 360, type locality: Costa Rica.
1874a. *Dendrobates ignitus* Cope: 68-69, six syntypes: ANSP 2724–29, Machuca, Nicaragua.
1882a. *Dendrobates typographus.* Boulenger: 143–144.
1952. *Dendrobates typographus.* Taylor: 633–635.
1953. *Dendrobates galindoi* Trapido: 181–187, fig. 36, holotype: FMNH 71053, Bastimentos, Bastimentos Island, Bocas del Toro, Panamá.
1968. *Dendrobates pumilio.* Savage: 761–763, fig. 5C.

Definition.—Snout-vent length of adults 17.5–24 mm; skin of back smooth to slightly granular; tarsal tubercle absent or slightly developed; color in life (except western Panamá): dorsum red, often with black dots; limbs and venter red, or partly or entirely blue or black; omosternum present.

Diagnosis.—*D. pumilio* is a member of the *pumilio* group, differing from *D. granuliferus* in having less granular skin, often with black dots or spots, and from *D. speciosus* in smaller size. *D. pumilio* differs from *D. opisthomelas* and *D. steyermarki* in larger size and in lacking a well-developed tarsal tubercle. *D. pumilio* differs from *D. altobueyensis* in larger size, in usually having red color in life, and in sometimes having the venter and limbs a different color than the dorsum.

Description.—Measurements are in Table 3. The skin is smooth or slightly granular, except in one specimen from Sixaola (BM 1956.1.6.54), which is nearly as granular as *D. granuliferus.* The tympanum is round, and its diameter equals one-half of the diameter of the eye. The finger disks are not sexually dimorphic. The tarsal tubercle is absent or slightly developed.

In life, the throat of males is darker than the throat of females (Kitasako 1967). In specimens from Nicaragua and Costa Rica, the head and back are red. The dorsum and venter often have black dots (Fig. 11I); southern specimens have more dots than do northern specimens. The hind limbs are black in southern specimens and purple or blue in northern specimens (Savage 1968). The venter is entirely red or red-orange, partly red and partly blue (Fig. 12M), or entirely blue (Kitasako 1967).

In specimens from western Panamá (Figs. 11J–K), the dorsum is red, red-orange, blue, green, or olive-

green, and the venter is red, yellow, blue, or white; dorsal black spotting is present or absent (Daly and Myers 1967). Usually, there is only one color pattern in each population. One of these western Panamanian populations, containing both red and green color morphs, was described as *D. galindoi* (Trapido 1953).

Breeding call.—The breeding call has been described as an insectlike "buzz-buzz-buzz," pause, repeat, similar to the call of *D. granuliferus* (Savage 1968); as a hasty, long-continued rattling, similar to a child's rattle (Oertter 1951); and as 20 to 30 grating, insectlike chirps, starting well spaced, increasing in frequency, and ending almost in a trill (Trapido 1953: *D. galindoi*). The calling site is a fallen log or branch (Kitasako 1967).

Tadpoles (Fig. 21).—Measurements are in Table 4. The tadpoles are distinctive, and resemble those of *D. histrionicus*, in having few, large oral papillae and a reduced number of denticles. The oral papillae are few, large, in one row, and border the entire posterior lip, but border only the lateral portions of the anterior lip. The oral disk is not laterally indented. The denticle formula of tadpoles from Bastimentos Island, Panamá (*D. galindoi*), is $\frac{0}{1}$, $\frac{1}{1}$, $\frac{1}{1\text{-}0}$, $\frac{1}{0\text{-}1}$, $\frac{1\text{-}1}{1}$, $\frac{1\text{-}0}{1}$, $\frac{0\text{-}1}{1}$, or $\frac{0}{1}$. The incomplete denticle rows are median or lateral, and often are reduced to a few denticles. The beaks are massive and serrate, and the lower beak is not indented. The eyes are dorsal. The spiracle is sinistral and low. The dorsal fin varies from not reaching the body to reaching it. The anus is median. The tip of the tail is rounded. In preservative, the head-body is uniform dark brown dorsally and laterally, and uniform light brown ventrally. The tail is tan with light brown dots; the dots extend onto the transparent fins.

Adults deposit tadpoles in water in the leaf axils of bromeliads and terrestrial aroids (Trapido 1953; Savage 1968). J.T. Kitasako told me that of five tadpole-carrying adults (all females) that he took in Costa Rica, one bore two tadpoles, and four bore one tadpole apiece. Tadpoles of this species have been described by Starrett (1960).

Relationships.—*D. pumilio* is closely related to an allopatric species, *D. granuliferus*, with which it probably was geographically and genetically continuous before the onset of orogeny and aridity in Costa Rica. The similarity of a specimen from Sixaola, in the Caribbean drainage of Costa Rica (BM 1956.1.6.54), to *D. granuliferus* calls into question the specific distinctness of *D. pumilio* from *D. granuliferus*.

Life history.—Aggressive behavior (wrestling and calling) occurs between males of this species (Duellman 1966; Bunnell 1973). The courting female pursues the male, but not as closely as in *D. auratus*

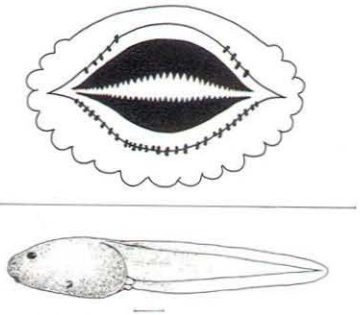


FIGURE 21. Tadpole of *Dendrobates pumilio*, Isla Bastimentos, Panamá (FMNH 71837), from leaf axil of *Xanthosoma violaceum* (Araceae); mouthparts and lateral aspect (Stage 28). Lines equal one millimeter.

(Kitasako 1967). Captive individuals laid eggs in bromeliad leaf axils. Clutch size in captives was six to 16; the period from fertilization to hatching was eight to 10 days at 19 to 21°C (Oertter 1953).

Predators.—Experienced ducks and chickens refused to eat *D. pumilio* (Belt 1874; Kitasako 1967). A. Starrett (California State University at Northridge) informed me that an unidentified captive snake in Costa Rica ate a specimen of *D. pumilio*.

Diseases.—Stolk (1959) found a red skin tumor, or erythrophoroma, in one specimen of *D. pumilio*.

Toxins.—Skin toxins have been investigated by Daly and Myers (1967).

Distribution and habitat (Fig. 7).—Elevation records are from sea level to 960 m (the type locality is higher, but see Savage [1968]). *D. pumilio* is known from the lowland forests of the Caribbean drainage of Central America, from northern Nicaragua through Costa Rica to western Panamá, in Holdridge's (1967) lowland tropical moist forest and lowland tropical wet forest zones, extending into the premontane moist forest and premontane wet forest zones in Nicaragua. In Costa Rica, it inhabits forests and cacao groves; in the latter, it occurs in relatively sunny, exposed areas among fallen bromeliads and logs, and occupies restricted areas within a relatively homogeneous habitat (Kitasako 1967).

Localities.—NICARAGUA. ***Matagalpa:*** near Matagalpa (MCZ 3538-39); Finca Tepeyac, 9 km E, 10.5 km N Matagalpa (KU 85277-79, 87696); Hacienda La Cumplida near

Matagalpa (UMMZ 118416, 118655); 19 km N Matagalpa (UMMZ 116478–81); 16 km S Matagalpa (KU 85280–82). ***Chontales:*** Chontales mines (BM 94.10.1.44–49). ***Zelaya:*** Río Grande (UMMZ 46459); Río Cama near Bluefields (ANSP 23512); Cukra (AMNH 8210, 8212, 8215–16, 8218–19, 8224–26); Kanawa (AMNH 7244); Wholesome Creek (AMNH 7356, 8051–52, 8201–04, 8206, 8208–09); Camp Santa Ana, Río Huahuashán (AMNH 54988–90); Camp Papel (AMNH 55006). ***Río San Juan:*** San Juan del Norte (=Greytown) (USNM 19769, 20725, 102278); Río San Juan (USNM 20726–35); Machuca (ANSP 2724–29); Los Sábalos (AMNH 5424); Río San Carlos (AMNH 52885); La Hunter (AMNH 7246).

COSTA RICA. ***Alajuela:*** Las Delicias (BM 1902.1.28.8–9); San Carlos (USNM 29884–90, 29979–83); 4.8 km S Tanque de San Carlos (CRE 7154); Río San Juan (USNM 19588–99, 19654–65; MCZ 26581–82); Río Frío (USNM 19666); El Ángel (CRE 506); Florencia (CRE 2626); 1.6 km W Jobillos (CRE 7148); Jobillos, 4.8 km N Santa Clara (CRE 8058); Río Ron-Ron, 8 km N Ciudad Quesada (CRE 7155–56); 9 km N Ciudad Quesada near La Florencia (CRE 8059). ***Heredia:*** Puerto Viejo (KU 65254–77, 68256–58, 86296–98, 94912–13; UMMZ 125471); Río Sarapiquí, 2-4 km W Puerto Viejo (CRE 2892); Finca La Selva, junction Ríos Sarapiquí and Puerto Viejo (CRE 64–65, 71–72, 512, 6573–74; UMMZ 122664, 123200, 123632); 16 km N Puerto Viejo (MCZ 75193–218); La Virgen (KU 65278–82). ***San José:*** Carrillo, junction Ríos Sucio and Hondura (Wettstein 1934). ***Cartago:*** Vere near Río Pacuare (CRE 118); headwaters Río Pacuare near San Vicente (CRE 119); Jicotea (CRE 120); Bonilla, on San José-Limón railroad (USNM 35716–21); Río Chitaría, 9.9 km NE bridge over Río Reventazón, on Turrialba-Peralta road (CRE 7196); Tuis (BM 98.10.26.28–29). ***Limón:*** Limón (MCZ 16161–62; ANSP 19509–14; CRE 2857); Finca Montecristo, Río Reventazón (USNM 70651–52); Finca Hamburgo, Río Reventazón (USNM 70650); Finca Wauchope, 11.2 km SW Limón (FMNH 67690–98); Colombiana (USNM 67344–46); Parismina (USNM 75431–32); Vesta (AMNH 76444); Zent (CRE 132; USNM 67326–31, 137766; MCZ 2908–09, 3961, 8002–10, 30461); Finca Philadelphia South near Finca Wauchope (ANSP 19650–51); Pandora (CRE 505; UMMZ 122663; MCZ 69184); Suretka (KU 35935–84, 35986–87, 36058–103, 36355–60, 36544–60; MCZ 10058, 10074–75, 10104–07); 0.8 km N Suretka (CRE 7185); Batán (Taylor 1952); Monteverde near Siquirres (MCZ 7930); 1.5 km E Siquirres (CM 41501); El Tigre, 9–14 km from Siquirres on road to Turrialba (CRE 290); Los Diamantes (CRE 210–13, 7002, 8044, 8076; KU 24884–901, 30451–58, 33048–56; UMMZ 118417, 118656; FMNH 103170–82, 172247; AMNH 54490); 1.6 km N Los Diamantes (CRE 849); 2.4 km E Los Diamantes (CRE 8049); Guápiles (AMNH 3810, 3812–13; ANSP 19564, 19567); Río Toro Amarillo near Guápiles (UMMZ 123632, 125470); Finca La Lola (KU 33036–47; UMMZ 118418; CRE 26, 127–28, 130–31, 133, 199–203, 205–09, 284–85, 657, 6099–100, 8061, 8068, 8072); near Guácimo (CRE 617); La Castilla, Río Reventazón (ANSP 23593–96, 23616, 24994); Cerro Tortuguero (AMNH 69053–55, 75607–71; CRE 2848); 3.2 km S, 16 km W, and 22.4 km S, 1.6 km W mouth Río Tortuguero (AMNH 69051–52); Caño Palmas, 1–4.8 km NW Cerro Tortuguero (UMMZ 126036; AMNH 75072–81); Puerto Viejo (=Old Harbour) (KU 35985, 35988, 36523–50); Valle de Talamanca (MCZ 10068–73); Río Lari, 8–16 km SW Amubre (CRE 7175–76, 7180); junction Ríos Lari and Dipari, 20.8 km SW Amubre (CRE 7178); Sixaola (BM 1956.1.6.54); Mountain Cow Creek near Banano (KU 33057); Barra de Colorado (AMNH 8199–200).

PANAMA. ***Bocas del Toro:*** Almirante (MCZ 15051–55; KU 80016–53; FMNH 83471–75, 97981, 152068–69, 152086–90, 153683); 4.8–12.8 km W Almirante (KU 95282–318, 95401, 115514–21, 115577–603, 117014); 10–11 km NW Almirante (FMNH 67661–89, 67699–707, 71088–101, 153781–841); road between Bocas del Toro and Volcán Chiriquí (KM 1018/1346); La Loma on Boquete trail (MCZ 56201); Chiriquí Grande (KU 95110–28); Guabo (MCZ 10057); Isla Bastimentos (KU 94914–58, 94965–95005, 95406, 95410, 116849; FMNH 71053–61, 71063–66, 71068–84, 71837, 153604–15, 153674–82; UMMZ 120385; MCZ 28288–89; USNM 149996); Cayo de Agua (KU 95230–38, 95242–67, 95404; USNM 149990–95); Isla Popa (KU 95093–108, 95408; AMNH 62904–05); Isla Escudo de Veraguas (KU 115522–61, 116745; AMNH 148231–35); Isla Providence (BM 91.11.7.10); Cayo Nancy (KU 95129–44, 95147–64, 95409); Isla Shepherd (KU 95269–78, 95280–81, 95411, 115624–31, 116746); Isla San Cristóbal (KU 95171–227, 95405, 115605–23); Isla de Colón (KU 95064–66, 95068–89, 95091, 95412, 95417); Isla Split Hill (KU 95009–41, 95407); mainland NW Isla Split Hill (KU 95044–62, 95403); Boca del Drago (USNM 142319–31); Península Valiente, Bluefield (KU 95319–86, 116747); across bay from Bluefield (KU 95387–98, 95402); Río Cricamola, 9.6 km from coast (KU 95167–70); Río Cahuita, mouth and 5 km above mouth (KU 115504–13); 5 km W mouth Río Calovébora (KU 115604). ***Veraguas:*** mouth Río Concepción (KU 115562–75).

DOUBTFUL RECORDS. NICARAGUA. ***Managua:*** Managua (USNM 115940–58; UMMZ 92455); ***Chinandega:*** Chinandega (MCZ 2633).

Cleared and stained material.—LACM 60992; JMS 1665, 1667–70.

Dendrobates speciosus O. Schmidt 1857
Splendid Poison-arrow Frog
Figure 17

1857. *Dendrobates speciosus* O. Schmidt: 12, three syntypes: KM 1017/1345 (now lost), road between Bocas del Toro and Volcán Chiriquí, Panamá, 5000–7000 ft.
1858. *Dendrobates speciosus* O. Schmidt: 249, plate 1, fig. 11, plate 2, fig. 12.
1858. *Hylaplesia speciosa.* Günther: 126.
1968. *Dendrobates speciosus.* Savage: 763.

Definition.—Snout-vent length of adults 27.5–30 mm; skin of back smooth; tarsal tubercle absent or slightly developed; color in life: uniform red; omosternum present.

Diagnosis.—*D. speciosus* is a member of the *pumilio* group, differing from *D. granuliferus* in larger size and in having smooth skin, and from *D. pumilio* in larger size. *D. speciosus* differs from *D. opisthomelas* in larger size, in having smooth skin, and in lacking a tarsal tubercle, from *D. steyermarki* in larger size and in lacking a tarsal tubercle, and from *D. histrionicus* in having an omosternum.

Description.—Measurements are in Table 3. The skin is smooth, except the posterior belly and ventral surface of the thighs, which are rugose. The tym-

panum is round, and its diameter is slightly greater than one-half of the diameter of the eye. The finger disks are not sexually dimorphic. The tarsal tubercle is absent or slightly developed.

In life, specimens from the type locality are uniform red (O. Schmidt 1858). In preservative, specimens from Gutiérrez and above Boquete are entirely gray, except for one or two small light spots in a few specimens.

Stomach contents (one specimen).—From LACM 60982: HYMENOPTERA: Formicidae: *Eurhopalothrix* sp (3), *Stenomma* ? sp (2), *Strumigenys* sp (1), *Apterostigma* sp (1), *Pachycondyla* sp (2); COLEOPTERA: Curculionidae: Cossoninae (2); ACARINA: mites of six families (50).

Distribution and habitat (Fig. 9).—An elevation record from Gutiérrez is 1372 m (the type locality may be higher, 1100–1580 m, see Savage [1968]). *D. speciosus* is known from the mountains of western Panamá in Holdridge's (1967) lower montane wet forest zone.

Localities.—PANAMÁ. ***Bocas del Toro:*** Gutiérrez (MCZ 9916–21, 52847–54; BM 1925.11.7.6; LACM 60998; AMNH 59676); road between Bocas del Toro and Volcán Chiriquí (KM 1017/1345). ***Chiriquí:*** above Boquete on trail to Bocas del Toro (MCZ 12127–31; USNM 118224; LACM 60982).

Cleared and stained material.—LACM 60982.

tinctorius group

This group contains five species (*D. auratus, D. azureus, D. galactonotus, D. tinctorius,* and *D. truncatus*).

Definition: snout-vent length of adults moderate to large (23.5–50 mm); stripes present or absent; color in life never red; dorsal skull bones often fused together and sculptured; omosternum present; tadpoles (known only in *D. auratus, D. azureus,* and *D. tinctorius*) have oral disk unindented, denticles not reduced in number, and anus median.

Dendrobates auratus (Girard 1855)
Green Poison-arrow Frog
Frontispiece II and Figures 11L–P, 12I–J

1855. *Phyllobates auratus* Girard: 226, holotype: USNM 10307, Taboga Island, Panamá.
1858. *Hylaplesia tinctoria* (part, var D). Günther: 125.
1858. *Dendrobates latimaculatus* Bibron. Günther: 125, holotype: BM 52.12.11.8, Isthmus of Darién, Panamá.
1863. *Hylaplesia aurata.* Cope: 49.
1874. *Dendrobates trivittatus auratus.* W. Peters: 618.
1874. *Dendrobates trivittatus maculatus* W. Peters: 617, type locality: Chiriquí, Panamá (I have not seen the type; according to Peters' description, the first finger is longer than the second, a *Phyllobates* character. Dunn [1941] saw the type and considered it *D. auratus*).
1882a. *Dendrobates tinctorius* (part, var Aa–e, C). Boulenger: 143.
1901. *Dendrobates tinctorius* (part). Werner: 631.
1901. *Dendrobates amoenus* Werner: 627–628, 632, holotype: NHMW 1904,111,95, Costa Rica (according to Dunn [1941], the type was said to be in Königsberg, but he saw the NHMW specimen labeled as the type).
1942. *Dendrobates tinctorius auratus.* Laurent: 12.
1961. *Dendrobates auratus.* Cochran: 107, plate 40 (color photo).
1968. *Dendrobates auratus.* Savage: 759–760, fig. 5A.
1970. *Dendrobates lugubris* (part). Cochran and Goin: 19–21 (not the plate).
1970. *Phyllobates bicolor* (part). Cochran and Goin: 35–37 (USNM 48865, 122104 only).

Definition.—Snout-vent length of adults 25–42 mm; skin of back smooth; tarsal tubercle absent or slightly developed; color in life: black, brown, or bronze with stripes, bands, or spots of blue, blue-green, green, or yellow-green; no red or orange; omosternum present.

Diagnosis.—*D. auratus* is a member of the *tinctorius* group, differing from *D. azureus* in lacking reticulation, from *D. galactonotus* in lacking a well-developed tarsal tubercle, from *D. tinctorius* in smaller size and in lacking reticulation, and from *D. truncatus* in having a smooth back, in usually lacking lateral stripes, and in sometimes having the dorsum spotted or banded instead of striped; when dorsolateral stripes are present, they are relatively broad, and are blue, blue-green, green, or yellow-green (*D. truncatus* has a slightly granular back, has lateral stripes, and always has dorsolateral stripes, which are relatively narrow and yellow).

Description.—Measurements are in Tables 3 and 7. The smallest specimens are from Isla Taboga, off the Pacific coast of Panamá; the largest are from El Valle de Antón, Panamá. Most Central American specimens are larger than those from Colombia and eastern Darién. The skin is smooth, except the posterior belly and ventral surface of the thighs, which are granular. The tympanum is round, and its diameter equals two-thirds of the diameter of the eye. The second, third, and fourth finger disks average wider in males than in females (e.g., in 67 Costa Rican specimens [CRE], the width of the third finger disk, expressed as a percentage of the snout-vent length [minimum-maximum-mean percentages], is: 50 females: 4.7–6.2–5.7; 17 males: 6.5–9.0–7.7). The finger disks of specimens from Isla Taboga, Panamá, average smaller than those of specimens from other populations of *D. auratus*, and are only slightly sexually dimorphic (19 females: 3.4–5.3–4.2; 13 males: 3.8–6.0–5.6). The tarsal tubercle is absent or slightly developed.

Specimens from Nicaragua, Costa Rica, and western Panamá usually have a light dorsal horseshoe

mark on the snout; this mark often continues onto the back as complete or broken dorsolateral stripes, which are sometimes interconnected by transverse stripes. The striped pattern sometimes becomes a longitudinal chain of two or two and one-half circles. Sometimes the dorsum lacks stripes and bears large spots or bands. The venter has light curving lines, bands, large spots, or circles; often, an ellipse or circle decorates the throat. In life, the light markings are blue, blue-green, green, or yellow-green on a black, light brown, or dark brown ground color.

C.W. Myers informed me that specimens from an aberrant population near Panamá City lack green, and are dark brown with tan markings.

Panamanian specimens from the San Blas coast and La Campana (on the Pacific coast near the Canal Zone) have a *D. histrionicus*like dorsal pattern of many small, light spots (Fig. 11L).

Specimens from extreme eastern Panamá and from the confluence of the Ríos Truandó and Nercua in northern Colombia have small, widely separated, longitudinal, light green (tinged with gold) or dark green dorsal and ventral spots on a black ground color (Fig. 11M).

Specimens from the middle Río Nercua, Colombia, have broken green or blue-green dorsolateral stripes on a chocolate brown or light bronze ground color; the venter has oblong blue spots.

Specimens from the western Atrato drainage (Cerro Los Hermanos and Camino de Yupe), Colombia, are similar to those from Nicaragua, Costa Rica, and western Panamá; the dorsum has bands, large spots, or dorsolateral stripes (Frontispiece II; Figs. 11N–P), and the throat has a horseshoe mark, circle (complete or broken), or median longitudinal stripe (Figs. 12I–J).

Breeding call.—The breeding call has been described as a slurred, high, musical "cheez-cheez-cheez," three to five notes (Savage 1968); a low buzzing, two seconds duration (Dunn 1941); and four to five clicking notes, two seconds duration, pause five seconds, repeat (D. Goodman, unpublished data).

Tadpoles (Fig. 22).—Measurements are in Table 4. The oral papillae are in two rows, and border the entire posterior lip, but border only the lateral portions of the anterior lip. The oral disk is not laterally indented. The denticle formula is $\frac{1}{3}$. The beaks are massive and serrate, and the lower beak is indented. The eyes are dorsal. The spiracle is sinistral and low. The dorsal fin barely reaches the body. The anus is median. The tip of the tail is broadly rounded. In preservative, the head-body and tail are uniform light brown, dark brown, or blackish; the fins are uniformly dotted with brown, except for a narrow, transparent border.

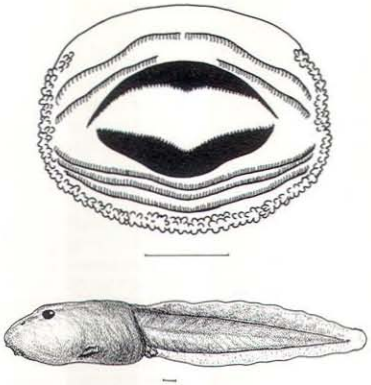


FIGURE 22. Tadpole of *Dendrobates auratus*, Rincón de Osa, Costa Rica (CRE 902), from hole in fallen log; mouthparts (Stage 38) and lateral aspect (Stage 34). Lines equal one millimeter.

Adults deposit tadpoles in water in tree-holes, leaf axils of bromeliads, and small, stagnant pools (Eaton 1941; Savage 1968). Stomachs of tadpoles collected in the field contained protozoans and rotifers (Eaton 1941). In captivity, tadpoles grazed on stones and ate algae, chopped liver, and other tadpoles (Senfft 1936). Several adults have been observed carrying one tadpole apiece (Dunn 1941; Eaton 1941). An adult male has been taken carrying two tadpoles (AMNH 51805).

Relationships.—*D. auratus* probably is closely related to *D. truncatus*. Their ranges appear to meet south of the Golfo de Urabá, but it is not known if they are sympatric there. Some Chocoan specimens that are called *D. auratus* herein resemble *D. truncatus*. Further study is needed to ascertain if one or two species are involved.

Life history.—Agonistic behavior occurs between females (Senfft 1936). During courtship, the female pursues the male (Dunn 1941; Kitasako 1967). Senfft (1936) reported that *D. auratus* does not carry out amplexus. In his captive animals, the male remained well separated from the female during oviposition; after the female left the eggs, the male sat on the eggs and fertilized them. During the breeding season, the same captive female laid eggs every eight to 10 days on herb leaves (Senfft 1936). Clutch size in captives was five to 13 (Oeser 1932). Senfft's (1936) captive male guarded the eggs for the first

three days after oviposition; when the eggs hatched, the tadpoles wriggled onto the male's back. He carried them in stages (two or three tadpoles at a time) to a water basin; when he entered the water, the tadpoles left his back.

In captivity, the period from fertilization to hatching was 13–16 days, from hatching to metamorphosis 68–102 days, and from metamorphosis to sexual maturity six to seven months (Oeser 1932; Senfft 1936). *D. auratus* survived at least four years in captivity (Senfft 1939).

Stomach contents (three specimens).—From LACM 44233: HYMENOPTERA: Formicidae: *Anochetus* sp (1), *Wasmannia auropunctata* (Roger) (24), *Solenopsis (Diplorhoptrum)* (5), *Pheidole* sp (6), *Apterostigma* sp (1); COLEOPTERA: Ptiliidae (4), Curculionidae (2), predaceous beetle larvae (20); LEPIDOPTERA: Microlepidoptera: larvae (25); CHILOPODA: (3).

From LACM 44239: HYMENOPTERA: Formicidae: *Pheidole* spp (4), *Solenopsis (Diplorhoptrum)* sp (9), *Strumigenys* sp (1), Myrmecinae (11), *Anochetus* sp (1); COLEOPTERA: Curculionidae (1), Bostrychidae (2); ACARINA: mites of six families (75).

From ANSP 23394: HYMENOPTERA: Formicidae: *Gnamptogenys* sp (3), *Cyphomyrmex* sp (6), *Pheidole* spp (21), *Apterostigma* sp (2), Myrmecinae (8); COLEOPTERA: two spp (3), fragments (4); COLLEMBOLA: Poduridae (1); ACARINA: mites of two families (5).

Predators.—Kayser (quoted in Oeser [1932]) saw a *Wasserfrosch (Rana esculenta)* eat a captive specimen of *D. auratus;* the predator was not harmed by his repast.

Parasites.—I found ticks attached to specimens of *D. auratus.*

Ethnozoology.—Breder (1946) reported that Indians in the Darién region of Panamá use *D. auratus* as a source of blowgun poison.

Teratology.—A juvenile 20.5 mm male from Panamá (FMNH 154404) has three left arms in addition to the normal right arm.

Nomenclature.—Taylor (1952:638) noted that if *Hyla aurata* Wied 1821 is a species of *Dendrobates,* the name *Dendrobates auratus* (Girard) 1855 would be a junior secondary homonym. *Hyla aurata* Wied is not a species of *Dendrobates* (see "species of uncertain status" in the generic section, above).

Distribution and habitat (Fig. 6).—Elevation records are from sea level to 800 m. *D. auratus* is known from the lowland forests of both coasts of Central America, on the Caribbean side from southern Nicaragua through Costa Rica and Panamá to the Golfo de Urabá in Colombia, and on the Pacific side from Costa Rica through Panamá and the western Atrato drainage of Colombia to the Baudó drainage, in Holdridge's (1967) lowland tropical wet forest and lowland tropical moist forest zones. In Costa Rica, it inhabits forests and cacao groves; in the latter, it occurs in shade near tree buttresses, and in dense secondary growth (Kitasako 1967). On the Camino de Yupe, in the Serranía de Baudó of Colombia, it occurs on the floor of shady virgin forest. In 1932, 206 specimens of *D. auratus* from Taboga or Taboguilla Islands, Panamá, were released in the upper Manoa Valley, Oahu, Hawaii; their descendants form a breeding population (Oliver and Shaw 1953; Ullman 1967).

Localities.—NICARAGUA. ***Río San Juan:*** Río San Juan (USNM 19587); San Juan del Norte (= Greytown) (USNM 15647, 19770-73, 24484-87, 102277; KU 42689); Río Machuca, San Juan drainage (ANSP 2730-38); Río San Carlos (AMNH 51509); San Miguelito (Dunn 1941); Los Sábalos (AMNH 5425); Río Tule (AMNH 7358-59).

TABLE 7

Snout-vent length of samples of adults from eight populations of *Dendrobates auratus,* arranged in order from northwest to southeast. Localities: COSTA RICA: (1) Finca La Lola, (2) Mountain Cow Creek near Banano, (3) Suretka, (4) Rincón de Osa. PANAMÁ: (5) 11 km NW Almirante, (6) El Valle de Antón, (7) Isla Taboga. COLOMBIA: (8) Camino de Yupe.

	All Specimens			Males			Females		
Locality	n	Range	$\bar{x}\pm SE$	n	Range	$\bar{x}$	n	Range	$\bar{x}$
(1) La Lola	41	30.5–36.5	33.8±0.28	15	30.5–33.5	31.7	26	33.5–36.5	35.1
(2) Banano	14	29.5–37.0	33.5±0.57	6	29.5–33.5	31.6	8	32.5–37.0	34.9
(3) Suretka	14	29.5–38.5	34.6±0.65	4	32.0–33.0	32.4	10	29.5–38.5	35.5
(4) Rincón	14	31.0–36.0	33.5±0.44	4	31.0–32.0	31.3	10	33.5–36.0	34.4
(5) Almirante	52	29.0–39.0	34.2±0.32	21	29.0–34.0	32.0	31	33.0–39.0	35.7
(6) El Valle	14	27.5–42.0	37.9±1.05	8	27.5–39.5	35.8	6	38.5–42.0	40.8
(7) Taboga	51	25.0–33.5	28.5±0.28	18	25.0–29.5	26.6	33	27.0–33.5	29.6
(8) Yupe	25	28.5–34.0	31.5±0.27	4	28.5–32.0	29.8	21	30.0–34.0	31.9

COSTA RICA. ***Alajuela:*** 8 km N Ciudad Quesada, Río Ron-Ron (CRE 7155); Muelle San Carlos (USNM 29977); Las Delicias (Günther 1900-1902); Santa Clara (Günther 1900-1902). ***Cartago:*** near Turrialba (KU 100626; MCZ 29271). ***Puntarenas:*** Rincón de Osa (MCZ 75190-92; UMMZ 123623; CRE 705, 902, 3114, 6026, 6325, 6391); 4.5 km W Rincón de Osa (KU 104294); 6.4 km inland near Río Rincón (CRE 752); Río Ferruviosa, 7.2 km S Rincón de Osa (CRE 7235); Villa Neily near Corredor (CRE 179); 8 km E Villa Neily (CRE 8038); Esquinas (KU 33082-89); Pozo Azul de Puris (BM 1907.6.28.5-12); Palmar Sur (CRE 2650); 4-5 km ESE Palmar Sur (KU 65244-46, 68343); 10 km SE Palmar Sur (KU 93902-06); 6 km W Palmar Norte (KU 93907-08, 95448); Río Zapote, 8 km E Palmar Norte (KU 93909-16); Quebrada Boruca, 22 km E Palmar Norte (KU 65247-53, 68255); Buenos Aires (FMNH 2542). ***Limón:*** Limón (ANSP 19509-14; KU 33090-91; CRE 2857; MCZ 10161); Suretka (KU 36051-57, 36348-54, 41019-23; MCZ 9773-75); Finca Wauchope, 11.2 km SW Limón (FMNH 67655-58); Finca La Lola (JMS 1671-73; CRE 126-27, 130-31, 133, 200-01, 203, 205-09, 8072; UMMZ 118415; KU 33073-81, 33104); Finca Holanda, Río Limón (ANSP 19652); Victoria, 30 km W Limón (FMNH 5626); Siquirres (CRE 2813); 1.5 km E Siquirres (CM 41500); Portete, 4.8 km W Limón (CRE 6341; UMMZ 125469); Batán (KU 30292-98); Zent (CRE 132; MCZ 3958-60, 7944-47); Pandora, Río Estrella (CRE 505; UMMZ 122665; MCZ 65015); Guápiles (Fowler 1916); Finca Montecristo, Río Reventazón (USNM 70653); Finca La Castilla, Río Reventazón (ANSP 23589–96, 23615–16); Finca Vesta, Río Estrella (ANSP 21431–34); Valle de Talamanca (MCZ 10063–67); Mountain Cow Creek near Banano (KU 33058–72); Cahuita (LACM 74769).

PANAMÁ. ***Bocas del Toro:*** Punta de Peña (USNM 38735); Almirante (USNM 142276-80; FMNH 60343-48, 83476, 152091-98; KU 79998-80015; MCZ 10061-62); 11 km NW Almirante (FMNH 67659-60, 154101-16, 154118-21, 154123-72); 4.8-12.8 km W Almirante (KU 94855-68, 100356, 115463); 5 km W mouth Río Calovébora (KU 115464-65); mainland NW Isla Split Hill (KU 94869-74); Punta Gallinazo, mainland WNW Isla Shepherd (KU 94875); Isla Shepherd (KU 94876-89); hill above Miramar (KU 94890-91); La Loma, inland from Chiriquicito on Boquete trail (MCZ 10059-60). ***Chiriquí:*** Progreso (UMMZ 58250); Puerto Armuelles (BM 1935.4.3.1). ***Veraguas:*** Soná (USNM 133041). ***Herrera:*** Parita (USNM 127253-60). ***Los Santos:*** Cerro Hoya (USNM 148215); 0.4 km W Macaracas (CM 43582); Lajamina (KU 67991-68009); Cerro Cambutal (KU 115469). ***Coclé:*** El Valle de Antón (LACM 44279; FMNH 60354, 154117, 173175-76; MRHN 6754; ANSP 21801, 23392-400; AMNH 45991, 55512-13, 59664-65; UMMZ 84719). ***Colón:*** Cerro Santa Rita (AMNH 59667-70; FMNH 154100; CAS-SU 4444–50); Cerro Bruja (FMNH 16678-82; USNM 54024-28); SW Cerro Bruja (KU 94892-93, 116732); Signal Loma (USNM 55322-27); Brazo del Medio near Palenque (FMNH 153702-03); 3.5 km SE Puerto Pilón (KU 115453-62, 115470). ***Canal Zone:*** Isla Barro Colorado (FMNH 13355, 13373, 13450, 16667-78, 22838-39, 67616–54, 121253, 174363–64; KU 33513, 76582–88; CM 8210-11, 8238, 8447, 8473, 8482; AMNH 20893, 40464, 44289, 52748-50, 55514-16, 60524, 62313-14, 64722, 69816; ANSP 23133; JMS 1482-84; MCZ 10149, 15246, 24196; UMMZ 61621, 63579, 63581-82, 63584-86); Isla Slothia (Eaton 1941); Ancón (USNM 54296-98, 63003; MCZ 10148; UMMZ 58207, 58251); Castilla (CAS-SU 3293); near Gamboa (KU 116991-117005); Fort Kobbe (KU 117006-13); Punta Bruja (MCZ 15723); Chilibrillo Cave on Madden Dam Road (MCZ 19964); Gatún (UMMZ 52718; USNM 54168; ANSP 21445-48); Balboa (ANSP 19557-60; AMNH 41764; UMMZ 98419-21; FMNH 55540). ***Panamá:*** Isla Taboga (FMNH 109777, 153720-29, 154122, 154173-84, 154384-97; USNM 10307, 48520-22, 51955-56, 51963-65, 66495-509, 80327, 102763-805, 129218-45; KU 67966-70, 76589-98, 115451-52; ANSP 21066-67, 21848-99; BM 83.11.9.1-4, 1926.1.20.57-63; MCZ 2498, 10127-32; AMNH 59671–75); Isla Taboguilla (USNM 66322–25, 89287–361, 102811-46; MCZ 25679-80); Cerro La Victoria (AMNH 59666; FMNH 153706, 153870); Chorrera (UMMZ 95478); Cerro Azul (USNM 140055-56); La Campana (ANSP 21824); near Boquerón, between Candelaria and Peluca Stations (AMNH 53721–22); Río Pequení, head of Madden Lake (ANSP 21755); Río Puente near Madden Dam (ANSP 23383); Río Silugandí (UMMZ 125587–90). ***San Blas:*** Nicuesa (MCZ 16015); Caledonia (AMNH 40546, 41099); Camp Summit (KU 115466). ***Darién:*** Serranía de Pirre (KU 115467); Río Tuquesa, 10 km above mouth (KU 115468); Tacarcuna (KU 77596); junction Ríos Tuira and Mono (KU 94899–900, 116733); Río Mono, 5 km above Río Tuira junction (KU 94901); Cerro Quia (KU 94894–98, 94902–11, 116734–37); Laguna de la Pita (Peracca 1896); Río Lara (Peracca 1896); Río Esnape (MCZ 9162–63); Río Aruza, Tuira drainage (USNM 54235); Río Chico (AMNH 40976–78, 41172; CM 23484–85); Camp Townsend, Three Falls Creek, and Camp Creek, all near Yavisa (AMNH 40940–48, 41006–09, 41170, 51805); Río Sucubtí, Chalichiman's Creek (AMNH 39770, 40524, 40536, 40882–84, 51767; USNM 68057).

COLOMBIA. ***Chocó:*** Río Truandó (USNM 48865, 122104); junction Ríos Truandó and Nercua (LACM 60983, 61052–55); Río Nercua (LACM 61051); Cerro Los Hermanos (LACM 44224–28); upper Río Opogadó (LACM 44229, 44264); Camino de Yupe, Serranía de Baudó, between upper Opogadó and Domingodó drainages (LACM 44230–63); Serranía de Baudó (ANSP 25617); La Victoria, junction Ríos Pepé and Baudó (USNM 150168); Unguía (FMNH 63877).

HAWAII (introduced). Oahu (CAS-SU 20380-83; BM 1963.481; AMNH 62122-27; LACM 74746).

Cleared and stained material.—LACM 60983; JMS 1482–84, 1671–76; ANSP 23394.

Dendrobates azureus Hoogmoed 1969
Blue Poison-arrow Frog
Figures 11E, 12H

1969. *Dendrobates azureus* Hoogmoed: 133-141, text-figs. 1-2, plates 1-2, holotype: RMNH 13837a, Vier Gebroedersberg near Brasilian border, 2°0'N, 55°38'W, forest island in Sipaliwini Savannah, Nickerie, Suriname.

Definition.—Snout-vent length of adults 38.5–45 mm; skin of back smooth; tarsal tubercle absent; color in life: black with close-set blue reticulation; omosternum present.

Diagnosis.—*D. azureus* is a member of the *tinctorius* group, differing from *D. auratus* in having reticulation, from *D. galactonotus* in lacking a tarsal tubercle, from *D. truncatus* in larger size, in having reticulation, and in lacking stripes, and from *D. tinctorius* in having a hunch-backed posture in life and

a relatively small (diameter equals one-third of the diameter of the eye), indistinct, and oval tympanum; versus a straight posture in life and a relatively large (diameter equals one-half of the diameter of the eye), distinct, and round tympanum in *D. tinctorius*.

Description.—Measurements are in Table 3. The skin is smooth, except the posterior belly and ventral surface of the thighs, which are slightly granular. The tympanum is oval, and its diameter equals one-third of the diameter of the eye. The second, third, and fourth finger disks average wider in males than in females. The tarsal tubercle is absent.

In life, specimens from the type locality are covered with close-set blue reticulation on a black ground color. The blue reticulation often is expanded, reducing the ground color to small black spots (Fig. 12H). A transverse area across the mid-belly and sides is light blue, divided on the belly by a dark blue longitudinal stripe (Hoogmoed 1969).

Tadpoles (Hoogmoed 1969: 136, text-figs. 1–2).—Two tadpoles in Stage 26, taken from the back of an adult male (RMNH 13842), have a head-body length of 4 mm and a total length of 10 mm. The oral papillae are in two rows, and border the entire posterior lip, but border only the lateral portions of the anterior lip. The oral disk is not laterally indented. The denticle formula is $\frac{1-1}{1-2}$. The beaks are massive, and the lower beak is indented. The eyes are dorsal. The spiracle is sinistral and low. The anus is median.

Relationships.—*D. azureus* may have arisen by isolation of a population of *D. tinctorius* in forest islands surrounded by unsuitable habitat.

Life history.—In captive specimens of *D. azureus*, Polder (quoted in Hoogmoed [1972]) observed fertilization of the eggs by the male without amplexus (similar to Senfft's observations on *D. auratus* in 1936). He also noted that clutch size was two, that the period from fertilization to hatching was 18 days, that an adult female carried a tadpole on her back, and that adults wrestled with each other.

Stomach contents (one specimen).—From RMNH 13843c: HYMENOPTERA: Formicidae: *Solenopsis* sp (3); ISOPTERA: *Coptotermes* sp (6), *Nasutitermes* sp (4).

Distribution and habitat (Fig. 9).—Elevation records are from 315 to 430 m. *D. azureus* is known only from the type locality. It inhabits humid forest islands surrounded by savannah. It usually is found on the ground, although Hoogmoed saw one specimen five meters above the ground on a tree trunk. *D. azureus* inhabits only those forest islands containing a small stream among moss-covered rocks. The frogs are found only near the rocks. These frogs are diurnal; at night they hide between rocks and in holes at the bases of trees. The temperature in the forest islands is 22 to 27°C in the daytime, and falls to 20°C at night (Hoogmoed 1969; Hoogmoed 1972).

Localities.—SURINAME. ***Nickerie:*** Sipaliwini Savannah, forest islands on Vier Gebroedersberg near Brasilian border (RMNH 13837–43).

Cleared and stained material.—RMNH 13843c.

Dendrobates galactonotus Fitzinger *in* Steindachner 1864
Splash-backed Poison-arrow Frog
Figures 11F–G

1864. *Dendrobates galactonotus* Fitzinger. Steindachner: 260, 262, holotype: NHMW 19189, farm of Pedro Gurção, Rio do Muria, North of Vigia, Pará, Brasil. Steindachner listed *D. galactonotus* in the synonymy of *D. tinctorius* and treated the species as *D. tinctorius* var *galactonotus*.

1882a. *Dendrobates tinctorius* (part, var Af-g, B). Boulenger: 143.

1913. *Dendrobates paraensis* Boulenger: 1028, fig. 178, eight syntypes: BM 1904.7.26.9–12, Igarapé-Açu, Pará, Brasil; BM 45.8.25.142, 45.8.25.161, 96.1.7.1, 51.2.3.9, Pará, Brasil.

Definition.—Snout-vent length of adults 30.5–40.5 mm; skin of back smooth; tarsal tubercle well developed; color in life: dorsum black with large, irregularly margined yellow area, or dorsum entirely yellow, rarely bearing tiny dark dots; venter black; omosternum present.

Diagnosis.—*D. galactonotus* is a member of the *tinctorius* group, differing from *D. auratus*, *D. azureus*, *D. tinctorius*, and *D. truncatus* in having a well-developed tarsal tubercle.

Description.—Measurements are in Table 3. The skin is smooth, except the posterior belly and ventral surface of the thighs, which are granular. The tympanum is round, and its diameter equals one-half of the diameter of the eye. The second, third, and fourth finger disks average wider in males than in females. The tarsal tubercle is well developed.

In life, the holotype (Fig. 11F) was black with a large, irregularly margined yellow area on the head and back (Steindachner 1864). In preservative, one specimen (from Santarém) is entirely black (perhaps an artifact of preservation). All others have light dorsal coloration. In some specimens (from Cahy, Belém, Breu Branco, and Piratuba), most of the head, back, hind limbs, and upper sides of the body are light. One of these specimens (from Cahy) has tiny black dots on the entire head and back (Fig. 11G); the other specimens lack dots. In some specimens (from the Rio do Muria, Santarém, Belém,

and Carolina), the light coloration covers only part of the back, and often is interrupted by irregular black areas (Fig. 11F). The limbs often have small, light dorsal spots on a black ground color. The venter is immaculate black in all specimens examined except one, which has small light spots on the throat and ventral surface of the calves.

Stomach contents (one specimen).—From LACM 60990: HYMENOPTERA: Formicidae: *Pheidole* spp (21), *Crematogaster* sp (1), *Wasmannia auropunctata* (Roger) (10), *Solenopsis* sp (26), *Smithistruma* sp (2), Myrmecinae (35); COLEOPTERA: Pselaphidae (1), Curculionidae (1); ISOPTERA: *Coptotermes*? sp (45); ACARINA: mites of six families (35).

Nomenclature.—D. galactonotus is a Fitzinger label name first published by Steindachner (1864) as a synonym of *D. tinctorius* (Schneider). The name *D. galactonotus* was used in 1952 by Lutz and Kloss. See the nomenclature section under *D. leucomelas.*

I designate BM 1904.7.26.10, a 35.0 mm female from Igarapé-Açu, Pará, Brasil, collected on 31 January 1904 by A. Robert, as the lectotype of *Dendrobates paraensis* Boulenger, 1913.

Distribution and habitat (Fig. 6).—Elevation records are from 14 to 300 m. *D. galactonotus* is known from the lowland forests of the lower portions of the southern tributaries of the Amazon, from the Rio Tapajós east to the mouth of the Amazon.

Localities.—BRASIL. ***Pará:*** Rio do Muria, farm of Pedro Gurção, N Vigia (NHMW 19189); Belém (BM 45.8.25.142, 45.8.25.161, 51.2.3.9, 96.1.7.1; AMNH 6371; MHNP 4908); Belém, Parque do Museu Goeldi (MPEG 471–473); Igarapé-Açu (BM 1904.7.26.9–11; LACM 60990); Mangabeira, Municipio Mocajuba, Rio Tocantins (MPEG 530–531); Belém-Brasília road, 75 km from Belém (MPEG 365); Mazagão, Rio Tocantins (MCZ 17743); Santarém (BM 76.5.26.2, 1875.10.22.17); Piratuba, 18 km SE Abaeté (CAS-SU 10631); Cachoeira Cahy, Rio Jamanchim, Tapajós drainage (ZSBS 14/1914); Breu Branco, Rio Tocantins (ZSBS 11/1914). ***Maranhão:*** Carolina (WCAB 6695; KU 93143). ***Goiás:*** Araguainago, Belém-Brasília road, Rio Lontra (MPEG 693–94).

Cleared and stained material.—LACM 60990.

Dendrobates tinctorius (Schneider 1799)
Dyeing Poison-arrow Frog
Frontispiece I and Figures 11C–D, 12F–G, 15, 24

1788. *Hyla rubra* (part). Lacépède: 566–567, plate 39.
1799. *Calamita tinctorius* Schneider: 175, type locality: South America.
1802. *Rana tinctoria.* Shaw: 135.
1803. *Hyla tinctoria* (part). Daudin: 25–26, plate 8, figs. 1–2.
1826. *Hylaplesia tinctoria.* Boie in Schlegel: 239.
1830. *Dendrobates tinctorius* Wagler: 202.
1841. *Dendrobates tinctorius* (part, var A). Duméril and Bibron: 652–654.
1864. *Dendrobates tinctorius* (part, var *daudini*). Steindachner: 260–262.
1882a. *Dendrobates tinctorius* (part, var Dm). Boulenger: 142–143.
1913. *Dendrobates tinctorius* (part, typical form). Boulenger: 1026–1028.
1942. *Dendrobates tinctorius tinctorius.* Laurent: 12.
1958. *Dendrobates machadoi* Bokermann: 73–76, nine figs., holotype: WCAB 3083, Serra do Navio, Amapá, Brasil.

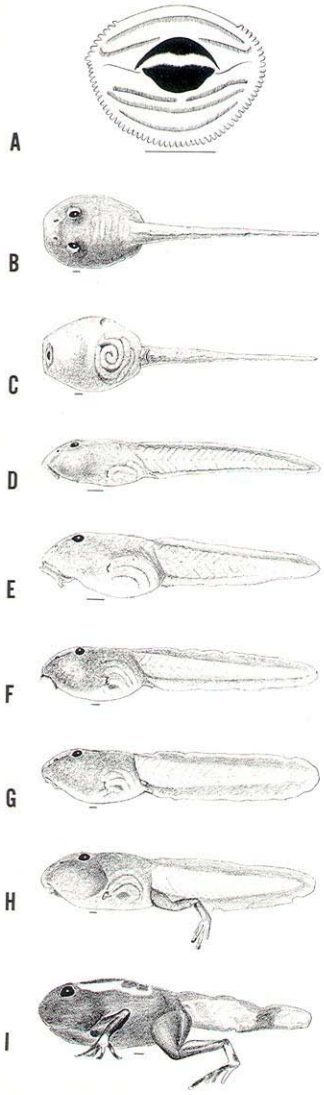
Definition.—Snout-vent length of adults 34–50 mm; skin of back smooth; tarsal tubercle absent; color in life: dorsum black with yellow, yellow-orange, or whitish dorsolateral stripes, which sometimes are interconnected by transverse band; sometimes stripes irregular or composed of yellow or blue reticulation; or dorsum uniform yellow; or dorsum black with few yellow or white spots; venter black (sometimes mostly yellow), usually reticulated with yellow or blue; omosternum present.

Diagnosis.—D. tinctorius is a member of the *tinctorius* group, differing from *D. auratus* and *D. truncatus* in larger size and in having reticulation, from *D. galactonotus* in lacking a tarsal tubercle, and from *D. azureus* in having a straight posture in life and a relatively large (diameter equals one-half of the diameter of the eye), distinct, and round tympanum; versus a hunchbacked posture in life and a relatively small (diameter equals one-third of the diameter of the eye), indistinct, and oval tympanum in *D. azureus.*

Description.—D. tinctorius is the largest species of the genus *Dendrobates.* Measurements are in Table 3. The skin is smooth, except the posterior belly and ventral surface of the thighs, which are granular. The tympanum is round, and its diameter equals one-half of the diameter of the eye. The second, third, and fourth finger disks average wider in males than in females. The tarsal tubercle is absent.

In life, specimens from the Rivière Matarony, French Guiana, are black with yellow or yellow-orange dorsolateral stripes meeting anteriorly in a solid snout color and posteriorly in a solid triangle or V; sometimes a transverse stripe connects the dorsolateral stripes at mid-back. The upper lips are yellow-orange. The sides of the body and the limbs are partly or entirely yellow or yellow-orange. The belly is partly reticulated with or nearly entirely bright yellow (Fig. 12G) or very pale yellow. The anterior throat sometimes is reticulated with yellow. The throat, posterior belly, posteroventral surface of the thighs, and sometimes the calves are reticulated with pale to medium blue, except in one specimen, which lacks blue.

Specimens from the Kayser Mountains, Suriname, are black with dorsolateral stripes; these stripes are



yellow on the snout and greenish white on the back, and connect with a greenish white reticulation on the sides of the body. The digital disks are light blue. The limbs and venter are black with dark purplish blue reticulation (M.S. Hoogmoed, field notes at RMNH).

One specimen (similar to Fig. 11D) from the Bakhuis Mountains, Suriname, is black with three dorsal white spots; it lacks yellow (M.S. Hoogmoed, unpublished data).

The transversely striped pattern (Fig. 15G) occurs in some specimens throughout the range. Specimens from Suriname and French Guiana (Fig. 15) have dorsal patterns varying from uniform yellow, to broad nearly fused stripes, to narrow stripes, to only a few spots. Most specimens from Guyana and a few specimens from Suriname have stripes composed of reticulation (Fig. 15H). Specimens from Shudikar-wau, Guyana, have a dorsal pattern transitional between stripes composed of reticulation and reticulation covering the whole back; some of these specimens are similar in pattern and color (blue in life, no yellow [R. Snedigar, field notes at AMNH]) to *D. azureus*, but the reticulation is broader (i.e., the interspaces are larger) and the tympanum is larger than in the type material of *D. azureus*. Provisionally, I include the Shudikar-wau population in *D. tinctorius*.

Tadpoles (Fig. 23).—Measurements are in Table 4. The oral papillae usually are in one row (one specimen has the papillae partially in two rows), and border the entire posterior lip, but border only the lateral portions of the anterior lip. The oral disk is not laterally indented. The denticle formula is $\frac{1}{3}$ or $\frac{1}{2}$. The beaks are massive and serrate, and the lower beak is slightly indented. The eyes are dorsal. The spiracle is sinistral and low. The dorsal fin varies from not reaching the body to reaching it. The anus is median. The tip of the tail is rounded. In life, the head-body and tail are entirely black. In preservative, the head-body is dark brown dorsally and laterally, and light brown ventrally, except for dark brown mottling on the posterior half of the venter; the tail is uniform light brown, and the fins are heavily dotted with brown, except for a narrow transparent border.

On 30 June 1968, I found 25 tadpoles of this species in water in a rusty, discarded oil drum in disturbed forest near the radio tower at Serra do Navio,

FIGURE 23. Tadpoles of *Dendrobates tinctorius*, Serra do Navio, Brasil (LACM 61069), from water-filled oil drum. (A) mouthparts, Stage 29; (B) dorsal aspect, Stage 29; (C) ventral aspect, Stage 29; (D-I) lateral aspect: (D-E) Stage 25; (F) Stage 27; (G) Stage 29; (H) Stage 41; (I) Stage 44, acquiring adult color pattern. Lines equal one millimeter.

Brasil, 300 m (LACM 61069). The tadpoles were in Stages 25–29, 37–38, 41, and 44; the oldest specimen bore the adult color pattern (black with yellow stripes). An adult male has been taken carrying one tadpole (BM 1936.4.2.4).

Relationships.—I have treated the closely related populations of the *tinctorius* group as five species, but further work may modify this arrangement. Some specimens from French Guiana *(D. tinctorius)* have the same dorsal color pattern as specimens from south of the Amazon (*D. galactonotus*), but the southern specimens always have a well-developed tarsal tubercle, and the northern specimens always lack it. Specimens bearing the *azureus* color pattern occur not only at the type locality in Suriname, but also at Shudikar-wau in Guyana near Brasil, and may occur at other localities along the border between Brasil and the Guianas.

Stomach contents (one specimen).—From LACM 43923: HYMENOPTERA: Formicidae: *Gnamptogenys* sp (1), *Hypoponera* sp (1), *Solenopsis* (*Diplorhoptrum*) sp (10), *Crematogaster* (*Orthocrema*), two spp (34), *Apterostigma* sp (2), *Pheidole*, two spp (12), *Anochetus* sp (1), Myrmecinae (75); COLEOPTERA: Staphylinidae (1), Byturidae (1).

Parasites.—I found larval nematodes parasitizing specimens of *D. tinctorius;* the nematodes were encysted in the abdominal muscles, stomach wall, and liver, and were free in the body cavity. W.E. Martin (University of Southern California), who examined the nematodes, told me that the frogs probably are intermediate hosts.

Toxins.—A specimen of *D. tinctorius* from the Rivière Matarony, French Guiana, released a white toxin from the back and axillae when I seized it. The toxin had an unpleasant taste similar to that of the toxin of *D. histrionicus,* and caused a cold sensation at the rear of the palate. At this site, several specimens of *D. tinctorius* were motionless on standing tree trunks and stumps from 1.2 to 1.7 m above the ground; in each case, the frog was in a vertical position, with the head upward and the belly pressed against the bark. The five-centimeter-long black frogs with their brilliant yellow stripes were conspicuous against the dark bark. One was visible about 35 m away in uncut forest, lending support to the hypothesis that their coloration has an aposematic function.

Ethnozoology.—Dendrobates tinctorius, the first of its family known to science, is famous as one of the means by which the Amerindians of the Amazon drainage and the Guianas were said to practise ***tapirage***, changing the color of the feathers of living parrots. According to the literature (Buffon 1780; Lacépède 1788; Sonnini and Latreille 1802; Métraux 1944; Wallace [1889] 1972), the Indians removed some of the green feathers of young parrots and rubbed the defeathered area with the blood or skin toxin of *Dendrobates tinctorius* (or with other substances). The new feathers that grew after rubbing were said to be red or yellow. I have been unable to confirm this story. A. Wetmore (personal communication) has not witnessed ***tapirage***, contrary to the implication in Métraux (1944). According to H. Sick (personal communication), no one has proved whether nor how Indians practise ***tapirage***; Sick was unable to obtain direct information about ***tapirage*** during many visits to the Indians of central Brasil. He stated that there are many known cases of naturally occurring xanthochroism in feral and captive green parrots of the genus *Amazona.* G.G. Villela (1968) experimented with ***tapirage***, using parrots as the subject and fat from the pirara fish (*Phractocephalus hemiliopterus*) as the rubbing agent, but failed to obtain consistent results. He thought that the mechanism of ***tapirage*** might be the uptake by the new feathers of xanthophylls from the rubbing agent.

At Shudikar-wau, Guyana, blue specimens of *D. tinctorius* are used as "dog 'medicine': the Wai-Wai [Indians] rub this frog on the dog's nose to make him more active in hunting and to increase the sensitivity of the smeller" (R. Snedigar, 1938 field notes at AMNH).

Nomenclature.—The name *Dendrobates tinctorius* has been applied to nine species in two genera. Schneider (1799), who described *Calamita tinctorius,* did not designate a type specimen. According to Boulenger (1913), Schneider never saw the frog, but based his description on that of Lacépède (1788), who based his description on that of Buffon (1780). Buffon said that the frog was used to dye parrots, that it was blue with yellow stripes, and that specimens were preserved in the Paris Museum. Two of these specimens were illustrated by Daudin (1803); Boulenger regarded the larger specimen illustrated as the "typical form" of *D. tinctorius,* similar to a specimen from Cayenne in the British Museum (BM 53.2.4.86).

Boulenger's reference to a British Museum specimen is not a designation of a neotype. I designate LACM 43927, a 49.0 mm female from the lower Rivière Matarony (Approuague drainage), Bruynzeel lumber camp, French Guiana, 35 m, collected by P.A. Silverstone on 18 August 1968, as the neotype of *Calamita tinctorius* Schneider 1799. The type locality probably is near that of Daudin's specimens, which are lost (J. Guibé, personal communication). The neotype (Fig. 24) has the same color pattern as Daudin's larger specimen (1803, plate 8, figs. 1–2), with dorsolateral stripes connected by a transverse stripe. The smaller specimen illustrated by Daudin (plate 8, fig. 3) is *D. quinquevittatus.*

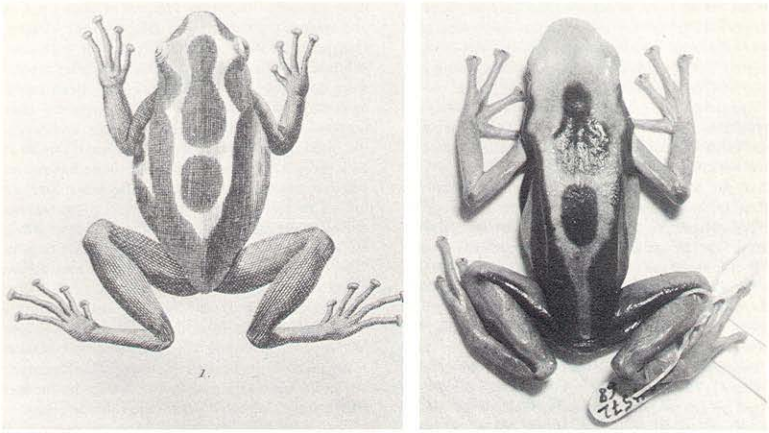


FIGURE 24. *Dendrobates tinctorius*, neotype (right), 49.0 mm female, Rivière Matarony, French Guiana (LACM 43927), compared with the larger of Daudin's (1803, plate 8, fig. 1) specimens (left).

Distribution and habitat (Fig. 9).—Elevation records are from near sea level to 300 m, but specimens from Itabu Creek, Guyana, may have been taken at E.R. Blake's base camp (610 m). *D. tinctorius* is known from the lowland forests of the three Guianas and adjacent northern Brasil. It has not been collected south of the Amazon, except for one doubtful record (see below). At the Rivière Matarony, French Guiana, I took it in shady forest on fallen palm leaves, branches, and logs, and also one to two meters above the ground on a vine, a stump, and standing trunks. At Serra do Navio, Brasil, I took a specimen on bare mine rubble.

Localities.—BRASIL. ***Amapá:*** Serra Tumucumaque, between Caiman and Ourouareu (MHNP 50.1–50.4, 50.A.6, 50.B.5); Serra do Navio, Rio Amapari (WCAB 2309, 2969, 3082–84, 37141–42; KU 93145–46, 93148–49; LACM 43905–08, 61069).

GUYANA. ***Rupununi:*** New River (BM 1936.4.2.3–6, 1938.9.3.1, 1939.1.1.16–19); Itabu Creek, upper New drainage (FMNH 30914); Kamoa Mountains (BM 1969.430; USNM 164813; AMNH 79874); Shudikar-wau, upper Essequibo drainage (AMNH 49297–328).

SURINAME. ***Nickerie:*** Frederik Willem IV-vallen, Corantijne Rivier (BM 1936.9.3.9–12); Kabalebo Rivier near airstrip (CM 44199–200); Blanche Marie-vallen, Nickerie Rivier (RMNH 13858); Kayser Gebergte (RMNH 13860). ***Saramacca:*** Linker Coppename Rivier, 3°54′N, 56°45′W (ZMA 157); upper Coppename Rivier (RMNH 13844); Wilhelmina Gebergte (RMNH 13849); Hebiweriberg, Coppename Rivier (RMNH 13854, 13856); Kroetoeberg near Coppename Rivier (RMNH 13859); Langa Soela, Coppename Rivier (RMNH 13845); Tafelberg (RMNH 13853). ***Brokopondo:*** Gran Rio, upper Suriname drainage (RMNH 5646, 5698); Toekoemoetoe Kreek, upper Saramacca drainage (RMNH 13847–48, 13851–52).

GUYANE FRANÇAISE. Cayenne-Kourou road, 16 km toward Kourou from Pointe Macouria (specimen in possession of Dr. LeClerc of Cayenne); trail between Dorlin and Sophie (MCZ 43509); Ouanary (MHNP 02.274–02.276); Village Camopi (MHNP 50.5); Yanioué (MHNP 50.6); Rivière Matarony just above its junction with Fleuve Approuague, Bruynzeel lumber camp (LACM 43909–19, 43921–31); near Saut Tortue, Fleuve Approuague just below its junction with Crique Tortue (LACM 43920); Lac des Américains, Île de Cayenne (LG 195); Chaumière, Île de Cayenne (LG 196); Crique Gabrielle, Mahury drainage (LG 197); Mont Atachi-Bacca (LG 567–620); Paramana, Matoury (LG 654); Roura (LG 702); Trois Sauts, upper Fleuve Oyapock (LG 1331–35, 1352–68); Mont Galbao (LG 1570–81); Massif du Mitaraca (LG 7292); Icholi Epoyan, upper Maroni drainage (LG 7215); Cayenne (MHNP 4905, 4909); Saut Sabbat, Fleuve Mana (Musée de Genève 1228.17–18).

DOUBTFUL RECORDS. (Workers at the virus research station at Utinga gave me a desiccated specimen [LACM 43904], saying they caught it at Utinga. There are no other records from south of the Amazon [I did not find this species at Utinga], and the workers could have brought the specimen from the virus research station at Serra do Navio; therefore, the Utinga record is doubtful. M.S. Hoogmoed, who has collected extensively in Suriname, considers the Koeroeni Kreek record doubtful.) BRASIL. ***Pará:*** Utinga

forest preserve near Belém (LACM 43904). SURINAME. ***Nickerie:*** Sipaliwini Rivier, Koeroeni Kreek (RMNH 13855).

Cleared and stained material.—LACM 43923; AMNH uncat.

Dendrobates truncatus (Cope 1861)
Yellow-striped Poison-arrow Frog
Frontispiece II and Figures 12K–L

1861. *Phyllobates truncatus* Cope: 372, two syntypes: ANSP 2251–52, New Grenada.
1863. *Hylaplesia truncata* Cope: 49.
1867b. *Dendrobates truncatus* Cope: 197.
1882a. *Dendrobates lugubris.* Boulenger: 145.
1968. *Dendrobates truncatus.* Savage: 765.
1970. *Dendrobates lugubris* (part). Cochran and Goin: 19–21, plate 2A–C.

Definition.—Snout-vent length of adults 23.5–31 mm; skin of back slightly granular; tarsal tubercle absent or slightly developed; color in life: dorsum black with yellow complete dorsolateral and incomplete lateral stripes; venter and sides black with pale blue curving lines or marbling; omosternum present.

Diagnosis.—*D. truncatus* is a member of the *tinctorius* group, differing from *D. azureus* in smaller size, in lacking reticulation, and in having stripes, from *D. galactonotus* in lacking a well-developed tarsal tubercle, from *D. tinctorius* in smaller size and in lacking reticulation, and from *D. auratus* in having a slightly granular back, in having lateral stripes, and in always having dorsolateral stripes, which are relatively narrow and yellow (*D. auratus* has a smooth back, usually lacks lateral stripes, and sometimes has the dorsum spotted or banded instead of striped; when dorsolateral stripes are present, they are relatively broad, and are blue, blue-green, green, or yellow-green). *D. truncatus* often is confused with *Phyllobates lugubris* (O. Schmidt), which was described as *Dendrobates lugubris* (see Savage 1968:765), from which *D. truncatus* differs in having the first finger shorter than (or rarely equal to) the second finger, in having relatively large finger disks, and in lacking teeth.

Description.—Measurements are in Table 3. The skin is slightly granular on the dorsum and smooth on the venter, except the posterior belly and ventral surface of the thighs, which are granular. The tympanum is round, and its diameter equals one-half of the diameter of the eye. The second, third, and fourth finger disks average wider in males than in females. The first finger is longer relative to the second finger than in most other species of *Dendrobates,* and rarely is equal to the second finger. The tarsal tubercle is absent or slightly developed.

In life, specimens from Mariquita, Colombia, are black with yellow complete dorsolateral stripes, hook-shaped proximodorsal marks on the thighs, undulating dorsal stripes on the limbs, and incomplete lateral stripes (Frontispiece II). One specimen has a short incomplete median stripe on the posterior back, connecting with the right dorsolateral stripe. The venter and ventral surface of the limbs are black with pale blue curving lines or marbling; the throat has a pale blue horseshoe mark (Fig. 12L). One specimen has two transverse bands on the belly instead of marbling, and the sides of the throat horseshoe are interconnected by a transverse stripe.

One specimen from Nechí, Colombia, has the throat horseshoe broken, and has a light semicircle on each side of the belly.

Specimens from Villa Arteaga and the Río Currulao, Colombia, have the ventral pattern, including the throat horseshoe, reduced to small light spots.

Tadpoles.—Three tadpoles from Volcanes, Caparrapí (near the Río Magdalena), Cundinamarca, Colombia (USNM 144985), labeled as this species (*Dendrobates lugubris*), probably are dendrobatids, but there is no apparent basis for identification as this species.

Relationships.—See the relationships section under *D. auratus.*

Stomach contents (one specimen). —From USNM 146851: HYMENOPTERA: Formicidae: *Dorymyrmex biconis* Forel ? (2), *Mycocepurus smithi* (Forel) (1), *Wasmannia auropunctata* (Roger) (7), *Cryptocerus maculatus* (F. Smith) (2), *Pheidole* sp (1), *Aphaenogaster ?* sp (15), Myrmecinae, two genera (43); COLEOPTERA: Staphylinidae (3); COLLEMBOLA: Entomobryidae (200).

Parasites. —I found ticks attached to specimens of *D. truncatus.*

Distribution and habitat (Fig. 6). —Elevation records are from 100 to 1133 m. *D. truncatus* is known only from Colombia, in the Río Magdalena drainage from Chaparral north to the Caribbean coast, and in the lowlands around the northern ends of the Cordilleras Central and Occidental west to the Golfo de Urabá, mainly in Holdridge's (1967) lowland tropical moist forest zone, although there are some records from the lowland tropical dry forest zone.

Localities.—COLOMBIA. ***Tolima:*** 8 km N Chaparral (MVZ 42005); Mesa Cucuana (USNM 145095–103); Espinal (USNM 98891–93; UMMZ 78304); Chicoral (ANSP 21030); Gualanday (ILS 146); Mariquita (USNM 144974–97, 146850–56; UMMZ 48612; FMNH 81826–28; LACM 44265–76); Río Guali (USNM 144978–79). ***Cundinamarca:*** 2 km W Pandi on Fusagasugá-Girardot road (AMNH 75157). ***Boyacá:*** Muzo (UMMZ 71221). ***Santander:*** Simacota (ANSP 25763); Floridablanca (USNM 163840; ILS 455); El Centro (USNM 144968–69); El Mosco and Finca Esmeralda, both near Lebrija (USNM 144970–73).

Magdalena: Ríofrío (USNM 118223; MCZ 16059–64). ***Sucre:*** Colosó, E Toluviejo (USNM 152654); Catival, upper Río San Jorge (FMNH 61181). ***Antioquia:*** Puerto Berrío (FMNH 30807); Nechí (FMNH 54275); Villa Arteaga (USNM 144948); Río Currulao near Golfo de Urabá (FMNH 63878).

DOUBTFUL RECORDS. COLOMBIA. ***Cundinamarca:*** eastern base of Cordillera of Bogotá and extreme limit of llanos east of Bogotá (ANSP 24324–31); Fusagasugá (AMNH 40309–12; ILS uncat); ***D.E.:*** Bogotá (BM RR.1934.9.1.11). ***Antioquia:*** Medellín (AMNH 39087); ***Chocó:*** Río San Juan (USNM 144949).

Cleared and stained material. –LACM 44265; USNM 146851.

ZOOGEOGRAPHY
Figures 6–9

Geographic groups.–The species of *Dendrobates* inhabit the following regions: Central America only–*D. granuliferus, D. pumilio, D. speciosus;* Central America and northwestern South America west of the Andes–*D. auratus, D. minutus;* northwestern South America west of the Andes (Chocó)–*D. altobueyensis, D. fulguritus, D. histrionicus;* northern Colombia north of the Andes and in the Magdalena Valley–*D. truncatus;* the Andes of Colombia–*D. opisthomelas;* east of the Andes in most of the Amazon drainage and into the Guianas–*D. quinquevittatus;* the lower Amazon drainage–*D. galactonotus;* the Guianan region–*D. azureus, D. leucomelas, D. steyermarki, D. tinctorius.*

Distribution within political units.–The species of *Dendrobates* occur in the following nations: Nicaragua (two species)–*D. auratus, D. pumilio;* Costa Rica (three species)–*D. auratus, D. granuliferus, D. pumilio;* Panamá (four species)–*D. auratus, D. minutus, D. pumilio, D. speciosus;* Colombia (nine species)–*D. altobueyensis, D. auratus, D. fulguritus, D. histrionicus, D. leucomelas, D. minutus, D. opisthomelas, D. quinquevittatus, D. truncatus;* Ecuador (two species)–*D. histrionicus, D. quinquevittatus;* Perú (one species)–*D. quinquevittatus;* Brasil (four species)–*D. galactonotus, D. leucomelas, D. quinquevittatus, D. tinctorius;* Venezuela (two species)–*D. leucomelas, D. steyermarki;* Guyana (two species)–*D. leucomelas, D. tinctorius;* Suriname (two species)–*D. azureus, D. tinctorius;* French Guiana (two species)–*D. quinquevittatus, D. tinctorius. Dendrobates* (as defined herein) is not known from Bolivia, Paraguay, Uruguay, Chile, or Argentina.

Sympatry.–The following species of *Dendrobates* have been taken in sympatry: *D. auratus* and *D. pumilio* (Nicaragua, Costa Rica, and Panamá); *D. auratus* and *D. granuliferus* (Costa Rica); *D. auratus* and *D. minutus* (Panamá); *D. auratus, D. fulguritus,* and *D. histrionicus* (Colombia); *D. histrionicus* and *D. minutus* (Colombia); *D. fulguritus* and *D. histrionicus* (Colombia); *D. fulguritus, D. histrionicus,* and *D. minutus* (Colombia); *D. altobueyensis, D. fulguritus, D. histrionicus,* and *D. minutus* (Colombia).

Correlation of distribution with climate, vegetation, and physiography.–I have used the following sources: Chapman (1917, 1926); Banco de la República (1959); Espinal and Montenegro (1963); Vivó (1964); Wagner (1964); Portig (1965); Stuart (1966); U.S. Department of Commerce (1966); Instituto Brasileiro de Geografia e Estatística (1966); Holdridge (1967) and the Holdridge system bioclimatic maps of Latin America; Haffer (1967a, 1967b, 1967c, 1969); and Ewel and Madriz (1968).

Because frogs of the genus *Dendrobates* lay noncleidoic eggs on land, they cannot reproduce in an arid microhabitat. Small, still bodies of water, such as those in leaf axils of aroids and bromeliads, tree holes, fallen fruit shells, or man-made objects, also must be present as tadpole release sites. Adults require humid, shady conditions and usually inhabit the floor of evergreen broadleaf forests.

Gaps in the distribution of *Dendrobates* are savannahs, some of which are seasonally flooded (the llanos of Colombia and Venezuela, the cerrado of Brasil, and the scattered savannahs of the Guianas and Central America), transitional areas of herbaceous and semideciduous woody plants (the pantanal of eastern Bolivia and western Mato Grosso), spiny deciduous scrub forest or bushes (the caatinga of northeastern Brasil and the semi-desert scrub of the Guajira and Paraguaná peninsulas of Colombia and Venezuela), the coastal desert of Ecuador and Perú, and the highest portions of the Andes.

West of the Andes, low rainfall and the resulting xeric habitats are the major factors limiting the southward distribution of *Dendrobates.* Because of the highly arid coastal desert extending from southwestern Ecuador through Perú into Chile, the southern limit of the range of *Dendrobates* west of the Andes is over 1000 km north of the southern limit east of the Andes. East of the Andes, in Brasil, there are eight lowland plant associations along 8°S latitude (Instituto Brasileiro de Geografia e Estatística 1966). Along this transect, the dry season is absent in the rain forests on the west, five to six months at the western edge of the cerrado (savannah), and over eight months in the caatinga (spiny scrub forest). Most of this transect lies between the 24 and 26°C mean annual isotherms. Thus the occurrence of these lowland plant associations is not determined by temperature, but by rainfall, in association with winds, edaphic factors, and human interference. *Dendrobates* occurs along this transect in the rain forests and probably in the transitional forests, but not in the cerrado or east of it, except perhaps in gallery forest. Thus lower precipitation (and associated veg-

etational changes), not temperature, is the principal limiting factor for *Dendrobates* on both sides of the Andes.

Temperature is probably important in limiting the vertical distribution of *Dendrobates*. Only *D. speciosus* and *D. opisthomelas* are highland species (Fig. 5). The latter reaches an elevation of at least 2200 m and withstands minimum temperatures of at least 10–12°C (Santa Rita, 1900 m), although by seeking shelter it probably escapes exposure to the minimum air temperatures.

At the northern end of the range of the genus, *D. pumilio* extends approximately to the 20°C isotherm in Nicaragua. In western Nicaragua and Honduras, a severe six-month dry season (perhaps supplemented by low temperature) is probably the major limiting factor. The Caribbean coast of Honduras and northeastern Nicaragua is pine savannah and probably unsuitable habitat. There is, however, an inland corridor of lowland tropical forest with a mean annual temperature of over 25°C, a mean annual rainfall of over 3000 mm, and a relatively mild three-month dry season; this seems suitable habitat, but for unknown reasons, *D. pumilio* has not advanced northward along the corridor.

Four dry forest regions along the Pacific coast of Central America act as distributional barriers. *D. granuliferus* formerly was continuous with *D. pumilio*, but now is confined on the Pacific coast of Costa Rica between dry regions to the northwest and southeast and mountains to the east. *D. auratus* probably is blocked by dry areas, but its separated populations have not differentiated to any great extent.

Dendrobates histrionicus is confined to the wet Chocoan region of the Pacific coast of Colombia and northwestern Ecuador. Thus it seems to require high, well-distributed precipitation. A decrease in precipitation and an increase in the length of the dry season probably limit the species to the north and south. Its southern limit in Ecuador roughly coincides with the 2500 mm isohyet. Its northern limit in Colombia is between the 4000 and 3000 mm isohyets. The range of *D. auratus* extends from Central America south into the Chocó of Colombia, but *D. auratus* is much less common in the Serranía de Baudó than is *D. histrionicus;* the latter may have a competitive advantage in regions of high precipitation. The two species share the same habitat in areas of sympatry.

Based on a comparison of collecting records with the Holdridge system bioclimatic maps (Espinal and Montenegro 1963), *D. truncatus* may be able to survive in climates too arid for other species of the genus. Its additional presence in moist areas, however, suggests that its populations in drier areas may occur in locally humid pockets.

Fossil record.—There are no published records of dendrobatid fossils.

Hypothesis on time of origin of dendrobatids.—My hypothesis is based on four assumptions. First, Central and South America were separated by a marine gap during Mesozoic (Lloyd 1963), connected during Paleocene, reseparated from Eocene to Miocene, and reconnected from Lower Pliocene to the present (Savage 1966). Second, the Eocene-Miocene marine gap was an effective distributional barrier for frogs (Savage 1966; Duellman 1970). Third, dendrobatids arose in South America (this is suggested by their present distribution). Fourth, dendrobatids were capable of reaching northwestern South America in Paleocene.

If dendrobatid frogs had crossed the Paleocene bridge into Central America, the Central American populations would have been isolated from the South American populations from Eocene through Miocene (about 44 million years). This is probably sufficient time for extensive speciation and differentiation. In actuality, only 12 of over 70 known species of dendrobatids occur in Central America. Only five of the 12 are endemic to Central America, and only one extends north as far as Nuclear Central America (the area that remained emergent during Tertiary). These 12 species are no more different from their South American congeners than the latter are from each other. Thus dendrobatids probably did not reach Central America until after the establishment of the Pliocene bridge. They did not cross the Paleocene bridge because they were not present in northwestern South America in Paleocene. They probably did not arise until after the beginning of Eocene.

Hypothesis on distributional history of Dendrobates.—Present distribution suggests that *Dendrobates* invaded Central America three times. The earliest arrival was probably the ancestor of the *D. pumilio* group, which has reached northern Nicaragua. The uplifting of the central mountains of Costa Rica and western Panamá split it into three species. Isolation was reinforced by the onset of aridity in portions of the Pacific coast of Central America. The second invader of Central America was probably the ancestor of *D. auratus.* Its descendants have reached southern Nicaragua and occur on both coasts of Costa Rica and Panamá, but comprise only one species. The most recent invader of Central America was probably *D. minutus,* which does not extend west of central Panamá.

According to Haffer (1967a, 1967b, 1969), Pleistocene glacial periods in South America were relatively wet and interglacials relatively dry. During interglacials, humid forests and their faunae were restricted to refuges. During glacials, forest refuges and their faunae were reconnected. Haffer's hypoth-

esis partially explains the present distribution of the lowland species of *Dendrobates*. During Pleistocene interglacials, the lowland species of *Dendrobates* probably were confined in Haffer's refuges as follows: Caribbean Costa Rica refuge (*D. auratus* and *D. pumilio*); Chiriquí refuge (*D. auratus* and *D. granuliferus*); Chocó refuge (*D. altobueyensis, D. fulguritus, D. histrionicus,* and *D. minutus*); Nechí refuge (*D. truncatus*); Napo refuge (*D. quinquevittatus*); Imerí refuge (*D. leucomelas*); Guiana refuge (*D. azureus* and *D. tinctorius*); and Belém refuge (*D. galactonotus*).

Based on present distribution, four species, *D. auratus, D. granuliferus, D. pumilio,* and *D. speciosus*, probably arose in Central America; the other 12 species arose in South America.

Resumen

Este estudio se trata de la biología, sistemática, y distribución del género *Dendrobates* (Amphibia: Anura: Dendrobatidae), y de la anatomía de ranas dendrobátidas. Se examinaron los huesos y músculos de 14 de las 16 especies de *Dendrobates,* 15 de las 20 especies de *Phyllobates,* y 12 de las numerosas (más de 40) especies de *Colostethus.* Los músculos del muslo y de la mandíbula diferen de los ránidos en todas las especies examinadas, incluyendo *C. bocagei* (el tendón del músculo *semitendinosus* atraviesa el tendón del músculo *gracilis major;* el músculo *adductor mandibularis externus superficialis* es ausente). La mayoría de los ejemplares de *Dendrobates* que se examinaron tienen las vértebras 1 + 2, 2 + 3, 1 + 2 + 3, u 8 + 9 coosificadas, mientras que casi todos los ejemplares de los otros dos géneros carecen de tal osificación. Todas las especies examinadas carecen de huesos palatinos menos dos especies de *Colostethus* (*C. palmatus* y *C. trinitatis*). Todas tienen un omoesternón menos dos especies de *Dendrobates* (*D. histrionicus* y *D. leucomelas*). Se propone que se cambie la especie típica de *Dendrobates* (reemplazando la especie típica actual, *D. nigerrimus,* con otra especie que Wagler incluyó en su descripción original de *Dendrobates, D. tinctorius*), y que se trasladen cinco especies (*D. bassleri, D. ingeri, D. parvulus, D. pictus,* y *D. trivittatus*) de *Dendrobates* a *Phyllobates. Dendrobates* abarca 16 especies, incluyendo dos nuevas especies procedentes del Chocó, Colombia, *D. altobueyensis* y *D. fulguritus.* Se pueden distribuir las 16 especies en cuatro grupos: grupo *histrionicus* (*D. histrionicus, D. leucomelas*); grupo *minutus* (*D. altobueyensis, D. fulguritus, D. minutus, D. opisthomelas, D. quinquevittatus, D. steyermarki*); grupo *pumilio* (*D. granuliferus, D. pumilio, D. speciosus);* y grupo *tinctorius* (*D. auratus, D. azureus, D. galactonotus, D. tinctorius, D. truncatus*). Dendrobátidos probablemente se originaron en la América del Sur después del comienzo del Eoceno, y entraron en la América Central luego del establecimiento del istmo en el Plioceno. *Dendrobates* probablemente entró en la America Central en tres invasiones distintas. La distribución actual de las especies de *Dendrobates* que habitan tierra baja se limita principalmente por la lluvia y formaciones vegetales, y se correlaciona con los refugios húmidos interglaciales del Pleistoceno de la hipótesis de Haffer. De las 16 especies de *Dendrobates,* cuatro probablemente se originaron en la América Central y 12 en la América del Sur. *Dendrobates* se alimenta principalmente de hormigas. Hay en esta obra una clave para la identificación de las especies del género *Dendrobates;* hay también una descripción, una lista de las localidades geográficas, y un mapa de la distribución de cada especie, y dibujos de quince especies (nueve de ellas en color).

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