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WITH DISCUSSION OF BLOWGUN  
FABRICATION AND DART POISONING

CHARLES W. MYERS, JOHN W. DALY, AND BORYS MALKIN

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## ABSTRACT

*Phyllobates terribilis*, a remarkably toxic new species of frog, is described from the vicinity of an Emberá Chocó settlement in lowland rain forest of Pacific coastal Colombia. It is the third frog definitely known to be used for poisoning darts; the other species are *P. aurotaenia* and *P. bicolor*. Toxicity of the skin secretions of *Phyllobates*, and of frog-poisoned darts, is due primarily to batrachotoxin and homobatrachotoxin, steroidal alkaloids that are stronger than curare mixtures. *Phyllobates terribilis* produces relatively massive quantities of these compounds and is at least twentyfold more toxic than other poison-dart frogs. *The new species is potentially dangerous to handle*: One freshly caught frog may contain up to 1900 micrograms ( $\mu\text{g}$ ) of toxins, only a fraction of which would be lethal to man if enough skin secretion came into contact with an open wound. A human lethal dose is indirectly judged as being somewhere in the range of 2-200  $\mu\text{g}$ , and the secretions also are irritating to porous skin and poisonous if ingested.

*Phyllobates terribilis* attains a snout-vent length of about 47 mm., making it one of the largest species in its family (Dendrobatidae). It is readily distinguished from all other dendrobatids in that body and limbs are a uniform golden or pale metallic green color above and below, except that small juveniles have a primitive pattern of golden dorsolateral stripes on a black ground. The ontogenetic color change, tadpoles, and other aspects of the life history and behavior are described. A component of aggressive grappling behavior of this and some other dendrobatids is suggested as being homologous with dendrobatid cephalic amplexus, an instance of which is photographically documented for *Dendrobates tricolor*. The trill call of *Phyllobates* is the third class of dendrobatid vocalizations to be defined. At the type locality, *Phyllobates terribilis* occurs in populations of predominantly adult frogs that probably have relatively long ( $> 5$  years) and secure lives; reproductive success or juvenile survivorship might be inversely correlated with population density. Emberá Indians are occasional predators, and the snake *Leimadophis epinephelus* is identified as a potential predator, at least of young frogs. This snake has an unusual capacity for tolerating a great chemical diversity of anuran skin secretions.

Piperidine-based skin alkaloids provide a shared, uniquely derived character (synapomorphy), seeming

to establish that frogs of the *Dendrobates-Phyllobates* complex share a monophyletic origin apart from a sister group (*Colostethus*). But, in the *Phyllobates bicolor* group, primitive piperidine alkaloids have been largely replaced by a more effective set of defensive skin toxins—the steroidal batrachotoxins. The latter are a novel synapomorphy that seems to establish the monophyly of *Phyllobates* (*sensu stricto*), a genus heretofore inadequately defined on the basis of shared primitive (symplesiomorphic) characters. Most of the species recently assigned to *Phyllobates* (by Silverstone, 1976) are here removed to *Dendrobates*, including the nomenclatural type species (*trivittatus*) on which the name *Dendrobates* must be based. *Dendrobates* is more diverse as now defined (vs. Silverstone, 1975). The diversity is due to a mixture of shared primitive characters, along with derived characters still to be tested for convergence or parallelism. These changes have minimal effect on the usefulness of Silverstone's (1975, 1976) monographs on the two genera, since his accounts of species and species groups are mostly well considered.

The laborious process of fabricating an Emberá Chocó blowgun, quiver, and darts is described and photographically illustrated. The Chocó blowgun is of Yde's type IV, two long and tapering, semi-cylindrical sections of palm wood glued together and wrapped with bast. There are two principal ways of making the bore in type-IV blowguns. Some tribes (Jívaro and Yagua) scratch initial grooves on the half-shafts, which are then joined and the bore enlarged and smoothed with a ramrod and sand. The Chocó and Cofán finish the grooves *before* the half-shafts are joined; use of metal implements by present-day Chocó and Cofán probably is a simple improvement over such objects as mammal teeth, said to have been used for the same purpose by Pasé Indians over a century ago. The Chocó weapon differs from most other type-IV blowguns in lacking a separate mouthpiece and in rarely being waterproofed. The blowgun is for hunting, but, unlike some Amazonian tribes, the Chocó may have no superstitious strictures against turning it occasionally on man.

The Chocó are the only Indians known with certainty to use frog toxins as the sole ingredient of dart poison, and the practice is documented only in the Río San Juan and Río Saija drainages of western

Colombia; use of a plant poison is more widespread, although the Chocó blowgun is on the decline and absent in some areas. The Emberá Chocó and Noanamá Chocó have two ways of obtaining frog poison: Frogs of the species *Phyllobates aurotaenia* and *P. bicolor* (San Juan drainage) are impaled on a special stick entering the mouth and exiting through

a hind leg; the spitted frog may sometimes, but not necessarily, be held near fire while darts are rubbed in its skin secretions. In contrast, dart tips are simply rubbed against the backs of living *Phyllobates terribilis* (Saija region). These different methods reflect more on the relative toxicity and abundance of the frogs than on cultural differences.

## INTRODUCTION AND WARNING

Blowguns and poisoned darts are widely used in northern South America, particularly in the Amazonian and Guayanian regions. The best known dart (and arrow) poisons are the curare alkaloids, derived mainly from plants of the genera *Strychnos* and *Curarea*. West of the Andes, however, a dart poison much stronger than most (if not all) curare mixtures is obtained from small, brightly colored frogs of the genus *Phyllobates*. Despite reports to the contrary, the use of frogs for the sole ingredient of dart poison may be geographically restricted to western Colombia, where the poison is applied to darts, *not* arrows. Until now, the custom seems to have been confirmed only in the Río San Juan drainage of northwestern Colombia, where frog poison is still employed by Chocó Indians of the Emberá group, and was also recently used by the Noanamá Chocó. *Phyllobates bicolor* ("neará") is the frog utilized by Emberá Chocó living near the headwaters of the Río San Juan, and, lower in the same drainage, *Phyllobates aurotaenia* ("kokoi") is the poison-dart frog of both the Emberá and the Noanamá Chocó. (See fig. 8.)

Some years ago, the Swedish anthropologist Henry Wassén acquired darts purportedly tipped with frog poison from Emberá Indians living on the Río Saija, some 150 km. south of the Río San Juan. Wassén (1935, p. 99) evidently did not see poison-dart frogs in the Saija area, and his accompanying illustration of a frog and description of dart poisoning were based on *Phyllobates aurotaenia* and its use by Noanamá Indians of the lower Río San Juan. We confirmed the existence of a poison-dart frog in the Río Saija drainage in 1971 and 1973, when we collected series of the frog and also

obtained information on its use by the Emberá Chocó. Our specimens represent a heretofore undescribed species of *Phyllobates*; it is only the third species of frog that is known with certainty to be used for poisoning blowgun darts.

The new species proved to be much more toxic than could have been predicted from our previous experience with other poison-dart frogs, and we heeded the advice of our Indian friends and handled it with appropriate caution, especially after accidentally killing a few of their domestic animals that got into our contaminated garbage. Subsequent analysis showed that the frog secretes essentially the same compounds as other species of *Phyllobates*, namely the potent batrachotoxin alkaloids, which are known to occur only in frogs of this genus. But the new species is characterized by having relatively massive quantities of batrachotoxins, and it is at least twentyfold more toxic than its relatives. Elsewhere in this paper we estimate that a small fraction of the poison from one of the new frogs would be lethal to man if gotten into the bloodstream through an open wound. The skin secretions are also irritating to porous skin and poisonous if ingested. *These frogs should be considered as potentially dangerous if improperly handled.* No effective antidote is known for batrachotoxin poisoning.

The epithet that we have chosen for the new species is "*terribilis*," a Latin adjective meaning terrible or frightful. The name describes the extraordinary toxicity of the frogs' skin secretions, and also alludes to the fear once evoked by the poisoned blowgun darts of a more warlike people.



***Phyllobates terribilis*, new species**

Plate 2 and text figures 1-3, 7, 8D, 11B, 12

**HOLOTYPE:** AMNH 88876 (field no. CWM 11920), an adult male obtained by Charles W. Myers and John W. Daly during February 18-19, 1973, in lowland rain forest at Quebrada Guanguí, about 0.5 km. above its junction with Río Patia,<sup>1</sup> 100-200 m. elevation, in upper Río Saija drainage, Department of Cauca, Colombia.

**PARATYPES:** A total of 393 specimens, as follows: AMNH 85990-86324, 88872-88875, 88877-88905, and 18 living specimens—all from same locality as the holotype. AMNH 88865-88871, La Brea, 50 m. elevation, on the Río Patia (upper tributary of Río Saija), at an estimated 15 km. by river below mouth of Quebrada Guanguí, Department of Cauca, Colombia.

The 18 living specimens, which comprise a breeding colony at the American Museum, have contributed to several aspects of the description; the colony presently consists of 13 paratopotypes collected in February 1973, and five of their offspring being raised from eggs laid on April 24, 1976, and May 18, 1977. Excluding the captive-reared specimens, all paratypes were collected in October-November

1971, or February 1973, by the authors, their assistants, and resident Indians.

**DEFINITION AND DIAGNOSIS:** A very large *Phyllobates* that attains a maximum snout-vent length of about 47 mm. Body and limbs overall golden yellow, golden orange, or pale metallic green in adults; small juveniles black with gold dorsolateral stripes. Teeth present on maxillary arch; appressed first finger slightly longer or equal to second; third finger disc 1.3-1.8 times wider than finger. *Extremely toxic*, producing large quantities of steroidal skin alkaloids of the batrachotoxin class.

*Phyllobates terribilis* is one of the largest dendrobatids and is by far the most toxic. It is readily distinguished from all other dendrobatids in that body and limbs are a nearly uniform golden or pale green color above and below (except that small juveniles have a primitively striped pattern). *Phyllobates terribilis* appears most similar to *P. bicolor*, which is distinguished by its smaller size and in having the venter and extremities colored differently from the dorsum (see Systematics section).

**COLOR AND MEASUREMENTS (IN MM.) OF HOLOTYPE:** The undissected holotype (fig. 1) is an average-sized male that is considered sex-



FIG. 1. *Phyllobates terribilis*, new species. The adult male holotype in life, approximately  $\times 1.5$ .

<sup>1</sup>The Quebrada Guanguí is shown as locality E in Myers and Daly (1976a, map 1); although not indicated on other maps known to us, the name has some permanence, being cited by Wassén (1935, p. 39) and listed in the "Diccionario Geográfico de Colombia" (Colombia, Inst. Geogr., 1971). The Río Patia is erroneously shown on maps as "Río Patía del Norte," an apparent cartographic invention. Local residents accent the first syllable of "Patia," this pronunciation apparently being unchanged since the time of Wassén (*loc. cit.*). [To those recent authors who advocate dropping Spanish accents from local place names, we would point out that *Patia* and *Patía* not only designate different rivers, they are different words, with different pronunciations, no small matter to the traveler seeking directions to one or the other. This is not to say that we support the practice of another class of American authors and editors, namely those who insist on foreign orthography (e.g., *México*, *Panamá*, *Guyane Française*) even of major political divisions having standard English equivalents. Such workers cause no confusion though, since they tend to balk at names (e.g., *Magyarország*) really unfamiliar to themselves and most of their readers.]

TABLE 1  
Size and Proportions of Adult *Phyllobates terribilis*, New Species, from Type Locality<sup>a</sup>

Character	N	Mean±1 S.E.	S.D.	C.V.(%)	Range
Snout-vent length (SVL) in mm.	150♂	41.05±0.11	1.36	3.31	37.3-44.6
	179♀	43.23±0.08	1.12	2.58	40.3-46.5
Tibia length/SVL	150♂	0.440±0.001	0.015	3.47	0.40-0.48
	179♀	0.428±0.001	0.014	3.35	0.41-0.47
Head width/SVL	25♂	0.332±0.003	0.013	3.86	0.31-0.35
	25♀	0.328±0.002	0.008	2.38	0.31-0.34
Eye length/tip of snout to eye	25♂	0.794±0.010	0.048	6.05	0.72-0.90
	25♀	0.789±0.010	0.048	6.05	0.72-0.89
Center naris to edge eye/lower edge tympanum to angle of jaws	25♂	2.142±0.046	0.229	10.69	1.89-2.67
	25♀	2.216±0.044	0.219	9.88	1.95-2.80
Width 3rd-finger disc/finger width below disc	25♂	1.507±0.024	0.121	7.99	1.30-1.78
	25♀	1.462±0.021	0.106	7.27	1.30-1.67

<sup>a</sup>Seven paratypes from another locality (La Brea) fall within the observed variational ranges of the paratopotypes, except that one male has a head width/SVL ratio of 0.36, and one female has an eye length/snout length ratio of 0.71.

ually mature because of its size and well-developed vocal slits. The subarticular tubercle on the first finger of each hand is rather large compared with that of other specimens, and there is a small lump (subcutaneous parasite?) on the posteroventral face of the right thigh, but the specimen otherwise appears normal. Its color in life was orange, changed in alcohol to light gray at the time of this description.

Length from snout to vent 41.6; tibia length from heel to fold of skin on knee 18.4; greatest width of body 14.7; greatest head width (between angles of jaws) 13.8; head width between edges upper eyelids 12.3; approximate width of interorbital area 5.0; head length from tip of snout to angle of jaws 12.6; tip of snout to center of naris 2.3; center of naris to anterior corner of eye 4.2; distance between centers of nares 5.2; eye length from anterior to posterior corner 5.3; horizontal diameter of tympanum (posteriorly indistinct) about 2.5; corner of mouth to lower edge tympanic ring 2.0; length from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger 11.4; width of disc of third finger 1.3; width of third finger (penultimate phalanx) below disc 0.8; width of discs of third and fourth toes, respectively, 1.5 and 1.6; width of third and fourth toes below discs both 0.9.

#### DESCRIPTION OF ADULTS

The following description is based on the approximately 350 adults in the type series, unless indication is given that a smaller sample was drawn from the series for some particular comparison. Larvae and juveniles are described in following sections.

*Phyllobates terribilis* is a very large dendrobatid, with males attaining a maximum snout to vent length (SVL) of about 45 mm. and females 47 mm. Males mature at about 37 mm., and females at 40-41 mm. SVL. See table 1 for data on size and proportions. Widest part of head lies between the jaw articulations. Greatest head width averages 87 percent of greatest body width in 28 preserved specimens (range 70-109%), but the body is wider and more distinctly rotund in well-fed living individuals. There is little external sexual dimorphism except in body length (table 1). Adult males have a shallow subgular vocal sac that is usually indicated externally by minute expansion wrinkles in a grayish area at base of throat. Adult males have well-developed vocal slits on the floor of the mouth, except that one or the other slits fails to open in about 18 percent of the population (see Postmetamorphic Changes).

TABLE 2  
Size and Proportions of Adult *Phyllobates bicolor* Bibron, from Upper Río San Juan<sup>a</sup>

Character	N	Mean±1 S.E.	S.D.	C.V.(%)	Range
Snout-vent length (SVL) in mm. <sup>b</sup>	27♂	36.17±0.30	1.55	4.28	32.1-39.5
	21♀	38.90±0.38	1.73	4.44	35.7-42.7
Tibia length/SVL	27♂	0.473±0.003	0.015	3.21	0.45-0.51
	21♀	0.462±0.003	0.014	3.05	0.44-0.49
Head width/SVL	27♂	0.350±0.003	0.014	4.16	0.33-0.39
	21♀	0.348±0.003	0.016	4.47	0.33-0.39
Eye length/tip of snout to eye	25♂	0.786±0.013	0.065	8.29	0.67-0.91
	21♀	0.792±0.014	0.065	8.19	0.68-0.93
Center naris to edge eye/lower edge tympanum to angle of jaws	27♂	2.589±0.064	0.366	12.96	2.06-3.36
	21♀	2.578±0.060	0.274	10.64	2.17-3.42
Width 3rd-finger disc/finger width below disc	24♂	1.569±0.033	0.162	10.36	1.30-1.86
	20♀	1.558±0.025	0.114	7.29	1.33-1.75

<sup>a</sup>Representing several local populations in vicinity of Santa Cecilia, Department of Risaralda, Colombia. Based on measurements from following 48 adult specimens: Amer. Mus. Nat. Hist. 98209-98224, 98226-98233, 98235, 98236; Field Mus. Nat. Hist. 54187, 54189, 54193, 54194, 54196, 54204, 54205, 54207, 54212, 54221, 54233; Natl. Mus. Nat. Hist. (Smithsonian Inst.) 137359-137362, 137364-137370, 147225, 147226.

<sup>b</sup>A seemingly precocious male (AMNH 98234) is excluded from the table; it has well-developed vocal slits but measures only 29.0 mm. SVL. A female (AMNH 98225) with small ova and enlarging oviducts was judged a subadult and is also excluded; it measures 35.2 mm. SVL, which, with the observed size range of adults, indicates that females mature at approximately 35-36 mm. SVL.

Color changing to gray in preservative, but in life most adults were *bright* golden yellow, golden orange, or pale metallic green (see Interpopulational Color Variation). Range of observed hues<sup>1</sup> included pale metallic green—pale greenish yellow—pale yellow—golden yellow—golden orange—orange; one uniformly medium-gray variant (AMNH 88870) was the only specimen lacking bright pigmentation. Dorsally, the body and limbs are uniformly colored, except for conspicuous black eyes and nares, black digit tips, usually black edging on lower rim of tympanum, and, often, black edging along the mouth and narrow black creases marking articulations of the limb segments.

<sup>1</sup>These hues are constant within individual adult frogs, which remain the same shade regardless of light or temperature changes. Absence of diel metachromatism appears to be characteristic of dendrobatids generally, although short-term changes have been observed in *Dendrobates pumilio* and *Colostethus trinitatis*, and some species show ontogenetic changes. *Phyllobates terribilis* undergoes ontogenetic change only (see Postmetamorphic Changes).

Ventrally, the coloration is the same or slightly lighter than the dorsal hue, except for black palms and soles, a black seat patch across undersides of thighs, and a black crease in axilla and groin; males usually have a light suffusion of gray on base of throat. The posterior venter, concealed part of shank, and, especially, the axilla and groin are lightly suffused with gray in some specimens; some pale metallic green specimens had a slight bluish tinge on the green venter, with the concealed part of the shank being a definite blue-green. Despite the aforesaid variations, the venters of all adults were colored mainly like the bright dorsal surfaces (as shown in color pl. 2).

Skin smooth in preservative; in life, smooth to finely rugose or finely granular, turning conspicuously rugose to very coarsely granular on upper surfaces of hind limbs, especially on the shank (fig. 1). Snout sloping, rounded in lateral profile, bluntly rounded to weakly truncate in dorsal or ventral aspect. Naris situated near tip of snout and directed posterolaterally; both



nares visible from front, barely visible from below, but not visible from above. Canthus rostralis rounded; loreal region vertical and slightly concave. Interorbital area wider than upper eyelid. Eye length somewhat greater than distance from anterior edge of naris to eye; eye/snout length 0.72-0.90 ( $N = 50$ , table 1). Tympanum concealed posterodorsally, where it subcutaneously dips under the anterior edge of *m. depressor mandibulae*; tympanum seen by dissection to be nearly circular or vertically elliptical, with an area less than 75 percent of eye.

Relative lengths of *appressed* fingers  $3 > 4 \geq 1 \geq 2$ , each terminating in moderately expanded disc; if measured from the base, finger 1 is distinctly longer than fingers 2 and 4, but when appressed their discs overlap and the three are nearly equal. Disc of third finger 1.30-1.78 times wider than distal end of adjacent phalanx, with no appreciable sexual dimorphism ( $N = 50$ , table 1). A large, circular tubercle on median base of palm, and a smaller elliptical one (inner metacarpal tubercle) on base of first finger; one or two subarticular tubercles on fingers (one each on fingers 1 and 2, two each on fingers 3 and 4). All tubercles low, with rounded surfaces.

Hind limbs of moderate length, heel of appressed limb usually reaching eye; tibia/snout-vent length 0.40-0.48 (table 1). Relative lengths of toes  $4 > 3 > 5 > 2 > 1$ , each terminating in moderately expanded disc, which on toes 3 and 4 is as wide or wider than third finger disc; appressed first toe reaching subarticular tubercle of second. Small inner and outer metatarsal tubercles, the inner being an elongated ellipse and the outer being smaller and nearly circular; an unpigmented area between aforesaid tubercles often has appearance of an incipient median metatarsal tubercle. One to three subarticular tubercles (one each on toes 1 and 2, two each on toes 3 and 5, three on toe 4). Distal third of tarsus with a keel-like ridge, usually extending from inner metatarsal tubercle and proximally continuous with the obliquely elongate and slightly elevated tarsal tubercle. All foot tubercles low, with rounded surfaces. Hands and feet lacking webbing, supernumerary tubercles, or lateral fringe (al-

though if digits are desiccated their ventrolateral keel might be mistaken for a low, unscalloped fringe).

#### INTERPOPULATIONAL COLOR VARIATION

*Phyllobates terribilis* has been collected only in the vicinity of Quebrada Guanguí and at La Brea, localities less than 15 km. apart in the upper Río Saija drainage. The species appears to be morphologically uniform within this region, and no significant difference in toxicity was detected in frogs from the two localities (see Skin Alkaloids and Toxicity). Nonetheless, there are striking differences in color (hue) that seem to reflect microgeographic variation. Such variation is commonplace among the toxic species of dendrobatids.

**QUEBRADA GUANGUÍ:** Well over 500 specimens were collected by resident Indians and ourselves at the type locality. Most of these frogs were various shades of golden yellow or golden orange (pl. 2); a relative few were pale greenish yellow or deep orange. The frogs were scattered through the forest and not to be taken in large numbers by any one collector in a single day, but, on a given day, up to a hundred specimens might be obtained by the combined efforts of six or more collectors. Each person's catch tended to consist predominantly of one color phase, depending on the ridge or slope area that was worked. Due to the enthusiasm and efficiency of our Indian collectors, the frog populations near camp were rapidly decimated (but by no means extirpated) and we were unable to determine the extent of intrademe variation or the nature of interdeme borders.

**LA BREA:** This is the site of a rural schoolhouse on a riverfront bluff, about 15 km. by river below the mouth of the Quebrada Guanguí. We collected here for three days and obtained 19 frogs, of which seven were preserved, six skinned for poison extraction, and the remainder lost in an accident of transport. The majority (17) differed strikingly from all Quebrada Guanguí specimens in being pale metallic *green*; these green frogs were found in forest on the riverfront bluff and on ridges

immediately adjacent. Two differently colored frogs were taken on ridges farther inland from the river: One specimen (AMNH 88865) was bright golden orange like many individuals from the type locality. The other specimen (AMNH 88870) was a uniformly medium gray, a coloration not seen in the large collection from the type locality. The lack of bright pigmentation on this specimen is assumed to be an aberration, since the vivid coloration of *Phyllobates terribilis* is probably aposematic and therefore under presumably strong selective pressure.

#### OSTEOLOGY

The following description emphasizes aspects of the skull (especially nasal region) and vertebrae that presently appear to be of potential use in dendrobatid systematics. It is based on six cleared and stained adult paratopotypes (AMNH 86319-86324), including three males (39.8-41.3 mm. SVL) and three females (40.6-42.6 mm. SVL).

Skull wider than long. Frontoparietals long and in close contact, their common suture being vague in most specimens. Sphenethmoid large, extending rostrad to halfway between nasals; often entirely or partly fused with anterior ends of frontoparietals (only two of six specimens having a distinct suture between sphenethmoid and frontoparietals). Sphenethmoid with a ventrolateral process extending toward preorbital process of maxillary; palatine bones absent. Nasal bones widely separated from one another; sometimes in narrow posteromedial contact with sphenethmoid (three of six specimens); posterolateral process of nasal narrow, ending above and slightly behind preorbital process of maxillary. Prevomers small, toothless, and widely separated, lying beneath nasals. Maxillary and premaxillary teeth present. Alary processes of premaxillae broad, tipped slightly forward. Maxillary posteriorly shallow, anteriorly with a high facial lobe bearing a small preorbital process. Eight presacral vertebrae, none fused either dorsally or ventrally. Neural spines of second and third vertebrae more massive than others, but not bearing dorsal shields. Omosternum present.

#### TADPOLES

The following description is based on three lots (AMNH 88979-88981) of stage-25 larvae taken from the backs of paratypic male frogs, and on one series of larvae (AMNH 97876, stages 24-37) reared in the laboratory from eggs laid and fertilized by captive frogs from the type locality. The clutch of terrestrial eggs was placed in water and commenced hatching 12 days after laying, when the larvae were at stage 24 (late); the first feeding was observed six days after hatching, at stage 26. Several tadpoles, from this and other laboratory clutches, were observed through metamorphosis. See the section on Natural History for additional comments on the life cycle. The staging system used here is that of Gosner (1960).

**HABITUS AND PROPORTIONS:** The head and body are depressed (width > depth), slightly convex above and flattened below. Eyes and nostrils are in a dorsal position, with the eyes directed dorsolaterally. One larva preserved a day before hatching was in early stage 24, with a long branching gill on the left side (longest gill filament = 1.3 mm., body length = 4.1 mm.); hatching of two other larvae occurred late in stage 24, with the gill greatly reduced in length. The spiracle is sinistral and the anus dextral (medial in several stage-25 larvae). Body length from hatching to stage 37 changes from 4.1 to 12.6 mm., and total length changes from 11.1 to 35.4 mm., as summarized in table 3.

The low-finned tail comprises 59-64 percent of the total length. There appears to be no significant ontogenetic change in tail length up to stage 37, as shown by the following ratios of tail length/total length: Stage 25,  $\bar{X} = 0.614 \pm 0.003$  (0.59-0.63,  $N = 11$ ); Stages 27, 29, 37 combined,  $\bar{X} = 0.613$  (0.58-0.64,  $N = 3$ ).

The greatest depth of the tail comprises only 12-15 percent of total body-tail length in stages 24-27, after which the depth of the tail *increases* to a maximum of at least 20 percent, relative to increasing total length. In 11 stage-25 larvae, the maximum distance from

the upper edge of dorsal fin to lower edge of the ventral fin averages  $0.142 \pm 0.004$  (range 0.12-0.15) of the total length. Two larvae in stages 29 and 37 have ratios of 0.20 and 0.18, respectively.

**PIGMENTATION:** Hatchlings have uniformly gray (grayish brown in preservative) bodies and throats, turning paler gray on the tail and tail fins; the abdominal region is pale yellow due to the contained yolk. Under magnification is seen a scattering of white flecks (probably bronze in life) over the body and tail, including fins.

The dark body pigmentation becomes sparser in later stages, giving the larvae a paler appearance; the belly becomes quite pale. The tail fins become more transparent in stage 26, and thereafter remain clear except for weak pigmentation basally along the fins and an overall sparse dispersion of white flecks.

There is a conspicuous color change at about stage 37, when the hind limbs have become fairly well developed. By this stage, the body has changed in a few days from gray to blackish gray, and has acquired a dense dorsal flecking of pale bronze. This bronze flecking is most densely concentrated dorsolaterally, forming paired dorsolateral stripes that diverge from the snout, pass over the eyes and extend to the tail base (fig. 2). To the naked eye, these stripes appear light gray against a grayish black body; the pale bronze color is apparent when the living tadpole is placed under magnification. By appearance of the forelimbs (stage 42), the body has turned black and the stripes a brighter bronze. The dorsolateral stripes then turn bronzy gold and are retained through metamorphosis (see Postmetamorphic Changes).

**MOUTH PARTS:** The mouth is directed anteroventrally. The tooth row formula is 2/3, with the second upper row being broken above the beak. The beak is shallowly keratinized, with very finely serrated cutting edges; the lower beak is broadly V-shaped. The oral disc is anteriorly nude and laterally indented; the lateral and posterior edges of the disc are continuously ornamented with one or two rows of blunt papillae. There is significant ontogenetic change in some of the aforesaid characters, as detailed below.

The beak is barely starting to become ker-

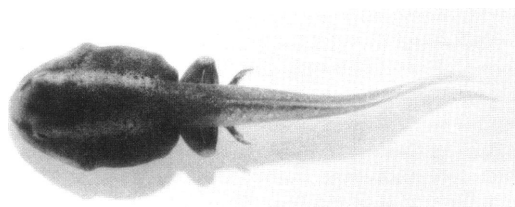


FIG. 2. Stage-40 larva of *Phyllobates terribilis*, new species. The dorsolateral stripes appear in about stage 37 and persist through metamorphosis (see fig. 3A). This tadpole, photographed in life, was laboratory reared from egg of paratopotypic parents.

atinized at hatching (stage 24), whereas the tooth-row denticles do not show keratinization until stage 25. In the latter stage, the two upper rows and the first one or two lower rows are keratinized; the third lower row was not keratinized in the stage-25 larvae and could not even be distinguished in a few individuals. All denticles are keratinized by stage 27. The fine serrations on the cutting edges of the beak are also evident by stage 27, whereas the beak edges appear smooth in some stage-25 larvae and barely serrated in others. The papillae fringing the lateral and posterior edges of the oral disc also show variation: Dorsal larvae in stage 25 have a *single*, uniform row of papillae (although one laboratory-reared larva in stage 26 has only the lateral and a few posterior papillae developed). However, larvae in stages 27-37 have *two* rows in close contact. A similar ontogenetic change from one to two rows of labial papillae occurs in some hylids (Zweifel, 1961).

Obviously, the mouth parts are incompletely developed in stage 25, which appears to be the stage in which many dendrobatid tadpoles mount the back of an attendant parent. Although species identification of such tadpoles requires only that the nurse frog be determined, caution is required in making interspecific comparisons with dendrobatid larvae of later stages.

#### POSTMETAMORPHIC CHANGES

During the first four to five months of growth, young *Phyllobates terribilis* change

strikingly in color and pattern; newly transformed frogs ( $\sim 13$  mm. SVL) have an evidently primitive color pattern that is virtually lost by attainment of only 20 mm. snout-vent length (SVL). Allometric changes in body proportions are slight, at least past 20 mm. SVL. There are few juveniles in our wild-caught sample of *P. terribilis* (see Natural History), and our smallest such preserved specimen measures 20.5 mm. However, several young raised at the American Museum, from eggs deposited and fertilized by captive paratopotypes, provide information on the early changes in coloration.

**COLOR AND PATTERN:** As described under Tadpoles, the aquatic larva acquires a blackish gray body and pale bronze dorsolateral stripes (fig. 2) at about stage 37, with the body turning black and the stripes becoming brighter by the time that the forelimbs appear in stage 42. Metamorphosis occurs at about 13 mm. SVL (as measured in life with dial calipers), at which time the dorsolateral stripes, upper arm, and upper lip are light bronzy gold, and the hind limbs and lower parts of the forelimbs are densely speckled with bronze on a black background. The dorsolateral stripes and upper arms become bright gold within a few days of metamorphosis, and the dense flecking on lower arms and on the hind limbs becomes brighter golden bronze. The undersides of the limbs are less strongly speckled with bronze and are mainly black; the venter is black except for a few golden specks scattered across the chest. Even at this early period there may be a few specks of gold on the back and sides of the body, although the general appearance is of a black frog with paired stripes of gold. There tends to be a faint suffusion of bronze or gold on the upper lip, which in one individual was sufficiently concentrated to form a gold labial stripe.

The dorsolateral stripes remain fairly well defined (fig. 3A) up to and slightly past 14 mm. SVL; at this size the ventral surfaces are still nearly pure black, except that the sparse bronze and gold speckling has slightly intensified underneath the limbs and across the chest, with a few scattered specks also appearing on the belly (fig. 3D).

By attainment of 15.5 mm. SVL (fig. 3B), an intense suffusion of gold has appeared dorsally between the stripes, which also are widened ventrad. Gold ventral speckling also has become more intense, although the ventral surfaces remain essentially black.

The dorsal and lateral spread and intensification of gold coloring proceeds rapidly, and by 21 mm. SVL the juvenile frog is almost uniformly golden above (fig. 3C). A strong suffusion of gold has developed ventrally across the chest (fig. 3E). The young frog in figure 3 acquired its bright dorsum in 18 weeks of postmetamorphic growth; an additional several weeks were required before the ventral surfaces turned uniformly bright as in adults (e.g., pl. 2). The adult coloration is thus acquired early, since it takes over a year to reach adult size.

**PROPORTIONS:** Some body proportions of the eight smallest preserved juveniles (20.5-29.6 mm. SVL) in the paratotypic series are compared with those of adults in table 4. Since the sample of juveniles is small, and because there is relatively little sexual dimorphism in these characters (table 1), the sexes are combined. The differences seen are very slight; allometric growth is probably of little or no taxonomic significance, assuming that closely related species have growth characteristics similar to *P. terribilis*.

The major difference in table 4 involves relative eye size compared to snout length (comparison of means:  $t = 3.342$ ,  $P < 0.01$ ). Linear regression analysis, using 50 adults and all 34 juveniles and subadults in the paratotypic series, confirms that relative eye size (eye length/snout-eye) decreases with increasing SVL ( $r = -0.50$ ,  $P < 0.001$ ). Although juvenile *P. terribilis* do have relatively larger eyes than adults (or relatively shorter snouts), the differences are little apparent by visual inspection (compare photographs herein).

Juvenile *P. terribilis* have relatively longer tibiae than adults, in keeping with an apparently common pattern of frog growth. The difference between the means in table 4 is of marginal significance ( $t = 2.094$ ,  $P < 0.05 > 0.02$ ), but regression analysis, using the sample mentioned above ( $N = 84$ ), shows that tibia/SVL decreases with increasing SVL ( $r =$



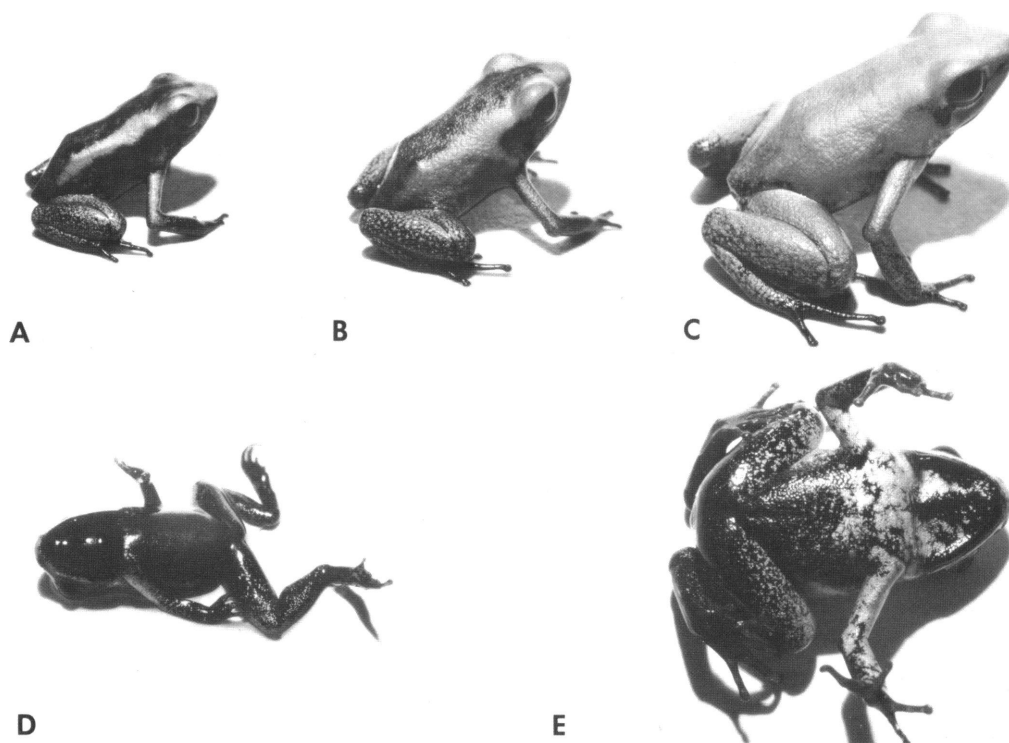


FIG. 3. Ontogenetic color change in juvenile *Phyllobates terribilis*, new species, during first 18 weeks of postmetamorphic growth. Laboratory-reared froglets of paratopotypic parents, approximately  $\times 2$ .

A and D. Frog of 14.2 mm. SVL, showing black dorsum and venter, with gold dorsolateral stripes. B. Dorsal surfaces becoming suffused with gold, 15.5 mm. SVL. C and E. By attainment of 21.4 mm. SVL, the dorsal surfaces have become almost uniformly golden, and gold pigmentation is starting to obliterate the black ventral color.

$-0.474$ ,  $P < 0.001$ ). However, the change is rather slight and there is complete overlap in ranges of variation (table 4).

*Phyllobates terribilis* shows no allometric growth in head width: The absence of relative change is indicated by the identical means in table 4 and confirmed by regression analysis ( $N = 84$ , see above), comparing head width/SVL with SVL ( $r = -0.162$ ,  $P > 0.1$ ). Differences between the means are not significant for the last two characters shown in table 4, where  $t = -0.126$ ,  $P > 0.9$  (naris-eye/tympanum-jaws) and  $t = -0.417$ ,  $P > 0.6$  (width of finger disc).

**ATTAINMENT OF SEXUAL MATURITY:** Males mature at about 37 mm. SVL, as determined by the criterion of open vocal slits; dissection

of selected specimens indicates that the presence of vocal slits is correlated with testicular enlargement. The smallest mature male, in the sample of 150 adult male paratopotypes, is 37.3 mm.; the largest immature male is 36.8 mm. SVL. No overlap was found between mature and immature sizes.

It should be noted that either the left-side or right-side vocal slit fails to open in about 18 percent of adult males (i.e., in 27 of 150 specimens). The presence of only one opening may be a permanent condition in some frogs, since the snout-vent lengths of such individuals are fairly representative of the population of adult males:  $N = 27$ ,  $\bar{X} = 40.39 \pm 0.30$  mm.,  $S.D. = 1.54$  mm., range = 37.5-42.9 mm. (compare with table 1).

Females mature at about 40-41 mm. SVL, as determined by gonadal development. The four smallest adults, in the sample of 179 adult female paratopotypes, measure 40.3, 40.6, 40.6, and 40.7 mm. SVL; these possess enlarged or enlarging ovarian ova and oviducts. The four largest immature females, 38.7, 40.3, 41.0, and 41.0 mm. SVL, have tiny ovarian ova and threadlike oviducts. The small size overlap (< 1 mm.) between mature and immature females is within the limits of measuring error. Some overlap, of course, is expected, due to the vagaries of individual growth rates, but attainment of maturity in both sexes of

*Phyllobates terribilis* does appear to be rather precisely correlated with body size.

#### NATURAL HISTORY

**HABITAT:** *Phyllobates terribilis* occurs in rough hilly country at the western foot of a northerly inclined spur of the Cordillera Occidental. The broken landscape (fig. 4) is the result of stream dissection of presumed Tertiary and Pleistocene sediments and gravels. Slopes are more often steep than gentle, and perpendicular surfaces are not uncommon. Hillside soils are gravelly in places. Drainage is by

TABLE 3  
Measurements (in Millimeters) of *Phyllobates terribilis* larvae

Stage	N	Head-Body Length	Total Length	Greatest Tail Depth
24 <sup>a</sup>	3	4.1-4.1 ( $\bar{X}$ = 4.10)	11.1-11.4 ( $\bar{X}$ = 11.27)	1.5-1.6 ( $\bar{X}$ = 1.57)
25 <sup>b</sup>	15 <sup>b</sup>	4.3-5.0 ( $\bar{X}$ = 4.66±0.05)	11.5-12.4 ( $\bar{X}$ = 12.09±0.09)	1.5-1.8 ( $\bar{X}$ = 1.70±0.04)
26 <sup>c</sup>	1	5.6	14.4	2.1
27 <sup>c</sup>	1	9.3	24.3	3.5
29 <sup>c</sup>	1	11.7	28.0	5.6
37 <sup>c</sup>	1	12.6	35.4	6.5

<sup>a</sup>Laboratory reared, including one preserved a day before hatching and two preserved within a few hours of hatching.

<sup>b</sup>Dorsal tadpoles from three male frogs. *N* = 11 for total length and tail measurements.

<sup>c</sup>Larvae reared in laboratory and preserved six days (stage 26), 13 days (stage 27), 19 days (stage 29), and 38 days (stage 37) after hatching.

TABLE 4  
Comparison of Body Proportions of Juvenile and Adult *Phyllobates terribilis* from the Type Locality

Character	Size <sup>a</sup>	N	Mean±1 S.E.	S.D.	Range
Tibia length/SVL	Juvenile	8	0.446±0.005	0.015	0.43-0.47
	Adult	329	0.434±0.001	0.016	0.40-0.48
Head width/SVL	Juvenile	8	0.330±0.002	0.008	0.32-0.34
	Adult	50	0.330±0.002	0.011	0.31-0.35
Eye length/tip of snout to eye	Juvenile	8	0.862±0.033	0.094	0.75-0.92
	Adult	50	0.792±0.007	0.047	0.72-0.90
Center naris to edge eye/lower edge tympanum to angle of jaws	Juvenile	8	2.168±0.092	0.260	1.83-2.64
	Adult	50	2.179±0.032	0.225	1.89-2.80
Width 3rd finger disc/finger width below disc	Juvenile	8	1.466±0.036	0.103	1.33-1.60
	Adult	50	1.484±0.016	0.115	1.30-1.78

<sup>a</sup>Data for sexually mature males and females (table 1) combined. The eight juveniles have snout-vent lengths of 20.5-29.6 mm. ( $\bar{X}$  = 25.98 mm.), and include four males and four females. Juveniles and subadults greater than 29.9 mm. SVL (*N* = 26) are excluded from this table, but were added to the total sample of immature specimens (*N* = 34) for purposes of regression analysis (see text).



FIG. 4. Topography of the type locality of *Phyllobates terribilis*, in Andean foothills on Pacific drainage of western Colombia, Department of Cauca. View is looking south toward Quebrada Guanguí (stream in center), above its junction with Río Patia (river on right, upstream view), in upper Río Saija drainage. The lowland rain forest (100-200 m. elev.) is extensively disturbed near major streams by slash-mulch agriculture (February 20, 1973).

clear-water streams flowing over rock, gravel, and sand. The principal stream, a tributary of the Río Saija, is the Río Patia (fig. 4), which originates along the western base of Cerro Tambor. The Quebrada Guanguí (see p. 313 n) is a southward flowing tributary that empties into the Río Patia at an elevation of about 90 m. above sea level. Hilltops in the immediate vicinity are about 200 m. above sea level.

The region has a decidedly tropical wet climate (*Af* in the Köppen system). Rainfall data are lacking, but extrapolation from distant stations and orographic considerations suggest that the Quebrada Guanguí area receives a yearly rainfall probably in excess of 5 m. (e.g., see map in West, 1957, p. 27). It seems certain that relative humidity is always very high, especially inside the forest.

There is no undisturbed forest along the larger streams, where small terraces and adja-

cent hillsides are either under cultivation, mainly for plantains, or in dense second growth. Inland, the native lowland rain forest (fig. 5) is relatively undisturbed but only of moderate height, probably due to the precipitous slopes. There are occasional tall emergents that break the uniformity of the forest canopy. Most of the larger trees have buttressed roots, and tall palms with stilt roots are common. Tree-trunk moss is sparse. Small bromeliads commonly grow low on the trunks, but the bromeliad population is not dense and they rarely occur on the ground. The understory and ground vegetation of saplings and treelets, small palms, and herbaceous plants and ferns, varies from dense to moderately open. The forest tends to be most open on gravelly slopes, some of which are quite wet due to seepage. Leaf litter is sparse. *Phyllobates terribilis* occurs throughout the forest, seeming to be as



FIG. 5. Rain-forest habitats of *Phyllobates terribilis* at type locality (February 20, 1973).



common on ridgetops as on moister slopes or near streams. We have the impression that this frog avoids second growth and cultivated areas.

**BEHAVIOR:** This is a diurnal frog, like other dendrobatids, and strictly terrestrial, like other species of *Phyllobates* (see list, p. 331). Specimens were found sitting on the ground or perched a few centimeters aboveground on tree roots or ground litter. None was seen climbing into the herbaceous ground stratum of vegetation, although such behavior characterizes many of the diverse species of *Dendrobates* (a few of which have strong arboreal tendencies). Most other species of *Phyllobates* are rather secretive and quick to seek cover, but *Phyllobates terribilis* is one of the boldest of all dendrobatids. It attempts to escape capture simply by hopping away, making no attempt to hide.

Captive *Phyllobates terribilis* show definite learning ability. The opening of their terrarium is rapidly associated with feeding, and they leap to snap at anything moving, be it their keeper's fingers or water spray from a misting bottle. The mere waving of a hand along one end of the terrarium is sufficient to cause an eager gathering of frogs "expecting" to be fed. They fare well on a diet of crickets dusted with vitamin and calcium powder.

*Phyllobates terribilis* was not found in dense aggregations; two individuals sometimes were found together, but otherwise they appeared to be well spaced in the forest. Territoriality might be inferred from such spacing, although captive *terribilis* thrive under crowded conditions and are nonaggressive, except sometimes during feeding. During the frenzy of feeding activity, captive individuals (of uncertain sex) may clasp one another in an amplexus-like embrace, sometimes around the body but often around the head. Clasping behavior occurs also in other species of *Phyllobates* and *Dendrobates*, which has led to suggestions that amplexant behavior has not been entirely lost<sup>1</sup>

<sup>1</sup>Amplexus probably is absent in the mating behavior of many dendrobatids, although data are available for only a few species (see Silverstone, 1976, p. 7, for summary). Amplexant behavior also appears to have been lost in *Rhinoderma* and in at least one genus of mantelline frogs (Janvier, 1935; Pflaumer, 1936; Blommers-Schlösser, 1975).

among dendrobatids, but rather has been incorporated into the aggressive repertory (Polder, 1974; Myers and Daly, 1976a, p. 238 n). Nonetheless, the high incidence of cephalic clasping, especially in captive *P. aurotaenia* and *P. terribilis*, has been puzzling to us. Cephalic amplexus is rare in normal anuran matings, and the presumed leptodactylid (Elosiinae) relatives of dendrobatids engage in the usual axillary amplexus (*vide* Lynch, 1971, pp. 22-24). The problem is partly resolved by a recent discovery that true mating amplexus *does* occur in at least one species of dendrobatid, and that the amplexus is cephalic in position (fig. 6). Is aggressive cephalic clasping in *Phyllobates* actually derived from a similar mating embrace, or has cephalic amplexus been newly derived from primitive aggressive clasping in dendrobatids? Or is the correlation strictly fortuitous and the result of different neural pathways? We favor the first hypothesis for its



FIG. 6. Amplexus in a dendrobatid mating: Cephalic amplexus has been repeatedly observed during successful matings of this captive pair of frogs, which represent two populations of *Dendrobates tricolor*, a geographically variable species (Myers and Daly, in progress). Cephalic clasping in aggressive behavior of *Phyllobates* spp. may be homologous with true amplexus, but evolutionary polarity is uncertain. Photograph by Charles J. Cole.

relative simplicity, by which cephalic amplexus would be primitive in the Dendrobatidae (albeit derived from some lower level) and aggressive cephalic clasping would be a derived condition. The matter remains to be tested by additional observations or experimentation, but one component of dendrobatid amplexus and aggressive clasping appears unusual enough to suggest homology. In the amplexus of *Dendrobates tricolor*, the male presses the upper surfaces of his hands against the female's chin (fig. 6). Neither the palms nor individual fingers are used in maintaining the grip. Identical chin-pressing behavior has been observed in captive *Phyllobates terribilis* during apparent aggression.

**VOCALIZATIONS:** The call of *Phyllobates terribilis* was described in field notes as a "long melodious trill," although it might sound slightly harsh to some ears. Two laboratory recordings are each six seconds in duration, and are comprised of a uniform train of notes uttered at a rate of 13 per second (at 27.0°C.), with a dominant frequency at about 1800 Hertz (fig. 7). The call is similar to vocalizations of related species but the dominant frequency is lower (< 1900 Hz in *P. terribilis*, > 2000 Hz in *P. aurotaenia*, *P. bicolor*, *P. lugubris*, *P. vittatus*).

We take this occasion to characterize the calls of *Phyllobates* as *trill calls*, the third class of dendrobatid vocalizations to be defined in a continuing study (Myers and Daly, 1976a). A trill call is a train of uniform notes uttered at a speed greater than 10 per second. This kind of call sounds quite different from the "chirp calls" of some *Dendrobates*, although each is comprised of a train of usually uniform, poorly modulated notes. The individual notes in a *Phyllobates* call are musical relative to the harsh notes in a chirp call, which contains more noise due to a sustentation of near maximum energy output over a broad frequency range (compare section in fig. 7 with chirp-call sections in Myers and Daly, 1976a, p. 237). The "trilled" aspect of a *Phyllobates* call is caused by the rapid succession of individual notes; the slight musical quality might also contribute to this aspect of the call. The fastest chirp calls recorded (some *D. pumilio*), with

note repetition rates of 9.5-10 per second, still sound harsh and lacking in any trilled quality.

During poorly studied social interactions, *Phyllobates* and some *Dendrobates* utter single or small groups of "chirps," which seem equivalent to individual notes in trill calls and chirp calls, respectively. Such isolated chirps are harsh-sounding in *Dendrobates*, but relatively musical in *Phyllobates*. *Dendrobates* chirp calls appear to have both territorial and female-attracting functions, but this subject is even less well understood in *Phyllobates*. In captivity, the trill call of *Phyllobates terribilis* often seems to excite other males to call and/or to engage in courtship activity, but does not induce the aggressive grappling observed in some *Dendrobates*, or at least not commonly (see below).

**REPRODUCTION AND LIFE HISTORY:** Courtship and egg laying have been observed several times, but only in a terrarium containing 13 frogs. Each occasion involved two or several calling males and at least one female. The interested individuals moved about together, crawled over one another, and clustered during egg laying. There was such jostling and movement that the actions of individual frogs could not be followed for any length of time, particularly since most activity occurred in a tangle of low-growing vegetation (noncourting frogs spend most of their time sitting in the open). Method of fertilization was not confirmed, but may involve vent to vent contact between frogs facing in opposite directions; observed instances of such behavior were brief, with the pair seemingly being disturbed by others of the group. One male was observed attempting to amplex a female that was depositing eggs, but the embrace was brief, with the male unable to maintain a grip and slipping off; it is not at all certain whether this behavior was an attempt at true amplexus or merely an instance of misplaced aggression (see Behavior, above).

The orgies described above are probably the result of unnatural crowding in captivity, where one female simultaneously excites several males. Many clutches deposited under such conditions were fragmented into small lots of often unfertilized eggs. Somewhat similar

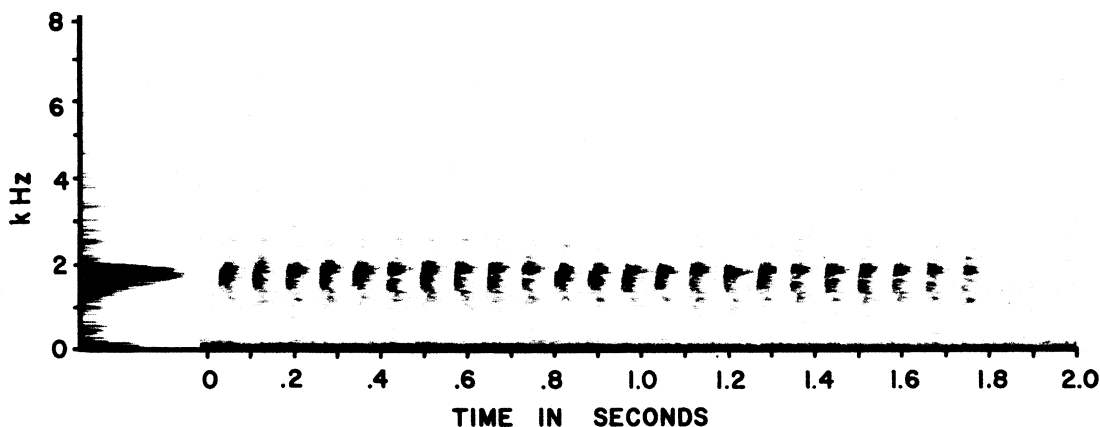


FIG. 7. Terminal portion of 6-second long trill call of *Phylllobates terribilis*, new species. Narrow-band sound spectrogram, 45-Hz filter; section is of first note on left. Topotypic specimen recorded in terrarium with air temperature of 27.0° C., April 4, 1972 (AMNH tape 177).

breeding frenzies occur among captive *P. aurotaenia* and *P. vittatus*, but neither these nor *P. terribilis* have been observed behaving so flagrantly under natural conditions. Field observations are needed, although the components of courtship and laying behavior also might be adequately determined from observations of a single pair of captive frogs.

Eggs were not found in the field, but one clutch of 15 black and white eggs (AMNH 88982) was laid, in February, in a plastic collecting bag, where they were evidently fertilized, since some are in second cleavage. Excluding the small jelly capsules, these eggs average 2.5 mm. in diameter (2.4-2.6 mm.). Captive breedings have produced several apparently entire clutches consisting of 11-17 eggs. *Dendrobatids* lay terrestrial eggs, but, if terrarium conditions are not suitable, the eggs often develop normally if moved to water soon after being laid. Two clutches of *P. terribilis* eggs each started hatching 11 days after they had been laid and placed in water, with hatching taking 2 or 4 days for completion. Fed liberally on boiled lettuce, the larvae metamorphosed and left the water about 55 days after hatching, and the froglets started feeding on *Drosophila* 10 days later.

Only three frogs, all males, were found in the field carrying tadpoles on their backs. One

male frog had a single tadpole and two males each carried nine larvae, but all were caught by Indians and some larvae might have been dislodged and lost during capture. The carrying period is perhaps brief, since the dorsal larvae are all in stage 25 (hatching in captivity occurred in late stage 24, see Tadpoles). Since the eggs can be artificially hatched in water, and the larvae develop normally, it seems that tadpole-carrying in *Phylllobates terribilis* serves only a mechanical function of moving larvae from the egg site to water.

It apparently takes *Phylllobates terribilis* a year or more of postmetamorphic growth to reach sexual maturity. Two living young frogs of uncertain sex measured only 37.5 and 38.5 mm. SVL, 13 months after metamorphosing in captivity. These measurements are barely equivalent to the smallest adult males and fall a few millimeters short of the size of recently matured females (table 1, which is based on preserved specimens). *Phylllobates terribilis* has a potentially long life span, since captive individuals are still alive five years after capture.

**PREDATION:** It seems a safe assumption that *Phylllobates terribilis* has few predators compared with other rain-forest frogs, none of which possesses such a combination of bright coloration, bold behavior, and *extreme* toxicity. Man, of course, must be reckoned as a preda-

tor, and probably so should one small frog-eating snake, *Leimadophis epinephelus* (Colubridae). This predator has a Chocoan distribution that probably places it within the habitats of all the species of *Phyllobates* (as herein defined). Captive specimens of this snake have shown themselves to be resistant to a great diversity of anuran skin toxins, including the ateloid toxins of *Atelopus elegans* and *Atelopus varius zeteki*, the piperidine alkaloids of *Dendrobates auratus*, and even the especially potent batrachotoxin alkaloids of *Phyllobates*.<sup>1</sup> Two uncontrolled experiments were performed with *Leimadophis epinephelus* and *Phyllobates terribilis*: (1) A *Leimadophis* from the type locality of *P. terribilis* was confined in a plastic bag with a recently caught juvenile frog of 25 mm. SVL. The frog was eaten and digested, with no apparent ill effect to the snake. (2) A caged *Leimadophis* from El Valle, central Panama, was offered an adult topotypic *P. terribilis* that had been collected seven months previously; such captive-held frogs have toxicities about 50 percent below normal (see Skin Alkaloids and Toxicity). At the outset the frog appeared too large to be swallowed, and it was released after the snake had chewed on it for 10 minutes. The snake showed no

<sup>1</sup>*Leimadophis epinephelus* seems to have an unusually high metabolic rate for a snake. Captive specimens have quickly become emaciated and have apparently starved to death after not being fed for several weeks. The nature of its immunity to frog poisons is not known, but, if the poisons are simply detoxified, the process must start with the snake's salivary secretions. The dendrobatid alkaloids appear to be rapidly absorbed by buccal tissue, causing some snakes (e.g., *Rhadinaea* spp.) to release the frogs almost immediately. The effect may be striking if the frog's secretions include batrachotoxin alkaloids: An adult *Rhadinaea taeniata aemula* (from Mexico) seized and released a proffered *Phyllobates vittatus* (which contains relatively small amounts of batrachotoxins), after which the snake gaped and attempted to rub its mouth on the substrate. Half an hour later the snake was in more obvious distress, resuming mouth gaping and also expanding the thoracic region and slowly contorting its entire body, after which it laid nearly motionless for at least four hours, with expanded thorax, contorted body, and head turned on one side. Observations were terminated late at night, but recovery was complete by the following morning.

immediate symptoms of distress, but on the following day it was noticed to be lethargic and was rather limp when handled; its behavior was normal on the third day. The frog also recovered.

*Leimadophis epinephelus* is moderately common at the type locality of *Phyllobates terribilis*, where we obtained nine specimens. But it is uncertain whether this snake (~ 500 mm. total length) is large enough to swallow the heavy-bodied adult frogs, or whether it could survive such a massive dose of batrachotoxins (~ 1.1 mg. per frog). However, *Leimadophis* does seem to be a likely predator of juvenile *Phyllobates terribilis*.

**POPULATION STRUCTURE:** The ratio of adult males to adult females (150:179) in the paratopotypic series shows no significant deviation from a 1:1 sex ratio ( $\chi^2 = 2.556$ ,  $P > 0.1$ ). The paratopotypic series is biased toward juveniles (10% of total), most of which were saved, whereas a very large number of adults were not preserved. Juvenile-sized frogs comprised only about 2.5 percent of all specimens collected. Inasmuch as captive juveniles exhibit no apparent behavioral differences from adults, we assume that their apparent rarity is not entirely due to sampling bias. Several observations on *P. terribilis* at the type locality are worth summarizing here:

1) Although density estimates were not obtained, the population was obviously large and rather evenly dispersed compared with other species of frogs in the area. No other forest frog could be collected in such large numbers in the Quebrada Guanguí area.

2) Reproductive potential is low (< 20 eggs per clutch) compared with many anurans, even if females were to breed monthly.

3) Few nurse frogs were found carrying tadpoles ( $N = 3$ ).

4) Juveniles take a year or more to attain maturity after metamorphosis, and appear to occupy the same microhabitat (surface of forest floor) as do adults.

5) Immature frogs comprise a small part of the population, probably less than ten percent (2.5% observed).

6) The species probably has few predators,



and individuals have a potentially long life span ( $> 5$  years in captivity, during which reproduction is still possible).

Taken together, the above observations suggest that *Phyllobates terribilis* maintains a relatively stable population comprised predominantly of adult frogs, which probably have long and secure lives. The small numbers of juveniles suggest that reproductive success or juvenile survivorship may be inversely density dependent and somehow suppressed in this population. This hypothesis is tenuously sup-

ported by observations that some dense populations of dendrobatid frogs are remarkably resilient to removal of large numbers in repeated years, and that harvesting might stimulate population growth toward a return to stability (Myers and Daly, 1976a, pp. 256-257). We present these perceptions not as confident descriptions of reality, but rather as suggestions that dendrobatid frogs would be well worth the attention of population biologists.

## SYSTEMATICS

The geographically and morphologically closest relatives of *Phyllobates terribilis* are *P. aurotaenia* and *P. bicolor*. These three species, confined to the Pacific versant of Colombia, also are the only frogs known with certainty to be used as sources of dart poison. Their skin alkaloids are qualitatively similar, but *P. terribilis* produces relatively massive amounts of the most potent compounds, batrachotoxin and homobatrachotoxin; quantitative comparisons are given in a following section on Skin Alkaloids and Toxicity. We here compare *P. terribilis* with its closest relatives and then suggest that the genus *Phyllobates* be redefined under a theory of monophyly.

### COMPARISON WITH RELATED SPECIES

*Phyllobates aurotaenia* (fig. 8A,B) is a smaller frog than *P. terribilis*: Its maximum body length is less than 32 mm. in males and less than 35 mm. in females, whereas male and female *terribilis* do not even mature until about 37 and 40 mm., respectively. *Phyllobates aurotaenia* is black with golden yellow, orange, or green dorsolateral stripes; the limbs are dotted with gold, blue, or green; the ventral surfaces of body and limbs are black with small spots of blue or green. This species is readily distinguished from *P. terribilis* by size and coloration, except that juvenile *terribilis* are also black with golden dorsolateral stripes; however, young *terribilis* lack the blue or green ventral spotting of *aurotaenia* and acquire a uniformly golden dorsum at about 20 mm. SVL.

*Phyllobates aurotaenia* occurs in low eleva-

tion rain forest west of the Cordillera Occidental, from the upper Río Atrato drainage southward nearly to Buenaventura (map in Silverstone, 1976, p. 17). The largest known specimens, which come from above Playa de Oro on the upper Río San Juan, have broad dorsolateral stripes that tend to fuse because of an intervening dorsal suffusion of bright pigmentation (fig. 8B). As noted by Silverstone (1976, p. 22), such specimens approach *Phyllobates bicolor* in size and coloration. The situation leads us to suspect the possibility of either hybridization or a cline between *aurotaenia* and *bicolor* in the upper San Juan drainage.

*Phyllobates bicolor* (fig. 8C) occurs along the western flank of the northern part of the Cordillera Occidental, at higher elevations ( $> 400$  m. to about 1500 m.) than the lowland *P. aurotaenia*, but distributional data are very scarce. Our own field work supports Silverstone's (1976, p. 24) claim that many museum specimens bear erroneous data, and that the most trustworthy records are from the Santa Cecilia region on the upper Río San Juan. Measurements and proportions of specimens of *P. bicolor* from this region are given in table 2.<sup>1</sup> *Phyllobates terribilis* (table 1) matures at a body length about 5 mm. larger than *P. bi-*

<sup>1</sup>The holotype of *Phyllobates bicolor* Bibron (Mus. Natl. d'Hist. Nat., Paris, No. 838) agrees well with this sample. The species was erroneously described from Cuba, but the holotype very likely came from the upper drainage of either the Río San Juan or Río Atrato, which were attracting gold miners and other travelers long before the early 1800s, when the specimen was probably collected.

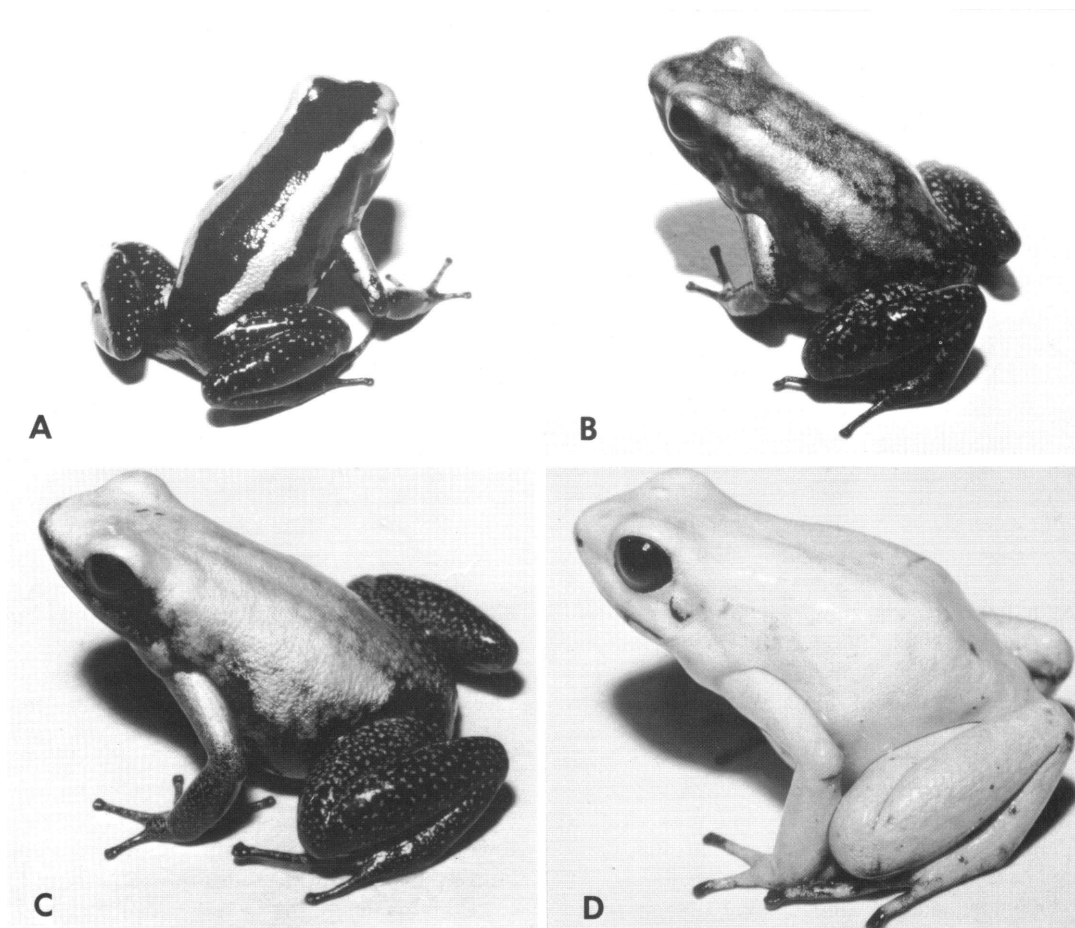


FIG. 8. Poison-dart frogs utilized by Chocó Indians of western Colombia. Approximately to scale (i.e., roughly  $1.5 \times$  SVL of maximum or near maximum size of females).

A and B. *Phyllobates aurotaenia* (Boulenger), from upper Río San Juan, Department of Chocó (specimen A from Playa de Oro, B from higher in same drainage, representing population of larger, less distinctly striped frogs). C. *Phyllobates bicolor* Bibron, from higher in Río San Juan drainage, probably Department of Risaralda; some populations of *bicolor* characterized by wash of bright pigmentation on limbs, but of different hue than body color. D. *Phyllobates terribilis*, new species, from type locality in Río Saija drainage, Department of Cauca. This, the largest and most toxic species, has body and limbs *uniformly* colored (see color plate), except that small juveniles are primitively striped (see fig. 3).

color, attains an average body size 4-5 mm. larger, and a maximum size also about 4-5 mm. larger. The two species are quite similar

in habitus, although *terribilis* tends to have a relatively shorter tibia, narrower head, and slightly smaller finger discs. Direct comparison of specimens indicated a difference in the positioning or size of the tympanum (size cannot be compared without dissection, since the tympanum is partly concealed); differences in proportions (tables 1, 2) confirmed that the lower edge of the tympanum tends to lie closer to the

Silverstone (1976, p. 23) incorrectly stated that the holotype is a male, possibly because the floor of the mouth has symmetrical ribs that resemble vocal slits. It is an adult female, 39.0 mm. SVL, with enlarged ova ( $\leq 2$  mm.) and oviducts.

angles of the jaws in *bicolor* than in *terribilis*. There is, however, extensive overlap in all the aforesaid characters except for that of snout-vent length, in which the largest specimens of *bicolor* are only about 2 mm. longer than the size at which *terribilis* attains sexual maturity.

Adult *Phyllobates bicolor* resemble *P. terribilis* in lacking dorsolateral stripes, since the backs and sides are uniformly colored in both (fig. 8C,D). The dorsum and sides of *bicolor* are golden yellow or orange; the limbs are mainly black with blue or gold spotting, or else covered with a light greenish or yellowish wash of different hue than the body color. The ventral surfaces may be mainly black or variably washed with light yellow, light orange, or bluish green, these hues being paler and less bright than the dorsal body color. Juveniles of *bicolor* are unknown, but they presumably pass through a striped phase resembling the primitive pattern that is exhibited by juvenile *terribilis* and retained by adults of *aurotaenia* and Central American *lugubris* and *vittatus*. The adult color pattern of *bicolor* is relatively less derived than that of *terribilis*, since the extremities and ventral surfaces of *bicolor* remain essentially black; some *bicolor* have the limbs and venter lightly pigmented, but it is a rather superficial color, less intense than the body color and quicker to fade in preservative.

As indicated by the above comparisons, *Phyllobates terribilis* most closely resembles *P. bicolor*, although living specimens are readily separated by coloration and nearly all specimens are separable by size. Minor differences in proportions and considerable differences in toxicity further establish the distinctiveness of *terribilis* from the upper Río San Juan population of *bicolor*. However, some dendrobatids are notorious for their extraordinary inter-populational variation, which causes complications in determining the taxonomic status of distinctive populations. Methods of distinguishing species in such populational complexes have included finding evidence of sympatry, and analysis of morphological, biochemical, and behavioral variation among and within populations (examples in Myers and Daly, 1976a, pp. 222-225, 232). But the present case is difficult to judge because *P. terribilis* and the Santa

Cecilia population of *P. bicolor* are separated by a distance of 300 km.—and *Phyllobates* appears not to be continuously distributed in the intervening area. Excluding *P. aurotaenia*, we are aware of only a single specimen of *Phyllobates* from a geographically intermediate locality: National Museum of Natural History (Smithsonian Inst.) No. 151381, from a former virology field station on the Río Raposa, Department of Valle; W. A. Thornton, collector. Recent examination of this specimen has provided the only independent test of a previously reached decision to consider *terribilis* and *bicolor* as separate species. Our attention was called to this specimen by Silverstone (1976), who considered it the southernmost reliable record of *bicolor*. We borrowed the specimen in order to determine if it displayed any tendencies towards *terribilis*.

The Río Raposa frog is a well-preserved adult female. It is pale gray over the dorsum, sides, and upper surfaces of the limbs, turning black on the hands and feet; the ventral surfaces are mostly black, except for ventrolateral extensions of the pale gray dorsal color. In life, the specimen presumably was a golden color above, with the extremities and ventral surfaces being mostly black or lightly pigmented; therefore, in coloration it more closely resembles *bicolor* than *terribilis*. Proportions are as follows: Tibia length/SVL = 0.46, head width/SVL = 0.35, eye length/snout-eye = 0.82, 3rd-finger disc/finger = 1.71, naris-eye/tympanum-jaw = 2.06. The specimen is closest to *bicolor* in the first four characters and closest to *terribilis* in the fifth character (compare tables 1, 2). Most surprising, however, is the small body size of this specimen, an adult female that measures only 33.5 mm. SVL.<sup>1</sup> Thus, the specimen is about 7 mm. smaller than the smallest adult female *terribilis*, 4 mm. smaller than male *terribilis*, and 2 mm. smaller than the smallest female *bicolor*; it falls only within the lower end of the range of male *bicolor* (tables 1, 2).

<sup>1</sup>This specimen either was not included in Silverstone's (1976, p. 4) list of measurements or was incorrectly sexed. It is an adult female, as revealed by its enlarged ovaries and oviducts; the body cavity had been opened prior to our examination.

The Río Raposa specimen may represent a population of distinctively small frogs that resemble *P. bicolor* in life. Its relationships need further investigation, but we tentatively consider it as representing a disjunct population of *bicolor*. In any case, the specimen seems to negate the possibility that *bicolor* and *terribilis* might represent extremes of a simple north-south cline in body size, and, in this regard, the specific status of *Phyllobates terribilis* is corroborated.

#### *Phyllobates*: A NEW HYPOTHESIS OF MONOPHYLY

*Phyllobates terribilis* is a member of the genus *Phyllobates* by virtue of its morphological and biochemical resemblance to *P. bicolor*, the generic type species. We presently recognize *Phyllobates* as being comprised only of the following named species:

- P. aurotaenia* (Boulenger), western Colombia
- P. bicolor* Bibron, western Colombia
- P. lugubris* (O. Schmidt), Atlantic-side Costa Rica and Panama
- P. terribilis*, new species, western Colombia
- P. vittatus* (Cope), Pacific-side Costa Rica

This arrangement differs from that of Silverstone (1976), who included a total of 20 species in the genus. We suggest that most of these are more closely related to *Dendrobates* (*sensu* Silverstone, 1975) than to *Phyllobates* (*sensu stricto*). Analyses of evolutionary trends in the Dendrobatidae are in progress, but, briefly, our rationale is as follows:

Silverstone (1976, p. 3) differentiated *Phyllobates* from *Dendrobates* on the basis of the relative lengths of the first and second fingers ( $1 \geq 2$  in *Phyllobates*) and on the relative widths of the finger discs (relatively unexpanded in *Phyllobates*). Silverstone based this diagnosis of *Phyllobates* on a set of character states that are primitive in the Dendrobatidae and hence unsuitable for demonstrating monophyly. In other words, Silverstone was unable to demonstrate that all the species placed in *Phyllobates* were more closely related (by recency of common ancestry) among themselves than to *Dendrobates*. Silverstone was not un-

aware of the problem, as evidenced by the following remarks: "I continue to recognize the . . . genera as categories of convenience, that is, as taxonomic units convenient to study, but not necessarily natural" (1975, p. 3), and "delineation of convincingly monophyletic genera of dendrobatids will require considerably more data" (1976, p. 1). Silverstone worked with the characters that he could find and produced two monographs that are remarkably useful at the level of species and species groups. Our disagreement with his generic arrangement is not based on subjective argumentation, but rather on an attempt to determine monophyletic groups through the discovery of shared, uniquely derived character states.

Consideration is being given to a variety of characters, but the initial emphasis is on a survey of skin alkaloids of dendrobatid frogs (Myers and Daly, 1976a; Daly et al., 1978). An ability to produce defensive skin toxins was a major evolutionary development that presumably opened new avenues of adaptation within the Dendrobatidae. The unexpected diversity and novel structures of the dendrobatid alkaloids seem to provide a new systematic character of potentially high information content. Most (> 80%) of the approximately 45 species suspected of being toxic have now been sampled for skin toxins, and about 100 novel alkaloids have been isolated; so far, all these compounds appear to be unique to the Dendrobatidae (although it would not be surprising if some of the simpler alkaloids proved to be convergent in plants or other animals). As an initial approach to problems of homology, it is parsimoniously assumed that identical alkaloids in different species of dendrobatids owe their existence to a common evolutionary event (Myers and Daly, 1976a, p. 197). A tentative, very simplified analysis of the evolutionary polarity of several classes of dendrobatid alkaloids is shown in figure 9, to which reference should be made for the following discussion.

The vast majority of dendrobatid alkaloids contain a piperidine ring (i.e., a 6-membered ring comprised of 5 carbons and 1 nitrogen) and appear to be biosynthetically related. The pumiliotoxin-C class compounds are relatively simple in structure, numerous in kind, and

widespread among the species included by Silverstone in *Dendrobates* and *Phyllobates*. They are the only piperidine alkaloids so far detected in *Phyllobates* as here restricted, but occur only in small amounts. The pumiliotoxin-C class alkaloids are tentatively considered as primitive relative to other dendrobatid alkaloids; they are, however, derived compared to the apparent alkaloid-free condition of *Colostethus*, which is treated as the plesiomorphic sister group of the *Dendrobates-Phyllobates* complex. This is the first clear evidence that this complex has a monophyletic origin apart from other members of the family (fig. 9).

Histrionicotoxins are a class of piperidine alkaloids characterized by an unusual spiro-ring system (two rings joined by a single carbon). It has been suggested (Daly et al., 1978) that the histrionicotoxins and pumiliotoxin-C alkaloids share a common precursor in the form of a disubstituted, unsaturated piperidine. There are fewer than a dozen known histrionicotoxins, but these are widely distributed among the species placed in *Dendrobates* and *Phyllobates* by Silverstone. So far, histrionicotoxins have not been detected in the *D. minutus* (fide Myers and Daly, 1976b) and *P. bicolor* groups and must be considered derived relative to the pumiliotoxin-C alkaloids.

Detailed analysis of the distribution of piperidine alkaloids among dendrobatids will be deferred until completion of an ongoing sampling program. However, we feel reasonably confident in considering some of the piperidine alkaloids as primitive relative to the steroidal batrachotoxins. The batrachotoxins are *much* more toxic than the piperidine alkaloids (e.g., see Myers and Daly, 1976a, p. 183) and a few laboratory observations indicate that they probably are more effective in deterring potential predators (see p. 327 n). The batrachotoxins are known to occur only in one group of morphologically similar frogs that today occupy remnants of what once was probably a continuous Chocoan distribution. The presence of small amounts of pumiliotoxin-C class alkaloids in species of this group indicates the presence of an old biosynthetic pathway that has been suppressed by the shift to a more effective set of defensive skin toxins. Therefore, we propose that the batrachotoxin alkaloids are a uniquely

derived (synapomorphic) character state that can be used to redefine *Phyllobates* so that it becomes monophyletic. A revision of *Phyllobates* as here restricted will be presented elsewhere (Myers and Daly, in progress).

**NOMENCLATURE SUGGESTION:** The hypothesis outlined above calls for removing 16 of the 20 species now in *Phyllobates* (*sensu* Silverstone, 1976). We share Silverstone's reluctance to establish new genera until necessary, and therefore we suggest that these species be transferred to *Dendrobates*<sup>1</sup> (*sensu lato*) until relationships can be further analyzed in this group of frogs, which has been difficult to treat taxonomically (see discussion by Silverstone, 1975, pp. 3-4). We acknowledge that the main basis for these changes rests on our present interpretation of the molecular data; a cautionary essay on the use of such data has already been presented (Myers and Daly, 1976a, pp. 194-197). We also acknowledge that transferring one species (*espinosai*) to *Dendrobates* differs from a previous view, in which it was claimed that, "molecular data should [not] be viewed as unequivocal criteria of 'close' relationship, unless morphological contradictions are otherwise explainable" (Myers and Daly, 1976a, pp. 238-239). The change lies in an increasing perception of what constitutes shared primitive characters in the Dendrobatidae (see also p. 180 n of previous reference). This matter is to be discussed more fully elsewhere, but we now see few contradictions between available biochemical and morphological data, so long as plesiomorphic characters are not allowed to interfere with the analysis of monophyly.

Some of the new assignments (e.g., *Dendro-*

<sup>1</sup>To formalize the matter, the following 15 species are removed from *Phyllobates* and placed in *Dendrobates*. New combinations are indicated by an asterisk: *Dendrobates anthonyi*\*, *Dendrobates bassleri*, *Dendrobates bolivianus*\*, *Dendrobates boulengeri*\*, *Dendrobates espinosai*\*, *Dendrobates femoralis*\*, *Dendrobates ingeri*, *Dendrobates parvulus*, *Dendrobates petersi*\*, *Dendrobates pictus*, *Dendrobates pulchripectus*\*, *Dendrobates smaragdinus*\*, *Dendrobates tricolor*\*, *Dendrobates trivittatus*, *Dendrobates zaparo*\*. A sixteenth species considered by Silverstone (1976, p. 20) remains to be described (Myers and Daly, in progress). See Silverstone (1976) for references to the above names.



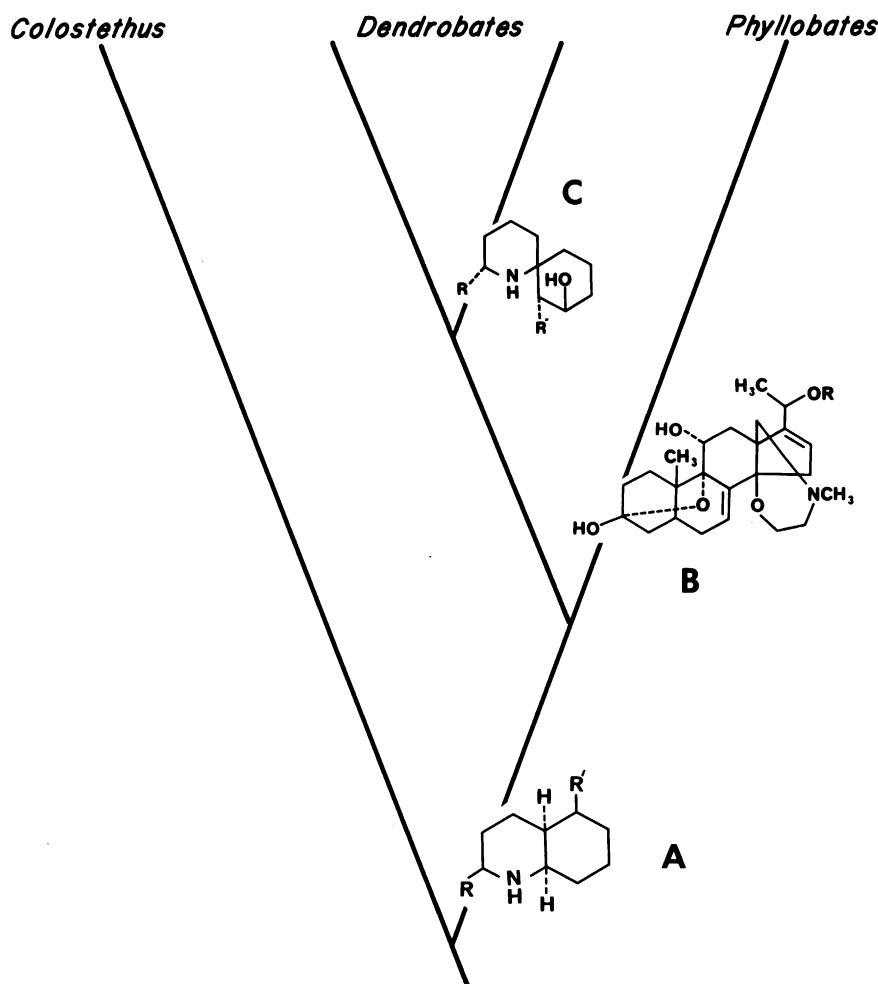


FIG. 9. Preliminary hypothesis of relationships among currently recognized genera of dendrobatid frogs, based on the distribution of skin alkaloids. Basic ring systems are shown for three major classes of toxic alkaloids, all of which are unique to the Dendrobatidae. Individual compounds within the classes differ only at the substituent points R and R'.

A. Pumiliotoxin-C class alkaloids occur in all species groups of *Dendrobates* and *Phyllobates*, marking this complex as monophyletic. Skin alkaloids have not been detected in *Colostethus*, the plesiomorphic sister group of *Dendrobates-Phyllobates*.

B. Highly toxic alkaloids of the steroidal batrachotoxin class mark the true poison-dart frogs as a monophyletic genus (*Phyllobates*, *sensu stricto*). Biosynthesis of primitive piperidine alkaloids has been suppressed, with pumiliotoxin-C alkaloids being produced in only small amounts.

C. Spiropiperidine alkaloids of the histrionicotoxin class have been found in all but one species group of *Dendrobates* (*sensu lato*). Studies are in progress to determine the taxonomic distribution of nearly 100 piperidine alkaloids in *Dendrobates*.

*bates femoralis*) will perhaps prove unsatisfactory, but specific epithets cannot float disembodied in a system of binominal nomenclature. Some workers might reasonably prefer to

follow Silverstone's arrangements, inasmuch as major revisions should not casually be set aside. We too hold the view that there should be a reasonable effort to balance phylogenetic

consistency with stability in classification, even though there is no agreed-upon method for achieving this elusive goal. But we would point out two important considerations in favor of the recommended changes: (1) At least *Phyllobates* appears to become monophyletic at the level of resolution shown by the second dichotomy in figure 9. (2) Our suggestion has the merit of *returning* the type species of *Dendrobates* to its rightful place.

Silverstone (1975, p. 4; 1976, p. 45) treated *Hyla nigerrima* [= *Dendrobates trivittatus*] as a *Phyllobates*, with full recognition that it is the nominal type species of *Dendrobates*. Silverstone (1971a) had earlier requested that the International Commission of Zoological Nomenclature set aside this designation and assign a new type species to *Dendrobates* (the petition has not been acted on at the time of this writing). Silverstone based his request on a subjective interpretation of "morphological and chromosomal evidence" that made it "clear that *Dendrobates trivittatus* (Spix), though it lacks teeth, is more closely related to the toothed brightly-colored dendrobatid frogs [i.e., *Phyllobates* in a traditional sense] than to the other toothless dendrobatids" [i.e., *Dendrobates* in a traditional sense]. The "chromosomal evidence," not fully discussed in Silverstone's published monographs, refers to the probably

primitive diploid number of 24 (Silverstone, 1971b). The "morphological . . . evidence" is the relatively long first finger and relatively unexpanded discs of *D. trivittatus*, which are almost surely primitive character states in the Dendrobatidae. We agree with Silverstone's implication that teeth have been lost in more than one lineage of dendrobatids, but we disagree with any belief that primitive character states can be used to make relationships "clear."<sup>1</sup> The *International Code* (International Commission . . . , 1964, p. v) stresses even in its preface that the name of a taxon is objectively determined by its type, but that the content of a taxon is otherwise a subjective "question of taxonomy, ignored by nomenclature." Silverstone had hoped to stabilize the nomenclature and avoid having to create a new generic name to fit his concept of *Dendrobates*, but we reaffirm a view (Myers and Daly, 1971) that the matter is a biological problem not to be resolved by decree. Furthermore, we would note that the skin toxins of *Dendrobates trivittatus* are a mixture of histrionicotoxins and pumiliotoxin-C class alkaloids (Daly et al., 1978)—indicating that *trivittatus* shares a more recent common ancestor with the species of *Dendrobates* (*sensu* Silverstone) than with *Phyllobates* (*sensu stricto*).

## SKIN ALKALOIDS AND TOXICITY

Several hundred *Phyllobates terribilis* were skinned in the field within two days of capture. Skins were accumulated in 100 percent methanol for transport to the National Institutes of Health, where skins and extracts were stored at -5° C. until use. The subsequent extraction, fractionation, and most analytical techniques are described in Myers and Daly (1976a).

The principal skin toxins of *Phyllobates terribilis* were isolated by thin-layer chromatography (fig. 11) and proved by mass spectrometry to be batrachotoxin ( $C_{31}H_{42}N_2O_6$ ), homobatrachotoxin ( $C_{32}H_{44}N_2O_6$ ), and batrachotoxin A ( $C_{24}H_{35}NO_5$ ). No pseudobatrachotoxin was detected, but this labile alkaloid (of unknown structure) cannot be presumed absent

because it readily converts to batrachotoxinin A during storage and/or fractionation of methanolic extracts.

Small amounts were detected of several minor compounds that appear related in structure to the batrachotoxin alkaloids; these represent less than 5 percent of total alkaloids and are under investigation by Dr. Takashi Tokuyama at Osaka City University, Japan. Also, trace amounts of alkaloid number **195B** ( $C_{13}H_{25}N$ ), a pumiliotoxin-C class compound

<sup>1</sup>Due to the influence of the late Willi Hennig, this point has been repeatedly mentioned in the literature on systematics for over a decade. Brief and especially lucid discussions include those of Hennig (1965, p. 104) and Eldredge and Tattersall (1975, pp. 226-230).

(Daly et al., 1978), were detected by combined gas chromatography-mass spectrometry.

### VARIATION

**INDIVIDUAL (AND GEOGRAPHIC) VARIATION:** The approximate amount of the two major steroidal alkaloids<sup>1</sup> was determined by bioassay in each of 16 adult frogs, from two localities less than 15 km. apart. The bioassay is based on the relationship between dose level of batrachotoxin and survival time in subcutaneously injected white mice (fig. 10). A small volume of each of the 16 methanolic extracts was diluted with isotonic NaCl so that methanol comprised less than 50  $\mu$ l of a final 0.2 ml. injection volume.<sup>2</sup> Methanol has no discernible toxic effects in mice at this level. Dilutions with isotonic NaCl were continued until the survival time of trial mice fell in the range of 5-10 minutes. Three mice were then assayed at this dosage and the concentration of batrachotoxin and homobatrachotoxin was determined from the curve based on pure batrachotoxin (fig. 10). The amount present in skin from individual frogs was calculated and rounded to the nearest 100  $\mu$ g, with the following results:

BATRACHOTOXIN-HOMOBATRACHOTOXIN,  
MICROGRAMS PER FROG

Locality	N	Mean $\pm$ 1 S.E.	S.D.	Range
La Brea	6	917 $\pm$ 31	75	800-1000
Que. Guanguí	10	1140 $\pm$ 144	455	700-1900
Comparison of means: $t = 1.175$ , $P < 0.3 > 0.2$				

Thus, individuals of *Phyllobates terribilis* have

<sup>1</sup>Batrachotoxin and homobatrachotoxin, the most toxic of the steroidal alkaloids, are responsible for the major portion of the toxicity of *Phyllobates* skin extracts. The limit of detection is about 0.05  $\mu$ g in both bioassay (mice) and by color reaction (dimethylaminocinnamaldehyde) after thin-layer chromatography.

<sup>2</sup>For other dendrobatid frogs, which are less toxic than *P. terribilis*, the methanol is first removed from the extract *in vacuo* and the residue then redissolved in a minimal volume of methanol prior to the dilution with isotonic NaCl. Alkaloids separated by chromatography are also dissolved in minimal volumes of methanol prior to dilution and assay.

an approximate range of 0.7-1.9 mg. of batrachotoxin-homobatrachotoxin per adult frog. Interpopulational variation is not documented, but we cannot reject a possibility that the greater variability at Quebrada Guanguí might be a reflection of interdeme variation. All extracts were collected within a month's time, but the La Brea frogs came from closely adjacent ridges and probably represent a single deme, whereas the 10 frogs from Quebrada Guanguí might represent more than one deme (a possibility not considered when the specimens were skinned). Coefficients of variation and their standard errors are  $8.18 \pm 2.26$  for La Brea, and  $39.91 \pm 8.92$  for Quebrada Guanguí. In any case, the above mean of 1140  $\mu$ g/frog, for Quebrada Guanguí, is confirmed by bioassay of a combined sample of 100 skins from the same locality; this large sample contained an average of 1100  $\mu$ g of batrachotoxin-homobatrachotoxin per frog.

The above figures, obtained by bioassay, are indirect but probably reliable estimations of amounts of the major toxins that are actually present in individual frogs. There is appreciable loss when the toxins are isolated by chromatographic techniques (table 5). For example, the aforesaid sample of 100 skins gave a total yield of 80 mg. of batrachotoxin and homobatrachotoxin, for an average of 800  $\mu$ g per frog (vs. 1100  $\mu$ g by bioassay), a recovery rate of 73 percent.

**ONTOGENETIC CHANGE:** A clutch of 13 captive-laid eggs, weighing 140 mg., was extracted in methanol and tested for toxicity by subcutaneous injection of the concentrate into white mice. The extract was not toxic, indicating that batrachotoxin-homobatrachotoxin, if present, occurred in an amount of less than 0.1  $\mu$ g. However, analysis of the egg extract by thin-layer chromatography revealed the presence of trace amounts of a compound or compounds having an  $R_f$  value similar to batrachotoxin-homobatrachotoxin and giving a blue color with dimethylaminocinnamaldehyde (see fig. 11, legend). The intensity of the colored spot was compatible with the presence of 0.2  $\mu$ g of batrachotoxin in the total extract. But identity of the compound(s) giving the blue color is uncertain, inasmuch as the bioassay

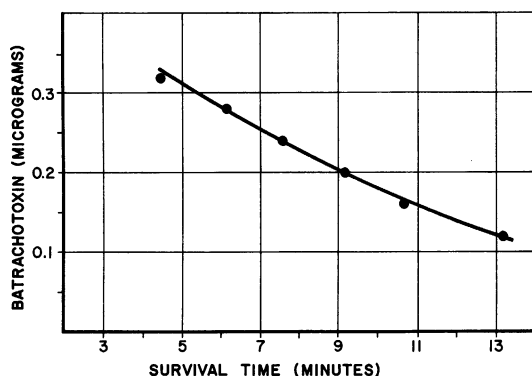


FIG. 10. Dose-response curve of batrachotoxin: assay of toxicity in white mice. Purified batrachotoxin was dissolved in a minimal volume of methanol, diluted with isotonic NaCl (0.9%) to a concentration of  $0.2 \mu\text{g}/0.2 \text{ ml.}$  and injected subcutaneously into 20-gram NIH general purpose white mice. Each point represents average of 4-5 determinations of death time at each dose (S.D.  $< 0.7 \text{ min.}$ ). The toxicity of homobatrachotoxin is only slightly less than batrachotoxin, with minimal lethal doses being about  $0.06$  and  $0.04 \mu\text{g}$ , respectively.

should have detected any batrachotoxin-homobatrachotoxin at such a concentration (detection limit  $\sim 0.05 \mu\text{g}$ ).

The skins of two tadpoles reared to stage 35 were also extracted in methanol; the combined skins weighed 23 mg. No batrachotoxin was detected by bioassay or color reaction after thin-layer chromatography.

A juvenile frog (27 mm. SVL) was skinned at Quebrada Guanguí and the extract later tested by bioassay. The toxicity was equivalent to the presence of  $200 \mu\text{g}$  of batrachotoxin-homobatrachotoxin in this small frog, compared with an average of about  $1100 \mu\text{g}$  in adults ( $700\text{--}1900 \mu\text{g}$ ) from the same locality. Its skin weight was 200 mg. as compared to an average of approximately 600 mg. for adult frogs (range about  $580\text{--}650 \text{ mg.}$ ).

The few data given above suggest that the batrachotoxin alkaloids of *Phyllobates terribilis* are formed in significant amounts only after metamorphosis.

**INFLUENCE OF CAPTIVITY:** Adult frogs from Quebrada Guanguí that were sacrificed three weeks to one year after capture had toxicities

equivalent to  $540 \pm 50 \mu\text{g}$  batrachotoxin-homobatrachotoxin per frog ( $400\text{--}600 \mu\text{g}$ ,  $N = 8$ ), or about 50 percent that of recently captured frogs (see preceding text table).

Two individuals sacrificed after three years of captivity had toxicity equivalents of 320 and  $480 \mu\text{g}$  per frog. Although reduced in total amounts, the relative proportions of batrachotoxin, homobatrachotoxin, and batrachotoxinin A, as assessed by thin-layer chromatography, appeared relatively unchanged in these frogs after three years on a laboratory diet of vitamin-fortified crickets and *Drosophila*. Levels of batrachotoxin alkaloids also appeared reduced in *P. aurotaenia* after prolonged periods in captivity (Tokuyama, Daly and Witkop, 1969).

The reason for such declines in toxicity is not clear, although conceivably related to stress. But the fact that the frogs are still appreciably toxic after long periods of captivity does provide evidence that the toxins are not sequestered from some natural food item. No traces of toxins or potential alkaloid precursors were found in extractions of stomach contents from wild-caught specimens of other dendrobatid species (*Dendrobates histrionicus*, *D. trivittatus*).

#### INTERSPECIFIC COMPARISONS

The major skin alkaloids of *Phyllobates terribilis* are identical with those of other frogs known to be used for poisoning blowgun darts, namely *P. aurotaenia* and *P. bicolor*. Structures of the batrachotoxin alkaloids were first determined from extracts of *Phyllobates aurotaenia* collected near Playa de Oro on the upper Río San Juan, Department of Chocó, Colombia (Tokuyama et al., 1968; Tokuyama, Daly and Witkop, 1969). The alkaloids of *P. aurotaenia* and *P. terribilis*, as visualized by thin-layer chromatography, are compared in figure 11. Comparison of relative intensities of the alkaloid spots allows visualization of the fact that *terribilis* contains a greater quantity of skin toxins than *aurotaenia*.

The large samples of skin extracts obtained from *Phyllobates terribilis* and *P. aurotaenia* allow more precise quantitative comparison.

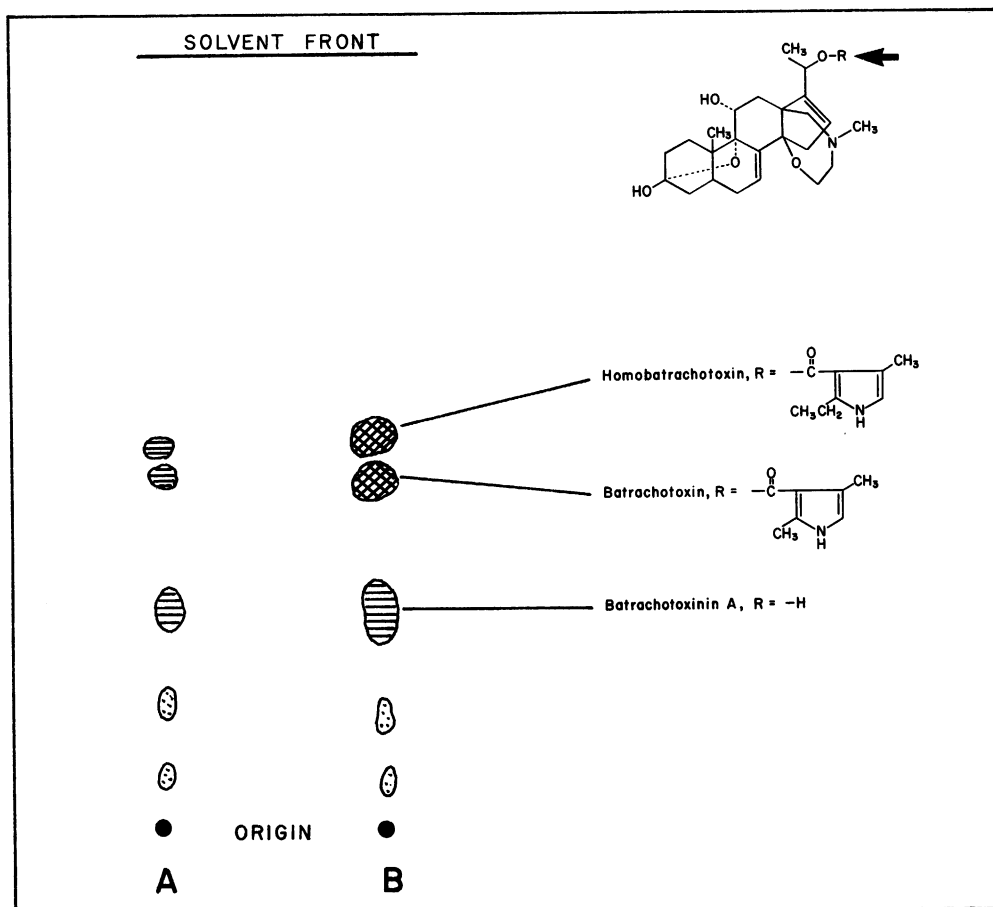


FIG. 11. Representation of thin-layer chromatoplate showing isolation of alkaloids from population samples (each > 100 skins) of two species of poison-dart frogs. A. *Phyllobates aurotaenia*, vicinity of Playa de Oro, upper Río San Juan, Chocó, Colombia. B. *Phyllobates terribilis*, new species, from type locality. Structures of major alkaloids as shown, each having same steroidal ring system but differing at the substituent R.

A sample of 10  $\mu$ l of methanolic alkaloids equivalent to the amount in 10 mg. wet skin was applied at each origin, and the silica gel GF plate (Analtech Co.) developed with 9:1 chloroform-methanol. Visualization, after chromatography and drying, by exposure to iodine vapor. For detailed methodology, see Appendix 1 in Myers and Daly (1976a). *Spot intensities depicted as follows:* Cross-hatched pattern=large amounts of alkaloids. Horizontal pattern=moderate amounts. Dots=small or trace amounts.

Structures confirmed by electron impact mass spectral analysis of material extracted from corresponding spots. The following diagnostic test for batrachotoxin alkaloids was utilized for some of the small sample analyses mentioned in text: Chromatography run as above, but, after drying, the plate was immediately sprayed with a 0.1 percent solution of 4-dimethylaminocinnamaldehyde in 1 N HCl. Batrachotoxinin A gives no color, but batrachotoxin and homobatrachotoxin turn an intense blue. The limit of detection of (homo)batrachotoxin with this reagent is about 0.05  $\mu$ g, comparable to the sensitivity of bioassay experiments on mice.

The relative amounts of the major toxins actually isolated from these species are compared in table 5. It must be emphasized that isolation results in a loss of 25 percent or more of the toxins. Therefore, the data in table 5 are presented only for the purpose of relative comparisons, and should not be interpreted as showing amounts of alkaloids present in the living frogs (see below). *Phyllobates terribilis* contains, per frog, about 27 times more batrachotoxin-homobatrachotoxin than the smaller *P. aurotaenia*; comparing equivalent skin weight (per 100 mg.), *P. terribilis* contains about nine times more of these powerful toxins. Individual *P. terribilis* contain about four times more batrachotoxinin A (combined with pseudobatrachotoxin for *aurotaenia*, see table 5, notes c, d), or about 1.3 times as much as *P. aurotaenia* by equivalent skin weight. As emphasized above, these comparisons are based on alkaloid isolation data in table 5. The amount of toxins actually present in living *P. terribilis* was previously given under Variation; such data are not available for *P. aurotaenia*. Conversely, isolation data are not available for a third species, *P. bicolor*, since our samples have been small, but individual toxicity estimates were obtained and are discussed next.

A sample of adult *Phyllobates bicolor* was collected near the upper Río San Juan, 7 km. SE Santa Cecilia in the Department of Risaralda. Ten individuals were assayed for toxicity in the manner described for *P. terribilis* (p. 335), using 3 or 4 mice for each final assay. These 10 frogs had an average toxicity equivalent to  $35.3 \pm 4.5$   $\mu$ g of batrachotoxin-homobatrachotoxin per frog, in a range of 17-56  $\mu$ g (S.D. =  $14.2 \pm 3.2$   $\mu$ g, C.V. =  $40.28 \pm 9.01\%$ ). An additional 10 adult *bicolor* skins were pooled and assayed in the same manner, yielding a slightly higher toxicity equivalent to 46.6  $\mu$ g per frog. Thus, *Phyllobates bicolor* is much less toxic than *P. terribilis*, which contained 700-1900  $\mu$ g of batrachotoxin-homobatrachotoxin per individual (p. 335).

*Phyllobates bicolor* does not appear to be appreciably more toxic than the neighboring *P. aurotaenia*, despite its larger size, brighter coloration, and bolder habits. This conclusion also was supported by a thin-layer chromatoplate of *bicolor* alkaloids, obtained from frogs collected by Indians at an indefinite locality in the upper Río San Juan drainage (represented by frog in fig. 8C). The *bicolor* chromatoplate showed a distribution and intensity of alkaloids similar to

TABLE 5  
Isolation of the Major Skin Toxins from Two Species of Poison-Dart Frogs

Species of Frog	Alkaloids ( $\mu$ g)					
	<i>Batrachotoxin</i>		<i>Homobatrachotoxin</i>		<i>Batrachotoxinin A</i>	
	per frog	per 100 mg. of wet skin	per frog	per 100 mg. of wet skin	per frog	per 100 mg. of wet skin
<i>Phyllobates aurotaenia</i> (Boulenger) <sup>a</sup> (1 skin ~ 200 mg.)	20	10	10	5	50 <sup>c</sup>	25
<i>Phyllobates terribilis</i> n. sp. <sup>b</sup> (1 skin ~ 600 mg.)	500	83	300	50	200 <sup>d</sup>	33

<sup>a</sup>Data based on thin-layer and column chromatographic isolation from > 100 adult frogs (Tokuyama, Daly, and Witkop, 1969).

<sup>b</sup>Data based on thin-layer chromatographic isolation from 100 adult frogs. Analysis of another sample, by column chromatography, gave the same total yield per frog (1000  $\mu$ g), but with individual differences in batrachotoxin (400  $\mu$ g) and batrachotoxinin A (300  $\mu$ g), *vide* Takashi Tokuyama (unpublished).

<sup>c</sup>Including pseudobatrachotoxin, initially present at about 20  $\mu$ g per frog (10  $\mu$ g/100 mg. skin). This labile compound underwent nearly complete conversion to batrachotoxinin A during column chromatographic isolation (Tokuyama, Daly, and Witkop, 1969).

<sup>d</sup>Pseudobatrachotoxin not detected (note c above).

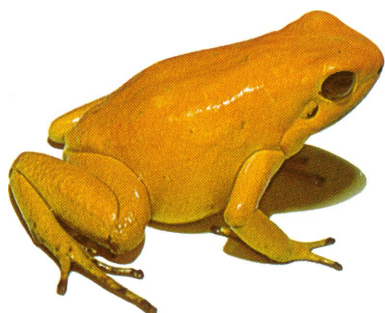




Plate 1. Emberá Indian with blowgun. The bamboo quiver holds darts poisoned with skin secretions from *Phyllobates terribilis*. Fruit shells attached to the quiver hold a fluffy plant fiber, used as wadding on the darts (see text fig. 28). Photograph taken in 1971, at Quebrada Guanguí, Pacific lowlands of Colombia.

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Plate 2. *Phyllobates terribilis*, new species. Common color variants at the type locality. The uniformly bright dorsal and ventral coloration, and the large size, are diagnostic. The extremely toxic skin secretions are used by southern Emberá Chocó for poisoning blowgun darts. Approximately natural size.







the illustration for *P. aurotaenia* (fig. 11A). Neither species can compare with the rather awesome toxicity of *Phyllobates terribilis*.

The other species of *Phyllobates*, the Central American *lugubris* and *vittatus*, produce much smaller amounts of batrachotoxins than any of the three Colombian species. Some Panamanian populations of the small *P. lugubris* are virtually nontoxic (Myers and Daly, in progress).

The relative toxicities of the main batrachotoxin alkaloids are as follows (see Myers and Daly, 1976a, table 1, for comparisons with some of the piperidine-based alkaloids of *Dendrobates*):

ALKALOID	TOXICITY <sup>a</sup>
Batrachotoxin	0.04 $\mu$ g
Homobatrachotoxin	0.06 $\mu$ g
Batrachotoxinin A	20 $\mu$ g

<sup>a</sup>Approximate minimal lethal dose by subcutaneous injection in 20-gram white mice.

Toxicity of the skin secretions of *Phyllobates*, therefore, is due primarily to the mixture of batrachotoxin and homobatrachotoxin, which occur in large quantity in the skin of *P. terribilis*. These are extraordinarily potent poisons, and *Phyllobates terribilis* is an extraordinarily poisonous frog, as is discussed next.

#### TOXICOLOGY

Batrachotoxin and homobatrachotoxin are among the most potent of all naturally occurring nonprotein poisons. They are strong cardiotoxins, whose selective effects on ionic permeability lead to an irreversible depolarization of nerve and muscle, thus eliciting arrhythmias, fibrillation, and cardiac failure (Albuquerque and Daly, 1977, and ref. therein). Externally observed symptoms in laboratory animals include strong muscle contraction, violent convulsions, salivation, gagging, and dyspnea (Märki and Witkop, 1963). Traces of *Phyllobates terribilis* skin secretions accidentally transferred from hand to face have caused a pronounced burning sensation that lasted several hours, seemingly because the low molecular-weight (< 600) toxins penetrated into beard follicles; contact with porous skin is evidently

to be avoided. Touching the tip of the tongue to the back of a Costa Rican *Phyllobates vittatus* resulted in a lingering, almost numb sensation on the tongue, followed by a disagreeable tightening sensation in the throat. A snake showed symptoms of great distress after biting a specimen of *P. vittatus*, and was rendered helpless for some hours (see p. 327 n). Such observations persuaded us against tasting<sup>1</sup> secretions from the more toxic species of *Phyllobates*, especially *P. terribilis*, since there seems a distinct possibility that respiratory difficulties might be encountered.

In 20-gram white mice, the minimal lethal dose of batrachotoxin-homobatrachotoxin is about 0.05  $\mu$ g when injected subcutaneously. Thus, an individual *Phyllobates terribilis*, with an average amount (1100  $\mu$ g) of these compounds, contains enough poison to kill upward of 20,000 mice. It is, of course, risky to extrapolate toxicity from species to species, such as from mouse to man, but we suppose that man is at least as susceptible as mice to the batrachotoxin alkaloids. If so, mouse toxicity (at about 2.5  $\mu$ g/kg. subcutaneously) would translate into a lethal dose of only about 170  $\mu$ g for a person weighing 68 kilograms. However, larger animals are usually more susceptible to toxins than smaller organisms, and, based on limited data, batrachotoxin does appear more toxic to guinea pigs and rabbits than to mice (unpublished data insufficient for estimating minimal lethal doses).<sup>2</sup>

The possible human toxicity of batrachotoxin might also be inferred by comparison with other, better known toxins of low molecu-

<sup>1</sup>A simple and fast bioassay, albeit not very elegant, for detecting the presence of pharmacologically active substances in frog skin (Myers and Daly, 1976a, p. 185).

<sup>2</sup>Mezey (1947a, 1947b) reported a much higher minimal lethal dose for dogs and rabbits, but his data are not comparable with recent studies, being based on material of uncertain composition that was obtained from darts 15 years old.

However, cats might be no more susceptible than mice. Märki and Witkop (1963, p. 337) cited an intravenous dose level of 3  $\mu$ g/kg. as being sublethal in a cat, although this is about the equivalent of the minimal lethal subcutaneous dose in mice. A second cat expired in nine minutes, after a dose equivalent to 5  $\mu$ g per kg. of body weight.

lar weight ( $< 800$ ), for example the plant alkaloids aconitine and strychnine, and digitoxin, a steroidal glycoside. Two of these compounds, aconitine and digitoxin, are cardiotoxins, as is batrachotoxin. In man, ingestion of 2 mg. of aconitine, 3 mg. of digitoxin, or 15 mg. of strychnine may be fatal (Dreisbach, 1977). If injected subcutaneously into mice, aconitine is 1/100 as toxic as batrachotoxin, and digitoxin and strychnine are 1/200 as toxic; the ratios of subcutaneous to oral potencies in mice are approximately 1:2 for digitoxin and 1:10 for aconitine and strychnine. Extrapolating from these figures, and *assuming* that the same relative relationships pertained to man, batrachotoxin would be expected to be lethal at injected doses of only 2-7.5  $\mu\text{g}$ , although such minute doses intuitively seem too low. By the same criteria, batrachotoxin would be expected to be fatal at ingested levels some 60 times higher (see below), that is, at doses of 120-450  $\mu\text{g}$ . However, attempting to estimate oral potency of batrachotoxin is frustrating for two reasons: (1) The ratio of subcutaneous to oral potency in mice is quite different than for the other toxins, since batrachotoxin is only one-sixtieth as toxic to mice when introduced directly into the stomach by tube.<sup>1</sup> (2) The toxin appears to be so readily absorbable by buccal and esophageal mucosa that asphyxiation might occur at lower doses than would be fatal by gastric absorption.

The main purpose of the above exercise is to emphasize that *Phylllobates terribilis* should be treated with the upmost respect, on account of the large amount of toxins in its defensive skin secretions. It should be remembered that a single frog may contain up to 1.9 mg. (1900  $\mu\text{g}$ ) of batrachotoxin and homobatrachotoxin, and that only a fraction of a milligram—almost certainly less than 200  $\mu\text{g}$ —would be fatal if it reached the bloodstream through an open

wound or by injection. The consequences of a case of sublethal poisoning are unpredictable, except to be unpleasant at best. The toxic sequelae to batrachotoxin poisoning—discoordination, gagging, convulsions, respiratory difficulty—have been detailed for mice and cats (Märki and Witkop, 1963). No effective antidote is known, but treatment of batrachotoxin poisoning might best be based on paradigms for aconitine or veratrum, agents with similar mechanisms of action, or for digitalis, an agent that produces somewhat similar cardiotoxic effects.

Our remarks are meant to be cautionary, not alarmist (after all, the frogs do not *bite*). *Phylllobates terribilis* is an interesting animal that can safely be maintained in the laboratory; furthermore, escapees would soon die at normal room humidity and therefore pose no threat. If one of the frogs were casually picked up, any small scratch or cut on the hand would likely be noticed because of a prompt burning sensation. We would anticipate no ill effect from brief contact with a tiny wound, especially if soon washed,<sup>2</sup> but we do strongly recommend that rubber gloves be used when handling these frogs, and that care be taken to keep the hands away from the face. It should be noted that the Emberá Indians protect their hands with leaves when catching *P. terribilis*. We used rubber gloves, goggles and disposable face masks when skinning specimens for toxin extraction. Contaminated gloves, plastic bags, etc. should be carefully disposed of; at our camp, we unintentionally caused the death of a dog and a chicken that got into garbage containing such items.

<sup>1</sup>Unpublished experiments. The important point is that *Phylllobates* secretion is poisonous if ingested. Statements to the contrary (e.g., Mezey, 1947a, 1947b; Märki and Witkop, 1963, p. 331) were based on studies of very old dart poison and probably on the fact that Indians eat game killed with poisoned darts. Batrachotoxin alkaloids are presumably decomposed when such game is cooked.

<sup>2</sup>**Disclaimer:** Although most dendrobatids appear not to release skin toxins until injured or rather strongly stressed, this is not the case with *Phylllobates terribilis*. We have noticed that merely handling specimens can result in toxin release, or possibly the frogs may constantly secrete small amounts from their large stores. *The amount of poison that could accidentally be introduced into a wound is unpredictable*, probably depending on the individual frog, length of its captivity, and the degree to which it feels stressed. Dendrobatid skin secretions often appear milky when released in large amounts, but the toxins are also secreted in colorless form.



## UTILIZATION OF FROGS FOR DART POISONING

The practice of using frogs for poisoning blowgun darts is not so common as indicated in the recent popular literature. Furthermore, we are unaware of any substantiated account of frog poison being applied to arrows or lances, even though it might seem likely that such experimentation has occurred. Dendrobatids are often called "poison-arrow frogs." Myers and Daly (1976a, p. 180) objected that this name, "is mildly misleading, based perhaps on the Spanish '*flecha*' (an arrow or dart), which is usually translated as 'arrow.'" Although a blowgun dart is a kind of small, unfeathered arrow, Myers and Daly (*loc. cit.*) coined the name "poison-dart frogs" as being more descriptive and more conformable to modern English—in which arrows and darts are clearly distinguished, as by Heath and Chiara (1977) for example. The matter would be unimportant, except that the poison-arrow name seems to feed imagination and perpetuate myth in a growing body of popular (e.g., Walsten, 1977) and technical literature (e.g., Heath and Chiara, 1977, p. 95).

### FROGS USED

*Phyllobates terribilis* is the third species of frog definitely known to be used as a source of dart poison. The other two are *P. aurotaenia* and *P. bicolor*, both of which have been erroneously called "*Dendrobates tinctorius*" in the anthropological literature. These three closely related species (fig. 8) are confined to western Colombia. Therefore, the known use of frog poison is likewise geographically restricted. By this restriction, we exclude secondhand, unverified reports that other anurans have been similarly used (e.g., see Vivante and Homero Palma, 1966, *re Bufo* spp.). We also exclude instances in which frogs and toads only provide some flavoring in a poison brew—other ingredients being such things as tree sap, snakes, ants, spiders, scorpions, menstrual blood, and men's testicles<sup>1</sup> (e.g., Kirchhoff,

1948; Wassén, 1934). We regard as questionable a report (Breder, 1946, p. 407) that *Dendrobates auratus* was used for poisoning darts in Panama. This was told to Breder in 1924, by Chocó Indians living on a tributary of the lower Río Chucunaque in extreme eastern Panama. But, the Chocó are travelers and we entertain the possibility that Breder's informants might have been emigrants from Colombia, where species of *Dendrobates* are recognized as being poisonous albeit much less so than *Phyllobates*. The blowgun is not used by Panamanian Chocó, at least in recent years in the Chucunaque-Tuira drainage, although the weapon and a supply of poisoned darts might have been occasionally carried up from Colombia. It may well be that Panamanian or Colombian Chocó have experimented with *Dendrobates* poison, but we have no proof of this for any species. We are uncertain whether the piperidine-based alkaloids of *Dendrobates* would be sufficiently toxic for hunting purposes.

Blowguns and poisoned darts were also used by Cuna Indians, northern neighbors of the Chocó. Suggestions (e.g., Stout, 1948, p. 260) that the weapon was obtained from the Chocó would seem erroneous, since the Cuna blowgun is of completely different manufacture (type I of Yde, 1948). Presumably the Cunas had a plant poison, although they conceivably might also have used species of *Phyllobates* in formerly occupied territory.

Blowgun darts tipped with plant poison are used by the Ecuadorian Cayapa Indians, southern neighbors of the Chocó (Barrett, 1925, p. 114). We recently (1975) received a report from a correspondent that the Cayapa also use a frog poison. The report was in no way substantiated, and we cannot imagine what frog might

<sup>1</sup>Such mixtures putrefy and, as can be imagined, would have varied pharmacological properties depending on the

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recipe and stage of decomposition. In the case of the extinct Amani and Patángoro Indians, who inhabited part of the central Andes of Colombia, Kirchhoff (1948, p. 345) passed on the following story from the sixteenth century: "The poison was prepared by old women, who were tired of living. The fumes of their poisonous concoction usually killed them."

supply a suitable poison for Indians living in northwestern Ecuador (*Dendrobates histrionicus* is the largest dendrobatid known from that region and it is not especially toxic), but the matter warrants investigation. It is of interest that the Cayapa were said to have contact with the "Cholos" [i.e., Emberá Chocó] of the Río Saija in Colombia (Barrett, 1925, p. 30), and so they could be expected to know of the usefulness of *Phyllobates terribilis* poison in that region.

#### METHODS OF POISONING DARTS

**RÍO SAN JUAN DRAINAGE:** So far as we have been able to determine, only the Noanamá Chocó and Emberá Chocó of western Colombia are known with certainty to have employed frogs for poisoning blowgun darts—a practice which still survives, at least among certain Emberá groups. There are several references for this practice in the Río San Juan region, in the present-day departments of Chocó and Risaralda; the most recent and authoritative accounts are those of Wassén (1935, 1957), who obtained information both from the Noanamá on the lower Río San Juan (*Phyllobates aurotaenia*) and from the Emberá on the upper part of the same river (*Phyllobates bicolor*).<sup>1</sup> By some accounts the frogs are impaled on a stick and held close to a fire while scraping darts against the animal's skin. But Wassén photographically illustrated and described an Emberá procedure in which fire is used only for drying the darts; the following observation (Wassén, 1957, pp. 85-86) was made at La Unión on the upper Río San Juan, in what is now the Department of Risaralda:

<sup>1</sup>Wassén was unable to get competent identifications from zoologists and used the misapplied name *Dendrobates tinctorius* for both species of *Phyllobates*. He was equally unable to interest pharmacologists or chemists in his sample of *P. bicolor* poison, being told in effect that it was the same as that of toads and had been well studied. One can only sympathize with Wassén's (1957, p. 88) sardonic observation that: "Whether the information [on Chinese toad poison] . . . can be automatically applied to the *Dendrobates* frogs from Colombia, I am not competent to judge." The novel structures of *Phyllobates* poison were demonstrated 11 years later (Tokuyama et al., 1968; Tokuyama, Daly and Witkop, 1969).

The forelegs of a frog [*P. bicolor*] are tied with a string and then the special stick *siurukida* is put through the mouth and body of the animal so that it comes out through one of the hind legs. Now the string from the forelegs is stretched so that the animal lies outstretched along the stick. The tips of the darts are hastily beaten against the back of the animal, while the frog is kept rotating on the stick. During the beating the yellow-red skin of the animal's back falls off and gets on to the tips of the darts. These should be dried quickly over a fire.

Wassén unknowingly substantiated an old description of dart poisoning in an area only about 50 km. south-southwest of his locality. Early in 1824, Capt. Charles Stuart Cochrane, traveling on leave from the British navy, crossed the Cordillera Occidental on an already old trail from Cartago to Las Juntas [Juntas del Tamaná on recent maps], on the upper Río Tamaná, a tributary of the Río San Juan. Although plagued by fever, he kept a detailed journal that was published in two volumes (Cochrane, 1825). Cochrane (vol. 2, p. 406) described a frog, "called *rana de veneno*, about three inches long, yellow on the back, with very large black eyes." Cochrane (p. 411) mentioned seeing the frogs "in the damp places in the wood" close above Las Juntas. From his description and the elevation (500-1000 m. from recent maps), it seems safe to identify the frogs as *Phyllobates bicolor*. It is uncertain whether Cochrane actually saw the dart-poisoning process, but his description is detailed enough and does not mention the use of fire. Cochrane (1825, vol. 2, p. 407) wrote:

Those who use this poison catch the frogs in the woods, and confine them in a hollow cane, where they regularly feed them until they want the poison, when they take one of the unfortunate reptiles, and *pass a pointed piece of wood down his throat, and out at one of his legs*. [Italics ours, compare with Wassén's description above.] This torture makes the poor frog perspire very much, especially on the back, which becomes covered with white froth: this is the most powerful poison that he yields, and in this they dip or roll the points of their arrows, which will preserve their destructive power for a year. Afterwards, below this white substance, appears a yellow oil [the dorsal pigment?], which is carefully scraped off,

and retains its deadly influence for four or six months, according to the goodness (as they say) of the frog. By this means, from one frog sufficient poison is obtained for about fifty arrows. [By "arrows," Cochrane was speaking of darts for a "blow-pipe."]

Cochrane's 1825 account seems to be the earliest description of a method of using frogs for poisoning blowgun darts. Descriptions by two later authors (Posada-Arango and Saffray) are discussed by Wassén (1957, pp. 428-431); a paper by one of these writers (Posada-Arango) also forms the basis for the frog section in Lewin's (1923, pp. 428-431) classic monograph on arrow poisons of the world. These descriptions (and also Wassén, 1935) agree that the frog is impaled on a stick before poison is obtained, but they differ from Cochrane (1825) and Wassén (1957) in claiming that the spitted frog is held near a fire. Regardless of this variation, the evidence suggests that *Phyllobates bicolor* and *P. aurotaenia* are customarily impaled, when used by Emberá and Noanamá Indians living in the Río San Juan drainage.

RÍO SAIJA DRAINAGE: The method used by

Emberá Indians in obtaining dart poison from *Phyllobates terribilis* is quite different and quite simple. The dart-poisoning process observed at Quebrada Guanguí was as follows: A number of *kokoi*<sup>1</sup> were collected in surrounding forest and confined in a plain wicker basket, with the top tied shut. When one of the Indians (Manuelito Maia) was ready to poison darts, he carried the basket and darts from the house to open ground, also taking a stick and a green plantain. He opened the basket and allowed one frog to emerge. This frog was carefully caught between two leaves and positioned on the ground, where it was temporarily kept in place with the stick held under foot (fig. 12). The point of a dart was rubbed several times along the frog's back, and the dart was then stuck, poisoned end up, into the plantain for drying. Only two or three darts were poisoned from

<sup>1</sup>The Emberá name for *Phyllobates terribilis* and also for the sympatric *Dendrobates histrionicus*, the latter being recognized as poisonous but not dangerous to handle. "Kokoi" is also the Noanamá and Emberá name for the more northern *Phyllobates aurotaenia*. At Quebrada Guanguí, the name is pronounced something like *co-coin*.



FIG. 12. Emberá Indian poisoning blowgun darts with skin secretions of *Phyllobates terribilis*, new species. Left: Frog (circled) is restrained by stick held under foot of man, who is careful to avoid skin contact (see p. 340); wicker basket contains supply of frogs. Plantain holds cluster of darts while poisoned tips dry in air; dart quiver also shown. Right: Tip of dart being drawn along back of live frog.

each of the frogs, which rapidly weakened in the sun. Some of the frogs expired, the others were allowed to hop away.

**COMPARISONS:** The two different methods of poisoning darts seem to reflect mainly on the relative toxicity and abundance of the frogs used. Since the art of making blowguns survives among the southern Emberá, there is no reason to suppose that they have merely forgotten about the simple method of using the special impaling stick, or *siurukida* ("bamboo tooth"), northern examples of which are figured in Wassén (1957, p. 84). *Phyllobates terribilis* simply does not need to be so cruelly stressed, so copious are the toxins in its skin secretions. Impaling specimens of *P. aurotaenia* or *P. bicolor* on a *siurukida*, with or without fire, is perhaps necessary in order to induce maximum secretion of poison from these less toxic species.

In addition to being relatively less toxic than *Phyllobates terribilis*, the more northern *P. aurotaenia* and *P. bicolor* are also smaller frogs that are harder to come by. *Phyllobates aurotaenia* is more secretive than *terribilis* and is harder to find even in places where it occurs in dense populations. *Phyllobates bicolor* is not secretive, but it appears to have a spotty distribution and may occur in sparser populations than *terribilis*. Wassén (1957, p. 86) observed 20 darts being poisoned from one specimen of *P. bicolor*, and was informed that "one animal very well could be enough for about 30 darts." Cochrane (1825) and Posada-Arango (1909 and earlier papers) independently claimed that 50 darts could be poisoned from a single specimen of *bicolor*. Therefore it might seem strange that only 2 or 3 darts were poisoned from single specimens of the more toxic *P. terribilis*. We conclude that the southern Emberá simply do not feel the need to be miserly with this resource, which is so easily come by.

#### A DECLINING CUSTOM

There are no statistics on use of the blowgun, but its distribution is somewhat less than that of the Chocó themselves. The historic range of the Chocó has been far from static: They are a riverine forest people living today in isolated family-group settlements in the Pacific

drainage of eastern Panama and western Colombia,<sup>1</sup> and also in the Caribbean lowlands of Colombia—on the upper Río Atrato drainage, and in the upper Río Sinú and adjacent areas at the northern base of the Andes.<sup>2</sup> At least the northernmost parts of this region were seemingly occupied within historic times, as the Emberá Chocó moved into areas vacated by the Cuna, Oromira, and Catío. Most of the areas presently occupied by the Emberá and Noanamá (or Waunana) Chocó, and the fragmented nature of their geographic range, are shown in an admirable map by West (1957, map 16), which however lacks present-day Emberá settlements in the Río Tuirá and lower Río Chucunaque drainages of eastern Panama.

In the interval since Wassén's 1935 report, blowguns have virtually disappeared among the Noanamá Chocó (Reichel-Dolmatoff, 1960; personal observ., 1968-1972). Among the Emberá Chocó, the blowgun appears not to be used in eastern Panama (see p. 341), where frogs of the genus *Phyllobates* do not occur,<sup>3</sup> but, according to Silverstone (1976, p. 23), neither are blowguns used in the nearby Serranía de Baudó region of Colombia, where *Phyllobates aurotaenia* does occur. In any case, blowgun use is not dependent on the presence of poison-dart frogs, because the Chocó also have *pa-*

<sup>1</sup>Although generally applicable, the term "riverine" does not accurately describe all the Emberá Chocó in the unnavigable headwater region of the upper Río San Juan, where Indians are found living on mountainsides high above the major streams (possibly a cultural retreat from other settlers who covet the valley floors). The Indians of this region are sometimes called "Chamf"; they speak a dialect of the Emberá tongue (Loewen, 1960).

<sup>2</sup>The Indians in the upper Sinú country are called "Catío" in much of the literature. Gorden (1957) noted that they call themselves "Emberá" and do not much differ from more western groups of Emberá (see also Reichel-Dolmatoff, 1963). The name Catío (or Katío) has also been applied to several dialects of the Emberá Chocó language (Loewen, 1960, pp. 14-15). The Catío appear to be extinct. Gorden (*op. cit.*, p. 53) suggested that Catío culture "may belong with Zenú and Cueva, but there is no indication that it was related to Chocó."

<sup>3</sup>There seems a possibility that the range of *Phyllobates aurotaenia* might barely extend into Panama along the western foot of the Serranía del Sapo, but this would be insignificant to the present discussion.

*kurú-neará* (Emberá), or *kierátchi* (Noanamá)—two names for a potent plant poison (*not curare*) obtained from a tree sap and said to contain a glycoside with cardiac effects (Santesson, 1931; Mezey et al., 1948). *Pakurú* dart poison is widely known in western Colombia, having been (or still being) used for example in the Río Saija drainage, in the lower Río San Juan drainage, and farther north on the Pacific coast opposite the Serranía de Baudó (Wassén, 1935; Reichel-Dolmatoff, 1960), and also far to the northeast in the Sinú region (Gorden, 1957; Reichel-Dolmatoff, 1963), although it is not certain whether the botanical source is the same in each region. However, Emberá on the headwaters of the Río San Juan are ignorant of plant poison, using only frogs (Wassén, 1957; personal observ., 1977), nor did Cochrane (1825) mention plant poison in an area some 50 km. southward in the same mountain system. Possibly, the trees from which poison is obtained do not grow in the lower montane areas where *Phyllobates bicolor* occurs, but written knowledge about these things seems exceedingly scant.<sup>1</sup> Where both plant and frog poisons are employed, there are no data on their relative usefulness, except that *pakurú* poison is reported from widely separated regions to be ineffective against chickens and jungle fowl such as curassow and guan (Wassén, 1935; Gorden, 1957). Wassén's (1935, pp. 94-95) Noanamá informant said that the addition of

frog poison rendered *kierátchi* (*pakurú*) poison effective against fowls. Wassén's report is the only information available to us that frog poison [from *Phyllobates aurotaenia*] was sometimes mixed with that of a plant. Frog poison is reputedly, and believably, effective against a wide variety of animals, including such large forms as jaguar, bear, deer, and man (Cochrane, 1825, vol. 2, p. 406; Greiff, 1827; Saffray, 1873, pp. 98-99; this paper, p. 362).

To summarize, it appears that, (1) either plant poison *or* frog poison may be known and employed in a given region, as in the Sinú and upper San Juan regions, respectively, or (2) both plant *and* frog poisons are used in the same area, occasionally in combination, or (3) the blowgun and poisoned darts have been abandoned, as in Panama. But each case is based on meager information.

Abandonment of the blowgun might simply be due to the absence (or lack of knowledge) of a suitable poison source, as might be the case in Panama, or it could be due to increased accessibility of firearms, as is certainly the case in Panama and probably in parts of Colombia. Because of the politically turbulent history south of Panama, modern weapons have been little available to the Chocó, although old-fashioned muzzle-loading shotguns are in use from the Sinú country to the Río Saija (Gorden, 1957; West, 1957; Isacson, 1976; personal observ.). The general scarcity of firearms, in the Pacific lowlands, is reflected in the fact that occasional Negro hunters have adopted the Chocó blowgun (Lafond, 1839; West, 1957; personal observ., 1971). Where conveniences such as guns are not readily available, the Chocó can maintain their superficial appearance of primitiveness with relatively few modern accouterments. Working in the Sinú country in the 1950s, Gorden (1957, p. 22) observed that there had been, "virtually no replacement of the aboriginal hunting instrument, the blowgun." In contrast, in the early 1970s, a family group in the upper Atrato drainage did not even own a blowgun, doing 78 percent of their hunting with a muzzle-loading shotgun (Isacson, 1976, p. 39). Change may come slowly in such back country as the Sinú and Saija, but, starting with the introduction of plantains, it has

<sup>1</sup>Perez (1863, p. 95) implied that both plant and frog poison were used by Chocó Indians in the Department of Antioquia. The frog, "una rana pequeña i amarilla," was probably *Phyllobates bicolor*, most likely from the border region between the departments of Antioquia and Chocó (then part of the State of Cauca). But Anzá, one of two localities given for the plant poison, is situated on the inter-Andean Río Cauca, outside the range of *P. bicolor*; the other locality, Quinua, is not listed in a recent gazetteer (Colombia, Inst. Geogr., 1971).

A similarly vague account, published by Greiff in 1827 and translated by Wassén (1934, p. 618), related that, "the bears living in the hills were shot by the Indians with blowguns and arrows smeared with a vegetable poison as well as with the poison of a frog. The preparation of both kinds of poison was a secret. Their effects were instantaneous." This may have been the source of some of Perez's information (*supra cit.*), since that author also mentioned bears and cited Greiff on another matter.

been coming inexorably for centuries. Even the fabrication process of the primitive blowgun has obviously been somewhat simplified by the post-Conquest adoption of machetes and other

metal tools. We take this opportunity to record a modern method of making a Chocó blowgun, quiver and darts.

## BLOWGUN AND DART FABRICATION

The fabrication process was observed and filmed in late October and early November 1971, in a small settlement of Emberá Chocó (fig. 13). The site is on the banks of Quebrada Guanguí, about half a kilometer above its junction with the Río Patia, in the upper Río Saija drainage, Pacific lowlands in the Department of Cauca (fig. 4). Although the Emberá often live in isolated houses, the Quebrada Guanguí settlement consisted of five houses on one bank and another on the opposite bank.

The making of a blowgun tends to be a lengthy affair, usually taking weeks or months for completion. However, a young head of a family, Manuelito Maia (nicknamed "Cocha-Cocha" by his friends), was persuaded to craft a blowgun, quiver and darts, with as few interruptions as possible. The entire task was thus completed in 12 days. Manuelito did his job carefully, and the finished work did not appear inferior to earlier made products that were available for examination. The blowgun and other objects described below are now in the collection of the Museum für Völkerkunde, Basel, Switzerland. A few supplementary materials are in the possession of the senior author at the American Museum of Natural History. A movie film of the fabrication process has been produced (Malkin, 1974).

**THE BLOWGUN:** The Chocó blowgun is always made of palm wood, and Manuelito's first task was to find a suitable palm. He followed a trail for a kilometer through the rain forest (fig. 5) before beginning his search. An appropriate palm was found a few hundred meters from the trail (fig. 14). On the basis of figure 14, which shows what appear to be slender flowering axes emerging from the inflorescence, Dr. Harold E. Moore, Jr., identified the tree as an iriarteoid palm, probably *Catoblastus inaequalis* (Cook and Doyle) Burret. This palm was judged to be between 15 and 18 meters high and roughly 25 centimeters in diameter.

The area about the palm was cleared of undergrowth and lianas and the tree felled with an ax. A straight section about 3 m. long was chopped from the rest of the trunk (fig. 14). This section was then split and quartered by ax (fig. 15). The two best sections were selected and the red inner core removed from the hard,



FIG. 13. Emberá Chocó at Quebrada Guanguí (February, 1973). Chocó houses are typically placed on piles and entered by means of a notched-log ladder. Walls are lacking, although a pole or board fence may be erected, possibly for restraining small children. Size, floor plan, and roof structure vary considerably (e.g., see Isacson, 1976, pp. 26-27).



FIG. 14. *Top*: Forest palm (probably *Catoblastus inaequalis*) to be used for making blowgun. *Bottom*: Chopping off a straight section of the felled trunk.





FIG. 15. *Left*: The palm trunk is split into halves and then quarter sections. *Right*: While still in the forest, the best two sections are further trimmed with machete.

blackish peripheral wood, which was further trimmed by machete into straight boards ready to be carried home (fig. 16). All the rest of the work was done near Manuelito's house.

The two boards—the future halves of the

blowgun shaft—were carefully thinned and tapered with a machete (fig. 17) and a small, modern plane. Next, a center groove had to be made along one side of each section. A black vegetable dye (fig. 18) was used to color a



FIG. 16. Two palm boards are ready to take home. These will become the longitudinal half-sections of a single blowgun.

length of cotton string, which was used like a chalkline to mark the course of each groove (fig. 19). A small chisel was used to cut out the grooves (fig. 20). This was tedious work requiring great care, because each groove must be a mate of the other. After carving out the

grooves, Manuelito returned to planing and carving the opposite sides of the tapered half-shafts, rounding these until each was a virtually perfect semicircle in cross section. This work required a week before the two sections were equally matched. The center grooves were



FIG. 17. One half-section is further trimmed and shaped at home.



FIG. 18. Black vegetable dye mixed in broken gourd.



FIG. 19. Straight line for the central groove is marked on each half-section of the future blowgun shaft, using a string coated with black vegetable dye.



FIG. 20. Chiseling out the central groove (left), and smoothing it with a small metal implement (right).



smoothed with a small, conveniently shaped piece of scrap iron (fig. 20), and both sides of each section were further polished by hard rubbing in wet sand at the edge of the river (fig. 21).

The next procedure was to glue together and tie the two longitudinal half-sections of the shaft. A locally obtained tree resin (the same as used for caulking and repairing dugout canoes) was heated over a small kerosene lamp and rubbed onto the edges, which were then carefully joined (fig. 22). After gluing, the blowgun was tied at intervals with plant fiber (fig. 23). The weapon was now ready to be wrapped with bast, which was done while the blowgun was suspended horizontally on fiber ropes (fig. 24).

The bast was made from strips of bark, of which Manuelito already had a supply in his house, although there was considerable discussion with friends as to whether the supply was adequate. The bark strips were soaked in water

for a day in order to make them more pliable and to prevent cracking. The bark was afterward scraped thin and smooth with a machete, and cut lengthwise with a knife into strips of about a centimeter or less in width. This bast was wrapped around the blowgun as a protective covering (fig. 24), starting at the tip of the muzzle end and completely covering a sight positioned about a centimeter from the muzzle. (This particular sight [see p. 360] was a separately carved oblong of wood, about 4 cm. long by 1 cm. high, affixed over the seam formed by the glued edges of the blowgun.) The first turn of bast was spot-glued in place and the free end so looped as to prevent slipping. The weapon was then wrapped toward its butt end with overlapping turns. At the end of one bast strip, another was started by bending an end under the earlier wrapping in such a way that subsequent winding would bind the previous end. Many strips were thus wound around in sequence to provide a uniform wrap-



FIG. 21. Polishing half of blowgun shaft against wet sand.



FIG. 22. *Left:* Applying heated resin to edges of blowgun section. *Right:* Fitting the two sections together.





FIG. 23. The two sections, after being glued together, are tied at intervals with slender fiber.



FIG. 24. Wrapping the blowgun with bast. (Method of suspending blowgun horizontally in string loops during this process is probably typical, having also been observed [1977] near Santa Cecilia on upper Río San Juan, Dept. Chocó.)

ping. The wrapping was continued to the very end of the gun, where the loose end of the last strip was tightly circled back under one of the final coils (fig. 25). The blowgun was then complete save for its several accessories.

**THE RAMROD:** A cleaning rod was carved and rounded from the same kind of hard palm wood used for making the blowgun. After the required diameter was attained, the rod was cut to match the length of the blowgun. The cleaning rod is left at home and not carried when hunting.

**THE QUIVER AND DARTS:** A dart quiver, 25 cm. by 7.5 cm., was made from a section of heavy bamboo (fig. 26). A suitable length of bamboo was cut off just below the node, the

septum of which forms the base. A bamboo cap was fitted by chiseling away peripheral wood around the top of the quiver. A shoulder strap of fiber was added, and two hard fruit shells were also tied on. The fruit shells were hollowed out with a knife and stuffed with a fluffy, cotton-like plant fiber (*Bombacaceae*) to be used as wadding on the darts, as described below.

Darts were made quickly from the woody stem (not the petioles) of a palm (fig. 27, probably *Bactris* sp., *vide* Dr. Harold E. Moore, Jr.); only the hard, blackish outer wood was used. The darts, 21 or 23 cm. long, were split from a section of the stem and then smoothed with a knife (fig. 27). One end of



FIG. 25. Method of binding the mouth end. (On many Chocó blowguns, the bast wrapping terminates several centimeters from the basal end, which is left bare. The Chocó do not add a separate mouthpiece.)

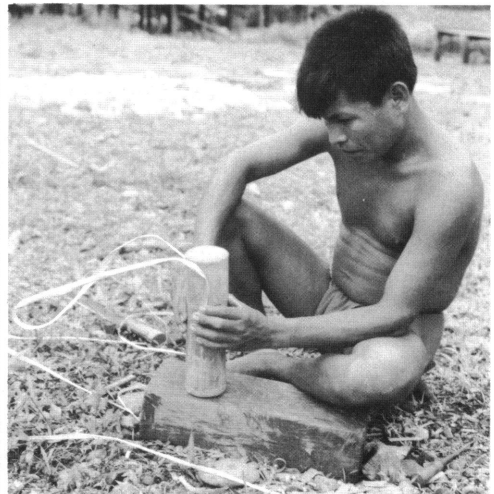


FIG. 26. *Top row*: Making the bamboo quiver. *Middle*: Making a cap for the quiver, and attaching carrying strap. *Bottom row*: Fruit shells are hollowed out and attached to the quiver, as containers for a fluffy plant fiber (*Bombacaceae*) used as wadding on the darts; see fig. 28.

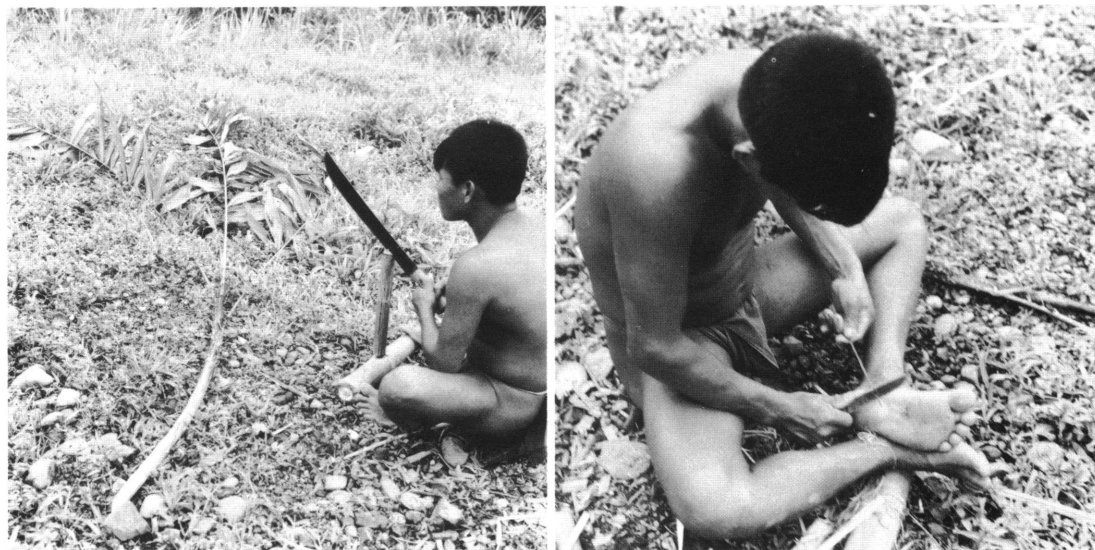


FIG. 27. Making the darts from the woody stem of a palm (probably *Bactris* sp.).

each dart was inscribed with fine spiral grooves for a distance extending about 2 or 3 cm. from the pointed tip. These grooves are characteristic of Chocó blowgun darts<sup>1</sup> and are intended to hold poison; they are too shallow to serve as breaking points, so a deeply cut break point is usually added just above the poison grooves, as illustrated in Wassén (1957, p. 81, fig. 5a). The darts were then ready for poisoning as described in an earlier section and shown in figure 12.

The plant-fiber wadding (fig. 28) is added last. This was tied around the basal end of the dart with a fine, threadlike fiber, as shown in Wassén's (*loc. cit.*) figures of darts from the upper Río San Juan.

#### COMPARISONS

Yde (1948) recognized four types of South American blowguns, based on features of their

<sup>1</sup>At least on the Pacific versant of Colombia, where darts resemble those described a century and a half ago by Cochrane (1825, vol. 2, p. 406): "The arrows are about eight inches long, formed of a fine-grained wood; the point very sharp, and cut like a corkscrew for an inch up, showing a very fine thread, that composes the spiral screw; this is rolled in the poison, which is permitted to dry on it." Cochrane did not mention the deeper break point, but

construction. The Chocó blowgun is of Yde's type IV—"two halves of a split palm stem, glued together and wound with bark strips or bast strings . . . two semicircular components [in cross section]." Yde showed that type-IV blowguns have their widest area of use in the upper Amazonian basin, but he cited an incorrect source to the effect that the weapon is rarely used by the Chocó (p. 289), "being only common with the Noanamá on the Río Dordó." Although on the decline (and virtually abandoned by the Noanamá), as already discussed, blowguns are still in widespread albeit spotty use by the Emberá Chocó.

There appears to be considerable variation in the fabrication of type-IV blowguns, both within and between tribes. The Jívaro, for example, hollow out the bore in a way entirely different from that described above: Using a bone awl and an animal tooth, grooves are carved in each of the two sections of shaft, which are then tied around a ramrod of slightly larger diameter; sand and water are poured into

this is sometimes omitted, perhaps dependent on the game to be hunted. Gorden (1957, p. 22) stated that a break point is made on Chocó darts in the Sinú country at the northern base of the Andes, but he did not mention the spiral poison grooves.



the bore while the rod is worked back and forth, until the bore is ground smooth and enlarged to the diameter of the ramrod (Stirling, 1938, p. 81). The Yagua, another Amazonian tribe, similarly round out a *square* hole in the tied shaft, using fine sand and a flexible ramrod (Fejos, 1943, pp. 48-49, pl. 36). The Cofán, of Amazonian Colombia, have recently been observed to make the bore of the blowgun in a manner very similar to that of the Chocó—using dyed string for marking the course of grooves on each half-shaft, and then metal implements for carving and smoothing the grooves *before* the two sections are joined (Malkin, 1975). Thus, there are essentially two different ways of making the bore in type-IV blowguns. Both methods probably predate the Conquest. Present-day use of metal tools by the Chocó and Cofán, for carving grooves in the separate half-shafts, would be a simple improvement over the use of such implements as mammal teeth, which were said to have been used for this purpose by the Pasé Indians in upper Amazonian Brazil (Bates, 1863, p. 236).

Most manufacturers of type-IV blowguns, including the aforementioned Jívaro, Yagua, Cofán, and Pasé tribes, attach a separate mouthpiece to the weapon. This appears never to be done by the Chocó, although their southern neighbors, the Cayapa of northwestern Ecuador, do attach a funnel-shaped mouthpiece (Barrett, 1925, p. 113). The Chocó blowguns seem primitive in this respect. The mouth end varies only in being either completely wrapped with bast or else left bare, the former type being shown in figure 25 and both types being illustrated in Wassén (1935, p. 91).

Type-IV blowguns are also commonly waterproofed with a covering of resin, rubber latex, or beeswax, as described in references already given for the Jívaro, Yagua, Cofán, Cayapa, and Pasé tribes. We have not noticed this refinement on any Chocó blowgun, and find no reference to it except that of Cochrane (1825, vol. 2, p. 405), who described a blowgun from the upper Río San Juan drainage (see p. 342) as being, "covered with a coat of milk from the *caucho*-tree; which, dried, prevents any air from entering, and appears of a dark-brown colour." It seems curious that such a custom would be lost or, if still known, not

extensively practiced, since the Chocóan rain forest is one of the wettest on earth.

Perhaps the greatest variation among Chocó blowguns involves the sight(s). Wassén (1957, fig. 7) illustrated blowguns that have sights near the butt, as well as the usual muzzle sights. The latter may involve a separate wooden piece, as described herein, or may be carved into the shaft itself, as figured for Río San Juan blowguns by Wassén (1935, fig. 26C; 1957, fig. 7B). Wassén's illustrations also show how the sight may either be covered over with the bast wrapping or left exposed, and how the sight may be placed near the very tip of the muzzle or positioned farther back. Wassén (1957, p. 82) mentioned one case in which a rodent's tooth was used as a sight, being "fastened on the blowgun with a lump of black material." Similarly, a blowgun from Quebrada Guanguí, now in the American Museum, has a piece of carved, red *plastic* that is affixed with resin 7 cm. from the muzzle.

There also is some variation in the quiver, which is left undecorated by the Chocó. Along the Pacific side of Colombia, the entire quiver is made of bamboo as shown in figure 26. But Emberá and Noanamá quivers from the Río San Juan seem to average somewhat slimmer and to have the top edge of the cap rounded, in contrast to Quebrada Guanguí (Saija drainage) quivers, which are thicker and have a sharp edge around the top of the cap; these differences can be visualized by comparing sketches A and B in Wassén (1935, p. 91). The Emberá Chocó in the Sinú region make the cap of the quiver from anteater skin rather than bamboo (Gordon, 1957, p. 22). A variety of fruit shells or small gourds are used to hold the fiber wadding for the darts, and Wassén (1957, p. 83) obtained one little rubber-coated bag that was used for the same purpose.

Stirling (1938, p. 83) said that the Jívaros make "short" blowguns of about 10 ft. (3 m.) and longer ones up to 15 ft. in length (4.5 m.). Chocó blowguns are normally shorter. Gordon (1957, p. 22) said that they are about 9-11 ft. long (2.7-3.3 m.) in the Sinú region, but along the Pacific versant of Colombia they seem to average about 2.5 m. in length.

In South America, blowguns with poisoned darts are primarily weapons of the hunt. They



FIG. 28. Loading the blowgun with a frog-poisoned dart. "Round the thicker end is wound fine cotton, in the natural state, until it will just easily enter the tube, which is applied to the mouth, and aim being taken with the eye, the arrow is blown out . . . certain death to man or animal wounded by it; no cure as yet having been discovered." (Cochrane's *Travels in Colombia*, 1825, vol. 2, p. 406.)

generally appear not to have been used in warfare, which, according to Yde's (1948) thesis, is why blowguns were so seldom mentioned in the earliest Spanish chronicles.<sup>1</sup> Stirling (1938, p. 85) was emphatic that the blowgun is never used in Jívaro warfare: "The Jivaros say that it was given them for the purpose of obtaining game. To use it against man would bring bad luck." Fejos (1943, p. 84) similarly reported that the Yagua believe their dart poison would

<sup>1</sup>Some authors had taken the lack of early records as indication of a post-Columbian introduction. Stirling (1938, p. 80), for example, thought it probable that, "the use of the blowgun and its equipment was brought into South America by southeastern Asiatics, possibly from the Philippines, who were carried across the Pacific on one or more of the many Spanish galleons which followed this route in the sixteenth century."

lose its power to kill game if used against man.<sup>2</sup> Stirling (*op. cit.*, p. 83) also noted that rigid dietary taboos must be observed during

<sup>2</sup>The Yagua also poison hunting spears with curare, but nonpoisoned spears are their only weapon of war (Fejos, *op. cit.*). The use of poisoned weapons in warfare has been often exaggerated even for groups in which the practice is documented. For example, although the fierce tribes of the Guayanan region are infamous for having tipped war arrows with plant poisons and even stingray spines, Roth (1924, pp. 155-156) noted that, "It is matter for surprise that the Guiana Indians did not make far more frequent use than they apparently did of the curare when engaged in fighting their enemies." It seems likely that many curares, which vary greatly in composition, simply were not sufficiently toxic to be effective in warfare. Indians are keenly aware of the strength of their hunting poisons. Cofán informants on the Río Putumayo, Colombia, recently (1970)



the manufacture of a Jívaro blowgun, and that the maker must be sexually continent.

The Chocó appear to observe no particular ceremony, either during blowgun fabrication or poisoning of the darts. And they are perhaps among the exceptions in having had no particular strictures against turning the weapon on man. The now peaceful Chocó fiercely resisted Spanish domination for more than a century, starting in the late 1500s in the upper Río San Juan drainage (West, 1957, p. 90), where it seems likely that blowguns with frog-poisoned darts would at least have been used in occasional ambush if not open warfare. A Chocó Indian at Playa de Oro, Río San Juan, was recently detained on suspicion of murder by frog-poisoned dart, and another Indian claimed that a man shot with such a dart could run but a few hundred meters before dropping dead.<sup>1</sup> Whatever the facts, the mental attitude is suggestive of a forgotten history. To this very day, out of a time as hazy as the mist that sweeps the western *cordillera*, it seems that frog-poisoned darts have been thought capable of bringing, in the words of Cochrane (1825), "certain death to man."

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confessed that their curare—obtained from the neighboring Siona—was not strong enough to stop tapir, jaguar, or man, although it was visibly effective on two peccaries.

<sup>1</sup>Personal communication from Drs. Eva Bartels de Bernal and Rosalina Cadenas Carrera, based on their inter-

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views with Indians and a government investigator at Playa de Oro, Department of Chocó, August 1977.

<sup>2</sup>Now the *Museo Departamental de Ciencias Naturales* "F. Carlos Lehmann Valencia," under the present directorship of Dr. Reinaldo Díaz.

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