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On the Type Specimens of Two Colombian Poison Frogs Described by A. A. Berthold (1845), and Their Bearing on the Locality "Provinz Popayan"

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ABSTRACT

The herpetological writings of the physician-zoologist Arnold Adolph Berthold (1803–1861) are reviewed. Berthold (1845) named two dendrobatid frogs and four lizards and snakes collected by a Mr. Degenhardt in Neu Granada, which Berthold later (1846a; "1847" [1846?]) clarified to "Provinz Popayan, etwa 2° N. B. und 301° L." Berthold (1859) later named another snake that was probably from the same collection.

Berthold's locality has been "restricted" by authors to the city of Popayán. However, knowledge of geographic ranges in conjunction with geographic variation in the two frogs demonstrates that Provinz Popayan must be construed in the broader sense of the old colonial Province of Popayán, which included nearly all of what is now western Colombia.

Seven of eight original syntypes of *Dendrobates histrionicus* Berthold (1845) survive in the collection transferred from the Zoological Museum of the University of Göttingen to the Alexander Koenig Zoological Research Institute and Museum at Bonn. A lectotype is designated. Color patterns and small body size show that the type series represents at least three local demes in the upper Río San Juan drainage. The prevalent color pattern, including that of the lectotype, is consistent with the Santa Cecilia regional population of *D. histrionicus*, in the upper Río San Juan drainage of the present-day Department of Risaralda.

Six of seven original syntypes survive for *Phyllobates melanorrhinus* Berthold (1845); a lectotype is designated. Among known species of true poison-dart frogs, *Phyllobates melanorrhinus* is similar only to *P. bicolor* Bibron, 1840, and *P. terribilis* Myers, Daly, and Malkin, 1978. Aspects of color pattern and statistical comparisons of body sizes and proportions show that *P. melan-*

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orrhinus should be continued in the synonymy of *P. bicolor*.

It is pointed out that species of *Phyllobates* always seem to occur in sympatry with a more conspicuous and more easily collected member of the *Dendrobates histrionicus* species group. The type series of *Phyllobates melanorrhinus* (= *P. bicolor*) probably was collected in sympatry with some part(s) of the type series of *Dendrobates histrionicus*, in the upper drainage of the Río San Juan.

Type localities of two lizards and three snakes named by Berthold can only be clarified as "western Colombia, probably on the Pacific versant," where all are known to occur. These species are *Anolis latifrons* Berthold, 1845, *Polychrus gutturosus* Berthold, 1845, *Bothrops schlegelii* (Berthold, 1845), *Stenorrhina degenhardtii* (Berthold, 1845), and *Urotheca lateristriga* (Berthold, 1859).

INTRODUCTION

In 1977, the Alexander Koenig Zoological Research Institute and Museum at Bonn took possession of the herpetological collection of the Zoological Museum of the University of Göttingen. The transfer occurred because the Göttingen Museum had to realize other priorities and could no longer maintain taxonomic collections solely for their historical value (Böhme and Bischoff 1984: 159). The Göttingen Museum was founded in 1773 as a department of the Royal[3] Academic Museum. The Museum received its own building in 1793 and developed as a significant herpetological center through the first half of the 19th century.

Johann Friedrich Blumenbach (1752–1840) was the first curator of the zoological holdings of the Göttingen Museum. His work as a systematist included the generic name *Marmota* for marmots and the species name for the African elephant, *Loxodonta africana* (Blumenbach). But in herpetology he named only the North American colubrid snake *Cemophora coccinea*, the type specimen of which has not been traced. Blumenbach authored the first basic treatise of comparative anatomy and was the academic teacher of several famous zoologists, including Prince Maximilian zu Wied-Neuwied (1782–1867) and A. A. Berthold.

Arnold Adolph Berthold (1803–1861) entered the museum as Blumenbach's successor in 1840. His curatorship of the zoological collections, however, was not his main professional obligation. As he had become extraordinary (1835) and ordinary professor of medicine (1836), he was absorbed by both practice and teaching in this field. Rush (1929) and Klein (1970) summarized some aspects of Berthold's rich and varied scientific career. His published scientific work covered an enormous range of subjects quite apart from herpetology. As summarized by Klein (1970: 72),

> [He published in 1829 the textbook] *Lehrbuch der Physiologie des Menschen und der Thiere*, which was reissued many times. His monographs, articles, and notes were published in medical, scientific, and even literary periodicals. A piece of research done with Bunsen . . . led to the discovery of hydrated iron oxide as an antidote for arsenic poisoning. Some of his other works dealt with myopia, the length of pregnancy, male hermaphroditism, and the formation of fingernails and hair. His short work commemorating Goethe's centennial in 1849 was one of the first German publications to do justice to Goethe as a naturalist.

Berthold nowadays is considered a founder of the field of endocrinology, owing to a short 1849 article on the effects of transplantation of testes in domestic fowl. A marginal herpetological paper of this time (Berthold, 1849), which experimentally evaluated older reports of amphibians and reptiles living inside human beings (e.g., after being accidentally swallowed), is of historical interest; Berthold's experiments dealt mainly with the ability of amphibians to survive in water heated to human body temperature.

Berthold's taxonomic interests are less well known although they developed early. He was only 24 when he published a 600 page translation of Latreille's *Familles naturelles du Règne Animal* (see Vanzolini, 1977: 39). He was in his late 30's when he started publishing in systematic herpetology. We are unaware of a published bibliography of Berthold's work, but, to our knowledge, he published about a dozen papers relevant

[3] "Royal" refers to the former Kingdom of Hannover.

to living amphibians and reptiles in 1840–1859 (see References, which include abstracts and separates). We cite below all the herpetological titles known to us, but there may be others.

Berthold's herpetological work includes the descriptions of 26 new species,[4] including four amphibians and 22 reptiles. Less than half of Berthold's species are considered valid today. All material forming the basis of his descriptions was deposited in his own institution—the Zoological Museum of the University of Göttingen.

Berthold's first herpetological paper (1840a, 1840b), published the same year that he became curator of the zoological collections, contains descriptions of new species of lizards and snakes, and taxonomic commentary on various named genera and species. This paper is actually a synopsis of a more useful, longer paper that was published both as a separate (1842) and as a regular journal article ("1843" [1842?])—but the new names date from the synopsis, which gives Latin diagnoses for the new taxa.

We are especially concerned here with additional new species that were named several years later under the title *Ueber verschiedene neue oder seltene Reptilien aus Neu-Granada und Crustaceen aus China* (Berthold, 1845). This paper—another synopsis—included Latin diagnoses (and additional text in German) that established the names of four crustaceans from China, and two frogs, two lizards, and two snakes from New Granada (Colombia). Berthold also listed and commented on specimens of additional, previously known taxa, including five crustaceans, one toad, five lizards, and 12 snakes. Many authors, starting with Troschel (1846, 1847), have ignored or have been unaware of this synopsis and have attributed Berthold's 1845 names to an illustrated 1846 or 1847 publication (see following).

Two subsequent papers have the same title as the foregoing 1845 synopsis. These longer papers give expanded descriptions and illustrations of all the new taxa. One published in the *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen* may have appeared in 1846 if the journal were issued in parts, but we can date it only as "1847" [1846?], after the title page of volume 3 for 1845–1847. Of more interest is a rare preprint or possibly reprint of the foregoing, which is dated 1846 and which has the plates hand-colored (Berthold, 1846a). These three citations (Berthold, 1845, 1846a, and "1847" [1846?]) are the ones most relevant to the descriptions of Berthold's two dendrobatid frogs—*Phyllobates melanorrhinus* and *Dendrobates histrionicus*—which are the subjects of the present study (fig. 1).

Berthold (1846b, 1846c) also published a catalog of the herpetological holdings of the Göttingen Museum that repeated the original Latin diagnoses of all taxa that he had previously described—including the aforesaid dendrobatids. Another paper of that year (Berthold, 1846d) contained his description of the salamander *Triton ophryticus* (= *Triturus vittatus ophryticus*), from a collection made by Moritz Wagner in Transcaucasia. Berthold identified and later reported on the entire collection from Wagner's expedition (Berthold, 1850a; Wagner, 1850). In the same year, he published on a specimen of the West African tortoise *Kinixys homeana* (Berthold, 1850b, 1850c).

Berthold's last paper containing herpetological descriptions appeared in September 1859 and consisted, except for the German title, only of the Latin diagnoses of a new genus and new species, among them another snake from "Nova-Granada."[5] Unfortunately, Berthold's 1859 paper was a synopsis (in the *Nachrichten*) that was not followed by an

[4] Böhme and Bischoff (1984) listed 27 Berthold species, but one of these attributions is based on Peters and Orejas-Miranda (1970: 80), who, in the synonymy of *Dendrophidion dendrophis* (Schlegel, 1837), inexplicably listed "1847 *Herpetodryas aestivus* Berthold ... Type-locality: Provincia Popayan, Colombia."

But Berthold (1845: 41; 1846a: 11; 1846b: 143; "1847" [1846?]) did not claim *H. aestivus* as a name for a new species but used it following Schlegel's *Essai sur la physionomie des serpens* (1837, 2: 186; pl. 7, figs. 12–13). See Peters and Orejas-Miranda (op. cit.: 241) for relevant commentary on the name *Herpetodryas aestivus* Schlegel.

[5] The snake is *Liophis lateristriga*, now in the genus *Urotheca*. The type(s), now lost, may originally have been cataloged as juvenile *Liophis merremii* from Popayán according to Böhme and Bischoff (1984: 171).

All the snake species listed in Berthold (1845, 1846a)

expanded, illustrated version in the *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen*, although the synopsis was mentioned as a meeting title in volume 8 (1860, page xi) of the *Abhandlungen*.

Berthold died not long after, in February 1861, a few weeks short of his 58th birthday.

Wilhelm M. Keferstein (1835–1870) was Berthold's successor at the museum. Keferstein worked mainly on anurans of Costa Rica and Australia and described a number of new species, thus increasing the number of type specimens in the Göttingen collection. Keferstein (1867) also tinkered with the two dendrobatid names proposed by his predecessor, emending one name and placing the other in synonymy. The active phase of a research collection ended with Keferstein's death at age 35. But under the following responsibility of Prof. Ernst Ehlers (1835–1925), Director of the Zoological Institute and Museum, at least a certain order was maintained and the collection continued to grow. The eminent herpetologists George Albert Boulenger, Giorgio Jan, and Franz Werner also published on material from Göttingen and left the collection with new types (see Böhme and Bischoff, 1984).

Collection-related research activities ended at the Göttingen Museum circa 1920 and new institutional priorities led to a decline in collection maintenance. The old catalog, fortunately still extant, contains entries made in the 1920s and early 1930s that specimens were found dried out and consequently discarded! The junior author first visited the Zoological Museum in Göttingen in 1976 and, on seeing the terrible state of the herpetological collection, inititated negotiations to transfer the remaining specimens to the Museum Alexander Koenig, Bonn. As two different German federal states were involved, the responsible ministry in Hanno-

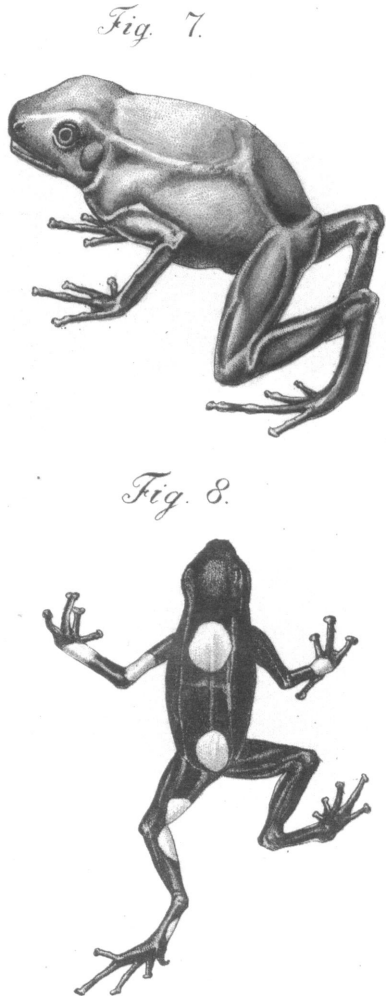

Fig. 1. First illustrations of *Phyllobates melanorrhinus* (upper) and *Dendrobates histrionicus* (lower), reproduced same size from Berthold (1846a, pl. 1, figs. 7, 8).

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except for "*Coronella Merremii*, Schleg." ("3 junge Exemplare") are also listed with Popayán specimens in Berthold's (1846b) catalog of the Göttingen collection. The published catalog (page 141) indicates only Brazilian specimens of *Coronella Merremii*, but it lists *Coronella reginae* with specimens from Popayán (the first such reference). The *merremii/reginae* determinations presumably involve a reidentification of the same specimens.

Thus, the description of *Liophis lateristriga* likely was based on material earlier misidentified as *merremii* and *reginae* in the original Degenhardt collection from Provinz Popayan, and there may have been syntypes rather than a single holotype.

Giorgio Jan, who had borrowed the *lateristriga* specimen(s) for illustration in the *Iconographie Générale*, also had been told that the species was from Popayán rather than simply "Nova-Granada" as originally published (references in Myers, 1974: 186).

ver, capital of Lower Saxony, had to give its agreement for moving the collection to Bonn in Northrhine-Westfalia. This transfer was accomplished in 1977 (Böhme and Bischoff, 1984).

As indicated above, a significant part of the Göttingen collection has been destroyed—lost not to the ravages of war but to simple lack of curatorial care. Nonetheless, much important material remains. Concerning the 26 new species described by Berthold, type material remains for 16 species (all four amphibians and 12 of 22 reptiles). Even the extant types had been presumed lost by some workers (e.g., Myers and Daly, 1976).

Two of Berthold's species names, *Dendrobates histrionicus* and *Phyllobates melanorrhinus*, are among the oldest names in the family Dendrobatidae. Examination of the surviving type specimens led us to the present study, which clarifies a few taxonomic and geographic problems that are associated with these 150-year-old names.

Materials and Methods

In addition to the Berthold syntypes of *Dendrobates histrionicus* and *Phyllobates melanorrhinus*, deposited in the Museum Alexander Koenig (ZFMK), we have used comparative specimens from the American Museum (AMNH) collections. This includes abundant material of *D. histrionicus*, *P. bicolor*, and *P. terribilis* collected by Myers and his colleagues in western Colombia; measurements, illustrations, and discussion of some of this material have been previously published (Myers and Daly, 1976; Myers et al., 1978).

Measurements were read to the nearest 0.1 mm with dial or digital calipers or (if < 12 mm) with an ocular micrometer fitted in a Wild dissecting microscope. All measurements were made by the first author over a span of years. Dimensions given herein for lectotypes are readings that were obtained more than once in series of sequential measurements made at one sitting.

It must be emphasized that it is difficult to obtain repeatable measurements of soft-bodied animals. For example, caliper readings of snout-to-vent length will vary from one observer to another and also within a series of readings made by the same observer. For small frogs in the size range of 20–50 mm, measuring "errors" of at least 5 percent will occur. Small distance measurements made with an ocular micrometer intuitively seem more repeatable but may have similar percentage errors. Caution is clearly required when making conclusions about statistical and biological significance based on small differences, even when (as in the present case) measurements were made by a single person. A priori assumptions of this paper are similar to those mentioned in Myers and Daly (1976: 201), with a significance level of 0.01 being selected prior to analysis for the few *t*-tests that seemed warranted.

Phyllobates melanorrhinus Berthold

Figures 1 (upper), 2–3

Phyllobates melanorrhinus Berthold, 1845: 43; 1846a: 14–15, pl. 1, fig. 7 (whole frog in dorsolateral view, hand-painted in AMNH copy of this preprint or reprint of following); "1847" [1846?]: 13–14, pl. 1, fig. 7 (same as preceding but uncolored).

Phyllobates melanorhinus Keferstein, 1867: 354 (emendation).

Lectotype: ZFMK 28130 (fig. 2) by present designation. This is the best preserved of the six surviving syntypes (Berthold [1846a: 15] mentioned seven specimens); it is an undissected male, determined to be adult by presence of vocal slits. In preservative, the specimen is light gray dorsally and laterally on head and body, with a pale gray frosting on dorsal surfaces of upper arms and thighs. The lower parts of the limbs are blackish, with punctuations and suffusions of pale gray; the ventral surfaces are blackish, suffused with pale gray across chest and near chin. *Measurements in mm*: Length from snout to vent 37.3; tibia length from heel to fold of skin on knee 17.5; greatest width of body > 13; greatest head width (between angles of jaws) 13.2; head width between edges upper eyelids 12.0; approximate width of interorbital area 5.0; diagonal head length from tip of snout to angle of jaws 12.1; tip of snout to center of naris in lateral view 1.5 (2.1 diagonally); center of naris to anterior corner of eye 4.2; distance between centers of nares 5.0; eye length from anterior to posterior cor-

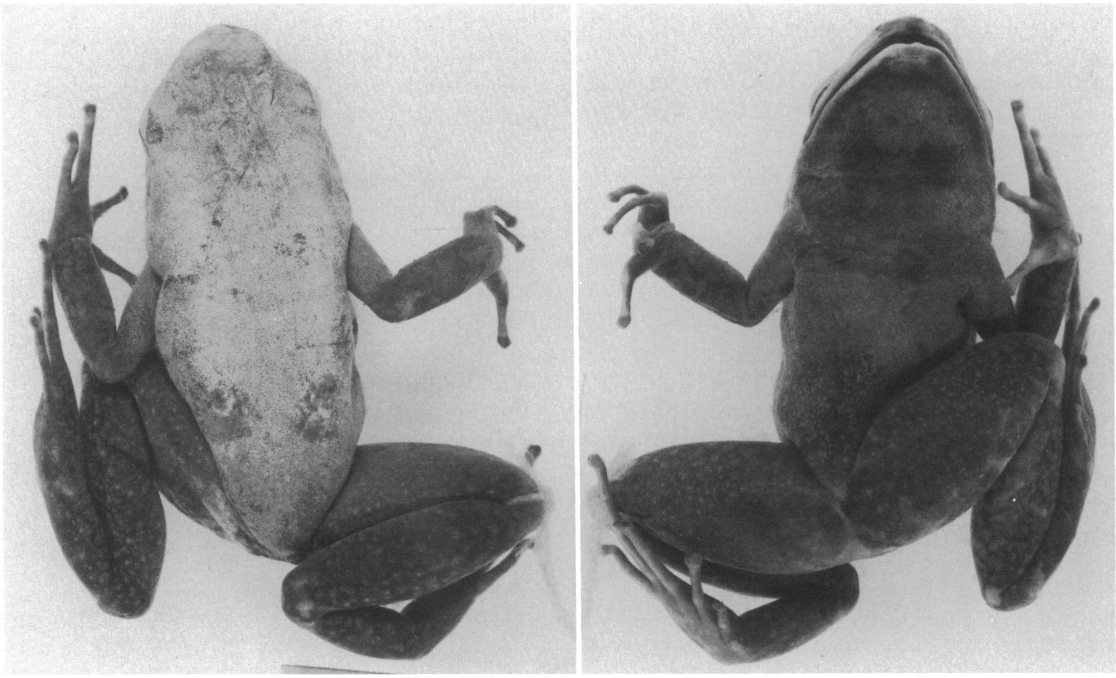

Fig. 2. Lectotype by present designation of *Phyllobates melanorrhinus* Berthold, 1845. ZFMK 28130 in dorsal and ventral view, ×1.9.

ner 4.5; horizontal diameter of tympanum (posteriorly indistinct) > 2; corner of mouth to lower edge tympanic ring 1.4; length from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger 10.5; width of disc of third finger 1.2; width of third finger (penultimate phalanx) below disc 0.8; width of discs of third and fourth toes, respectively, 1.2 and 1.3; width of third and fourth toes below discs both 0.8.

PARALECTOTYPES: The remaining extant specimens in the syntype series are ZFMK 28126♂, 28127♀, 28128♂ [now AMNH A-140864], 28129♀, and 28131♀. All are sexually mature specimens, as determined by presence of vocal slits or active ovaries and enlarged oviducts.

Measurements and proportions of the paralectotypes and lectotype are given in table 1. Color variation among the type series is shown in figure 3. The heads and bodies of these 150-year-old specimens are pale gray. The limbs and venters are mostly black, with variable amounts of paler gray suffusion. The pale limb coloring is most strongly developed in ZFMK 28126 (fig. 3, top left), which has the dorsal limb surfaces largely pale gray, with some dark pigment showing through on the lower extremities; the undersides of the head and limbs are darker, nearly black under the thighs (this specimen has been extensively dissected and the skin of the venter removed[6]). The largest specimen (ZFMK 28129) is one of the darkest dorsally and ventrally; the very pale areas on this specimen (fig. 3, bottom left) are areas of skin that seem to be completely faded or abraded of all pigmentation. Berthold (1846a: 14; "1847" [1846?]: 14) described the color as follows:

> Farbe oben schmutzig-gelbgrün, nach hinten hin etwas dunkler, unten blaugrau, Hinterschenkel oft sammetschwarz; Nasenspitze immer, und Lippenränder oft sammetschwarz.

The old hand-colored plate in Berthold's

[6] This specimen (ZFMK 28126) presumably was dissected by Berthold, who included observations on internal anatomy in his detailed descriptions (1846a; "1847" [1846?]).

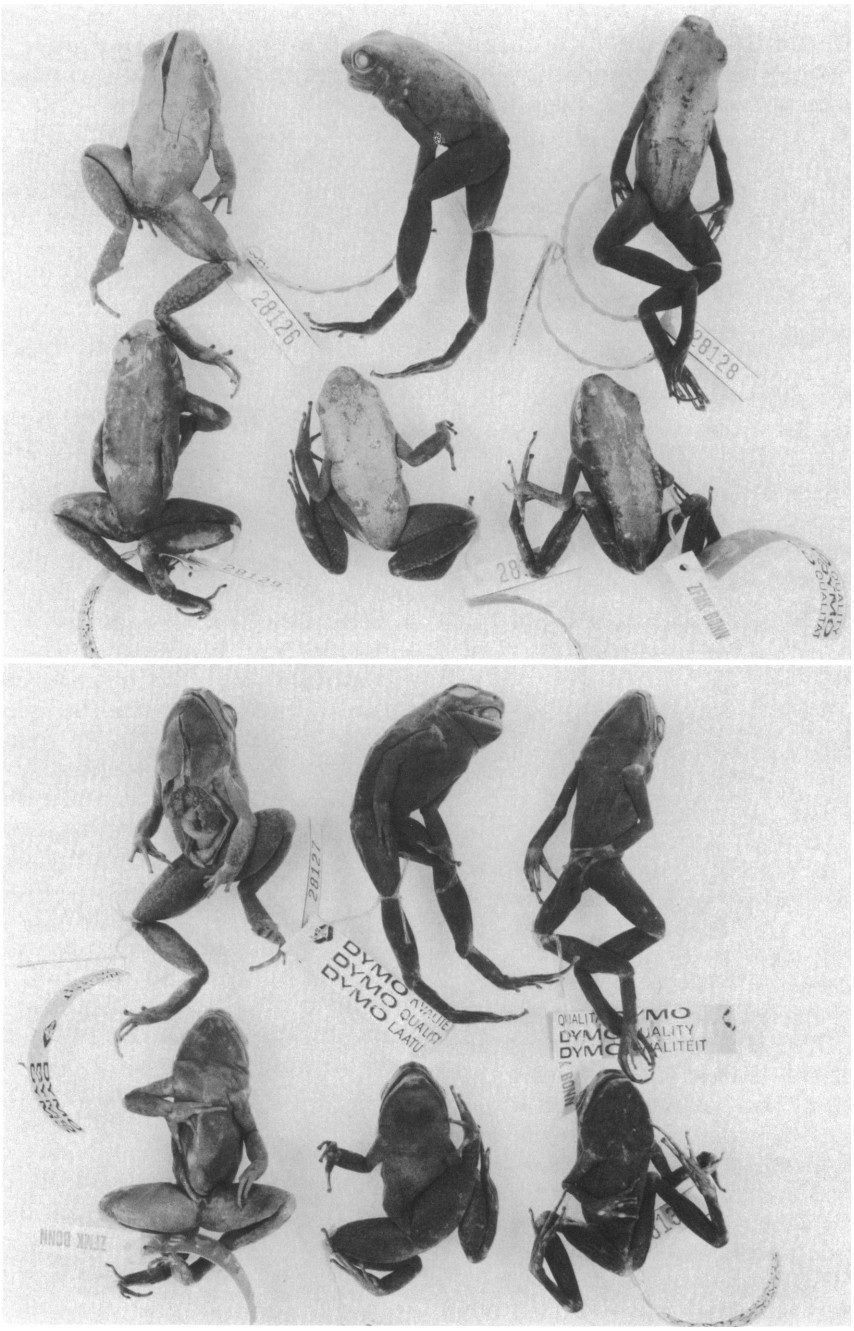

Fig. 3. Syntypes of *Phyllobates melanorrhinus* Berthold, 1845, in dorsal and ventral views. **Top Rows:** Left to right, ZFMK 28126, 28127, 28128 (now AMNH A-140864). **Bottom Rows:** Left to right, ZFMK 28129, 28130 (lectotype), 28131.

1846a preprint (reprint?) shows a green frog with a faint (faded?) yellow wash; the snout-tip and lower limbs are vaguely black.

The specimen of *Phyllobates melanorrhinus* illustrated in Berthold probably is the missing seventh specimen, inasmuch as none of the six surviving specimens fall easily into the illustrated pose (compare reproduction of original illustration in fig. 1 with specimens in fig. 3). Also missing is the illustrated specimen of *Dendrobates histrionicus*, as commented on below.

Dendrobates histrionicus Berthold

Figures 1 (lower), 4–5

Dendrobates histrionicus Berthold, 1845: 43; 1846a: 15–16, pl. 1, fig. 8 (whole frog in dorsal view, hand-painted in AMNH copy of this preprint or reprint of following); "1847" [1846?]: 15–16, pl. 1, fig. 8 (same as preceding but uncolored).

Dendrobates tinctorius (Schneider): Keferstein, 1867: 359–360 (*D. histrionicus* Berthold placed in synonymy).

LECTOTYPE: ZFMK 28123 by present designation. This is one of the best preserved of the seven surviving syntypes (originally eight, see closing remarks under Paralectotypes below); it is an undissected male, determined to be adult by presence of vocal slits and with vocal pouch externally evident by darkening on base of throat. Color blackish brown with vivid white markings (fig. 4, row 2, second from left) that were probably reddish or orange in life. *Measurements in mm*: Length from snout to vent 30.8; tibia length from heel to fold of skin on knee 12.8; greatest width of body about 11; head width between angles of jaws 9.1; head width between edges upper eyelids 9.5; width of interorbital area 3.0; diagonal head length from tip of snout to angle of jaw 7.7; tip of snout to center of naris in lateral view 1.2; center of naris to anterior corner of eye 2.6; distance between centers of nares 3.6; eye length from anterior to posterior corner 4.0; horizontal diameter of tympanum (posteriorly concealed) about 1.5; corner of mouth to lower edge tympanic ring 1.1; hand length from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger 8.6; width of disc of third finger 1.4, and width of penultimate phalanx below disc 0.6; width of discs of third and fourth toes 1.1 and 1.2, respectively, with each toe 0.7 below disc.

PARALECTOTYPES: The remaining extant specimens in the syntype series are ZFMK 28119♀, 28120♂, 28121♂, 28122♀ [now AMNH A-140863], 28124♀, and 28125♀. All are sexually mature, based on appearance of ovaries or presence of vocal slits.

Including the male lectotype, there are three males in the series and four females, with snout-vent lengths (SVL) and proportional tibial lengths (TL/SVL) as follow (mean ± 1 S.D., range):

SVL: 3♂ = 30.47 ± 0.85, 29.5–31.1 mm
4♀ = 29.60 ± 1.18, 28.5–30.9 mm
TL/SVL: 3♂ = 0.418 ± 2.373, 0.416–0.420
4♀ = 0.408 ± 1.581, 0.386–0.421

Color-pattern variation of the lectotype and extant paralectotypes is shown in figure 4. Five of the seven specimens (including the lectotype) have conspicuous white markings on an overall dark ground color of brown or (in most) blackish brown. The pale markings include a conspicuous, large round or oval dorsal spot, variably complete limb bracelets, and either separate throat and belly blotches or a single larger blotch that is continuous from throat to belly. A sixth specimen (fig. 4, row 2, third from left) differs from the preceding five in having paired dorsolateral spots that are well separated middorsally. The remaining specimen (fig. 4, last specimen in row 2), which is poorly preserved, lacks dorsal body markings but appears to have a large, irregular pale spot over the rear of the head; the ventral pale area is larger in this last specimen, extending from the groin nearly to the chin and up onto the lower sides of the body. Berthold's (1846a: 16; "1847" [1846?]: 16) description reflects the variation in color pattern seen in figure 4 except that one specimen (see below) is now missing:

> Russig schwarzbraun, Stirn schwarz, Schnurrbart (Oberkiefer von einem Auge bis zum andern) rosenroth; Hals, Brust und Bauch roth, manchmal Brust mit breiter schwarzer Querbinde; Rücken meist mit einem rothen ovalen Fleck in der Mitte, seltener mit 2 solchen Flecken auf jeder Seite, welche aber mit der rothen Bauchfläche nicht zusammenstossen, –die Individuen mit dem ovalen Mittelfleck zuweilen noch mit einem ähnlichen Fleck auf dem Ende des Steisses. Unterarm mit breiten rothen Handmanschetten, –

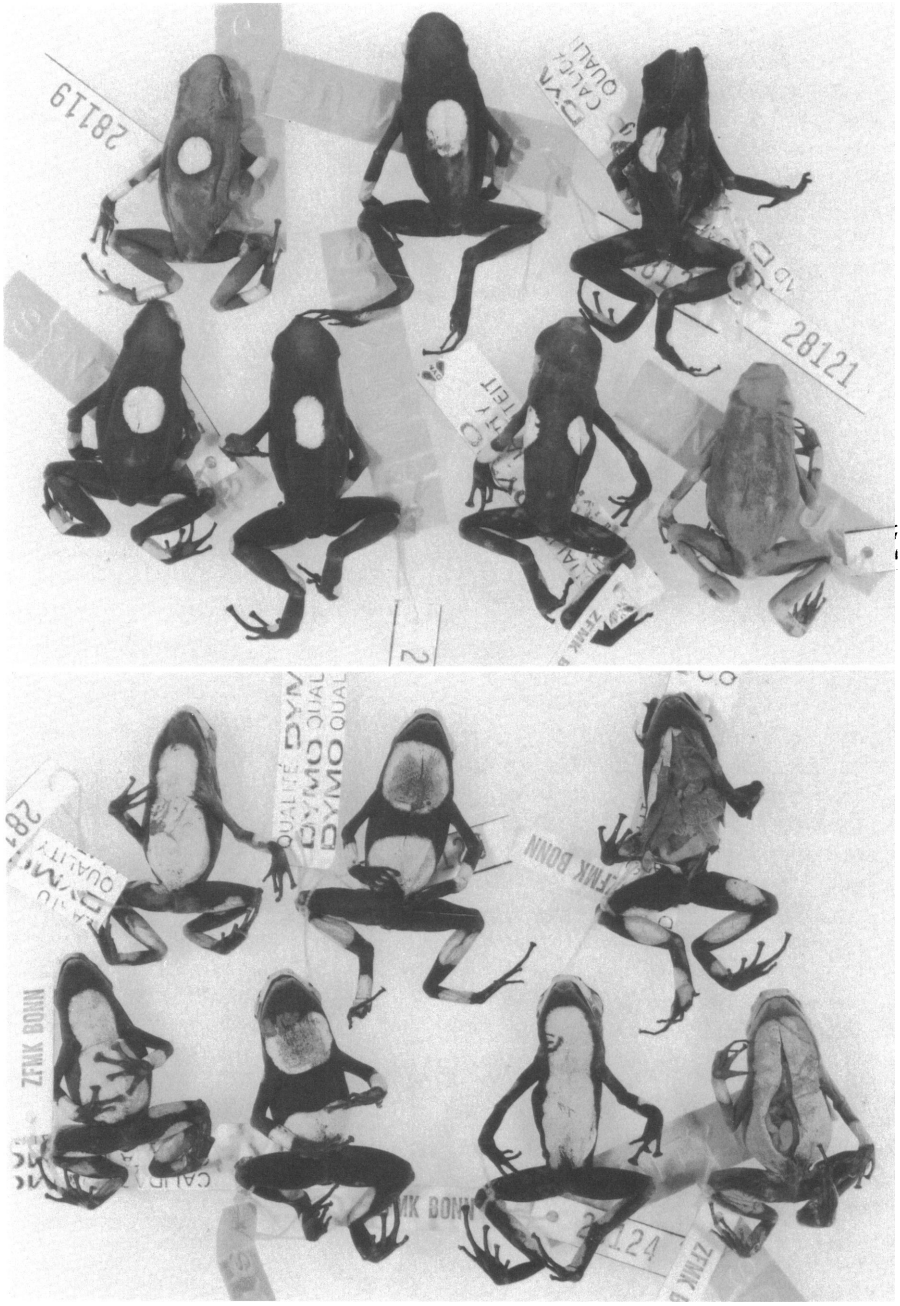

Fig. 4. Syntypes of *Dendrobates histrionicus* Berthold, 1845, in dorsal and ventral views. **Top Rows:** Left to right, ZFMK 28119, 28120, 28121. **Bottom Rows:** Left to right, ZFMK 28122 (now AMNH A-140863), 28123 (lectotype), 28124, 28125. See figure 1 for a reproduction of Berthold's (1846a) illustration of an additional syntype, which is lost.

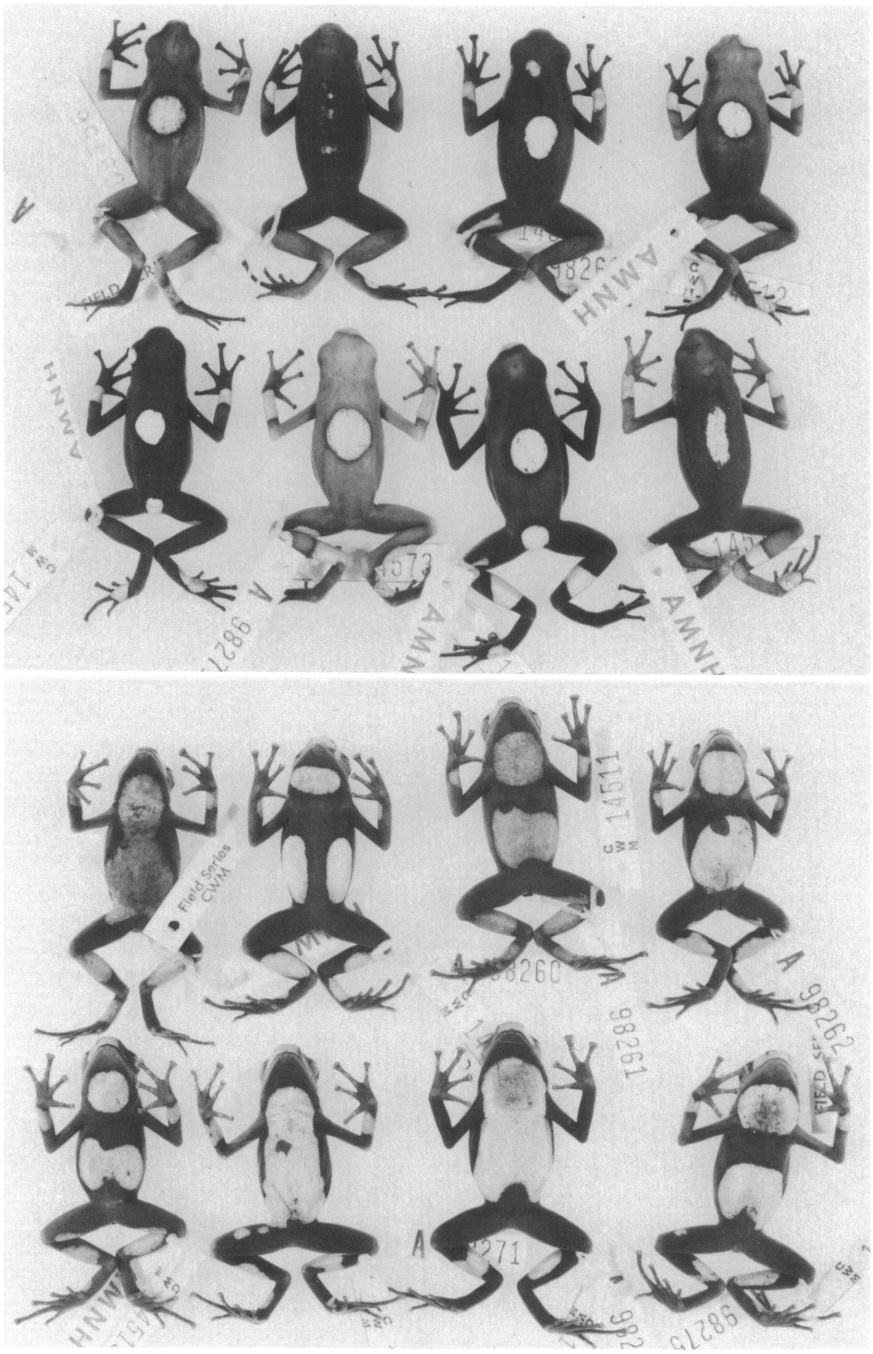

Fig. 5. *Dendrobates histrionicus* Berthold, 1845. Variation in a population sample from the region of Santa Cecilia, upper Río San Juan, Risaralda, Colombia. **Top Rows:** Left to right, AMNH 85159, 98260, 98261, 98262. **Bottom Rows:** Left to right, AMNH 98263, 98271, 98274, 98275.

ebenso gefärbte Kniekehle und Seite des untern Tarsalendes.

The old hand-colored plate in Berthold's 1846a preprint (reprint?) shows a black frog with pale reddish markings. This specimen (see fig. 1, lower) has been lost; the seven extant syntypes (fig. 4) lack the conspicuous sacral spot seen in Berthold's original illustration. Keferstein (1867: 359) confirmed that there were eight specimens in the original series.

Nomenclatural Remark

Myers and Daly (1976: 200) reproduced Berthold's figure of a specimen that is no longer associated with the type series and which is presumed lost. In the figure caption, Myers and Daly inadvertently referred to the specimen as the "holotype" of *Dendrobates histrionicus*—even though Berthold's (1846a; "1847" [1846?]) longer accounts showed that he had more than one specimen. According to the 1985 edition of the *International Code of Zoological Nomenclature*, such action may now constitute "designation of lectotype by inference of holotype" (art. 74b). But if such inadvertence is retrospectively construed as a binding designation, and if the specimen is now (or was already) lost, there can be no new designation of a primary type specimen unless extraordinary circumstances (which do not exist) call for a neotype (there are no provisions for designation of a second lectotype because paralectotypes do not regain status as syntypes [art. 73b(ii)]).

Such an unfortunate situation would be far removed from any intent held by Myers and Daly in 1976, since the first author has always believed that the procedure for modern type designations should be explicit and not subject to accident. There seems to be an arguable way out, however, based on the last sentence in article 74d: Inasmuch as Myers and Daly's reference to Berthold's figure as "holotype" did not "have as its object the definition of that taxon," we take the view that there has been no lectotype designation prior to the one made herein.

TAXONOMIC STATUS AND GEOGRAPHIC PROVENANCE

Phyllobates melanorrhinus

There is very little in the way of significant literature concerning this name (including the emendation "*melanorhinus*"). It has been listed primarily as a nominal species supposedly distinct from "Cuban" *Phyllobates bicolor* Bibron (e.g., Boulenger, 1882: 91; 1888: 206; Dunn, 1944: 491; 1957: 77). After growing recognition that the earlier named *P. bicolor* (the generic type) is a Colombian rather than a West Indian endemic,[7] *P. melanorrhinus* was relegated to its synonymy (Cochran and Goin, 1957: 36; Silverstone, 1976: 23). This assignment, however, was conjectural because it was not based on comparison of specimens. It is to be noted that the type locality of *Phyllobates terribilis* Myers et al., 1978, is little more than 100 km northwestward of Popayán, sometimes construed as the type locality of species named in Berthold's 1845 paper. *Phyllobates melanorrhinus* thus needs to be compared with *P. terribilis* and *P. bicolor*, the only more-or-less uniformly colored species of *Phyllobates* currently recognized.[8]

There can be no conclusive statement that the name *Phyllobates melanorrhinus* is not applicable to some otherwise unknown population characterized by autapomorphies of living color, toxicity, etc. But there seems to be nothing about the 150-year-old preserved specimens suggesting a species separate from *bicolor* and *terribilis*. Nor is there any compelling reason to suspect that the *melanor-*

[7] The literature involved in this recognition is essentially the same as for *Urotheca dumerilii* Bibron, a rare Colombian snake described in the same work as *Phyllobates bicolor*. See Myers (1974: 178) for citations and summary. Like *Urotheca dumerilii*, *Phyllobates bicolor* "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" (Myers et al., 1978: 328n).

[8] There is a possibly undescribed species known only from a single specimen, which appears to represent a population of frogs significantly smaller than the species considered in the present paper (discussion in Myers et al., 1978: 330–331).

rhinus syntypes (3♂, 3♀) might be samples drawn from more than one species, so we therefore assume that they probably represent a single regional population, if not in fact a single deme—an assumption implicit in the following comparisons of available "population" samples.

Known body size of *Phyllobates bicolor*—a significantly smaller species than *P. terribilis*—is based primarily on pooled samples (N = 48) from several demes in the Santa Cecilia region, upper Río San Juan. Male and female *Phyllobates melanorrhinus* fall within the upper size ranges of this sample (fig. 6A, B) and, statistically, it is not inconceivable that the syntypes were drawn from the Santa Cecilia regional population of *bicolor*: males, t = -2.46438, 27 df, P = 0.02038; females, t = -1.9456, 23 df, P = 0.06402.

The six adult syntypes of *P. melanorrhinus* fall at the *lower* end of the size range of *Phyllobates terribilis*, with one female being smaller than any of 182 adult female *terribilis* (fig. 6C, D). Statistically, it is extremely unlikely that the *melanorrhinus* sample could have been drawn from the large regional population to which the name *terribilis* is applied: males, t = 3.71707, 154 df, P = 0.00028; females, t = 3.44084, 183 df, P = 0.00072.

Preserved color patterns of the old *melanorrhinus* syntypes fit best within known variation of *Phyllobates bicolor* and differ from *P. terribilis*. Bodies and limbs of adult *P. terribilis* are a nearly *uniform* yellow, orange, or pale metallic green above *and* below (Myers et al., 1978: pl. 2)—a uniformity that is maintained when specimens fade to an overall gray in preservative. One of the *melanorrhinus* syntypes (fig. 3, top left) approaches this condition dorsally but not overall (vide supra, description associated with fn. 6). *Phyllobates bicolor* may be as brightly colored as *P. terribilis* in life (Myers and Daly, 1983: color pl.), but the venter and limbs tend to be partly black or else washed with bright, pale pigmentation that is more subject to fading than the body color. The *melanorrhinus* syntypes appear to have had limbs and venters suffused with bright pigment, but in preservative this coloring has faded to a greater extent than the body coloring, as exemplified by the lectotype (fig. 2). The adult colorations of *P. terribilis* and *P. bicolor*, and the differential fading in *bicolor*, are discussed in Myers et al. (1978: 315, 316–317, 330; also Myers and Daly, 1983: color pl.). However, intraspecific color variation doubtless has not been thoroughly documented, a generality applicable to most of the bright-hued dendrobatids.

Phyllobates terribilis differs from *P. bicolor* in having a relatively shorter tibia (P = < 0.001), narrower head (P = < 0.001), perhaps slightly smaller finger discs (P = 0.003♀, 0.189♂), and in having the lower edge of the tympanum positioned somewhat farther from the angle of the jaws (P = < 0.0001), as discussed in Myers et al. (1978: 329–330).

Various body proportions of the *melanorrhinus* syntypes fit comfortably with all data for *P. bicolor* (compare tables 1, 2); significance levels based on t-values for *bicolor-melanorrhinus* comparisons, by sex, vary from 0.13 to 0.99. In contrast, comparisons of the small *melanorrhinus* samples with *P. terribilis*[9] give highly significant differences for tibia length/SVL: males, t = -4.02389, 151 df, P = 0.00009; females, t = -2.95577, 180 df, P = 0.00353. Also a significant difference in the naris-eye/tympanum-jaw proportion for males only: males, t = -5.27697, 26 df, P = 0.00002; females, t = -1.00154, 26 df, P = 0.32580). Significance levels for the other proportions vary from 0.05 to 0.16. These data on proportions are of minimal value in identifying individual specimens but are strongly indicative of average differences between population samples, with the small *melanorrhinus* samples being much more compatible with *P. bicolor* than with *P. terribilis*.

Therefore, based on comparisons of accessible characters, the *melanorrhinus* lectotype and paralectotypes seem not to be separable from *Phyllobates bicolor* and the name is to be maintained as a junior synonym of *bicolor*. The size distributions of the *melanorrhin-*

[9] Except for tibia/SVL, where over 300 measurements were used for *Phyllobates terribilis*, the *melanorrhinus* proportions in table 1 were compared with samples of 25 adult males and 25 adult females drawn from the large type series of *P. terribilis* (see table 1 in Myers et al., 1978).

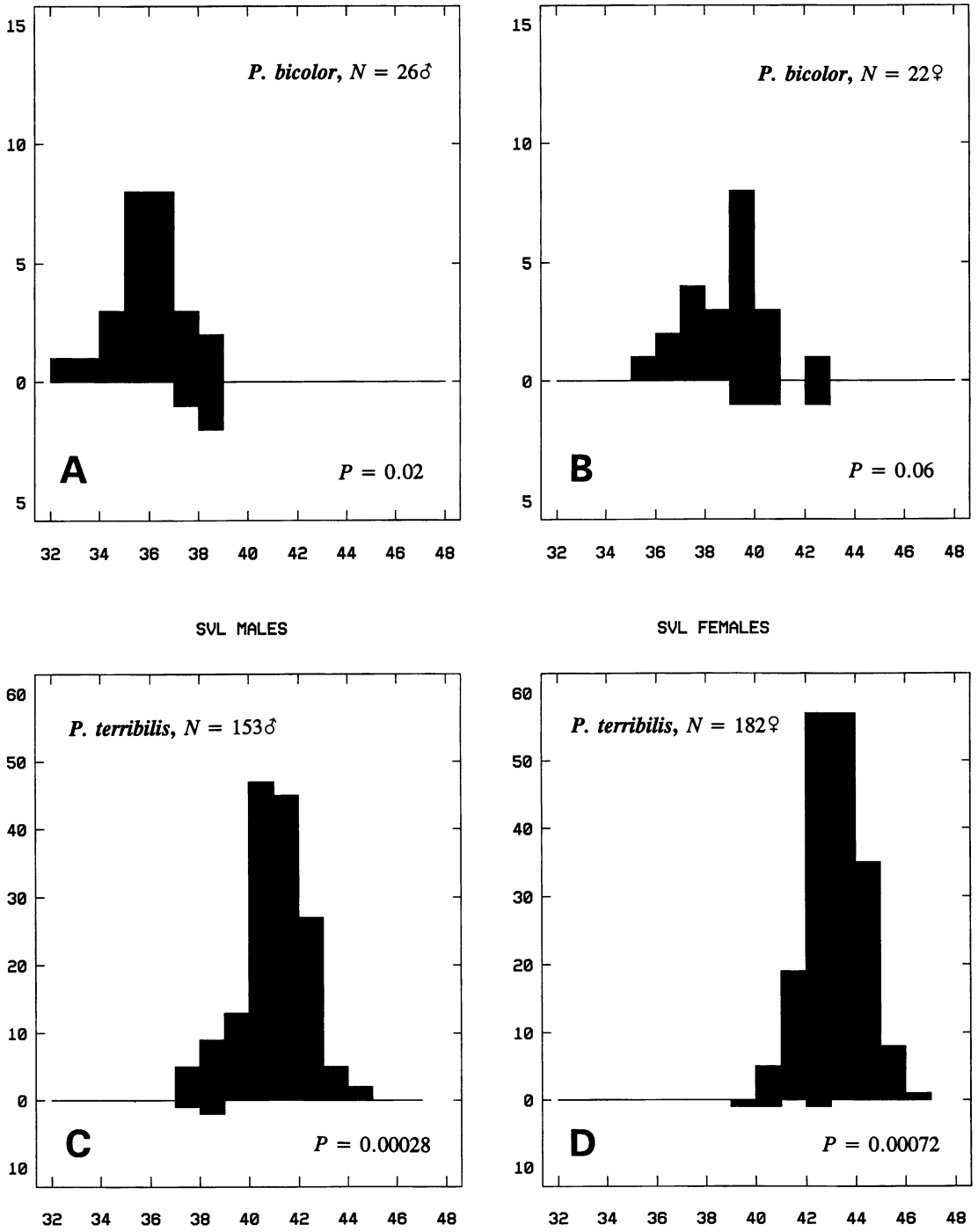

Fig. 6. Comparisons of adult sizes of *Phyllobates bicolor* (**A, B**) and *Phyllobates terribilis* (**C, D**) with the syntypes of *P. melanorrhinus* (3♂, 3♀, shown as hanging histograms).

TABLE 1
Size and Proportions of Syntypes of *Phyllobates melanorrhinus* Berthold[a]

Character	N	Mean	SD	Range
Snout-vent length (SVL) in mm	3♂	38.13	0.80	37.3–38.9
	3♀	40.93	1.56	39.5–42.6
Tibia length[b]/SVL	3♂	0.475	0.008	0.47–0.48
	3♀	0.452	0.010	0.44–0.46
Head width/SVL	3♂	0.344	0.019	0.32–0.36
	3♀	0.340	0.024	0.32–0.37
Eye length/tip of snout to eye[c]	3♂	0.815	0.032	0.78–0.83
	3♀	0.838	0.039	0.79–0.86
Center naris to edge eye/lower edge tympanum to angle of jaws	3♂	2.865	0.176	2.67–3.00
	3♀	2.353	0.263	2.10–2.63
Width 3rd-finger disc/finger width below disc	2♂	1.563	0.088	1.50–1.63
	2♀	1.625	0.177	1.50–1.75

[a] ZFMK 28126–28131.
[b] Tibia length measured from heel to fold of skin on knee, with joints flexed at right angles.
[c] Snout length measured on the diagonal, with calipers.

us types relative to sizes in a somewhat heterogeneous sample of *bicolor* (fig. 6A, B), and the relatively low significance value for males (see above),[10] suggest that the types might have come from a deme of relatively large *bicolor*.[11] The unknown type locality must be in northwestern Colombia, probably in the upper drainage of the Río San Juan in sympatry with a distinctive population of *Dendrobates histrionicus*, as follows.

Dendrobates histrionicus

This variable species is a characteristic inhabitant of low-elevation rain forest on the Pacific versant of western Colombia and northwestern Ecuador. Geographic variation in color pattern is extreme (Silverstone, 1975) and there also is detectable interpopulational variation in size, relative tibia length, skin alkaloids, and escape behavior (Myers and Daly, 1976; Daly et al., 1986). The data on skin toxins were taken to support the notion of conspecificity of populations currently assigned to *D. histrionicus*—which remains the only dendrobatid in which skin-alkaloid variation shows geographic patterns that do not seem to be explicable by presumptions of dietary variation (Myers et al., 1995: 16).

Geographic variation in color pattern of *D. histrionicus* is chaotic or patchwork in the extreme and some pattern types (e.g., numerous red spots on black) are repeated in geographically disjunct demes (Myers and Daly, 1976; Daly et al., 1986). Nonetheless, the color patterns in the type series of *D. histrionicus* allow geographic placement with relative precision. Firstly, the well-defined pale limb "bracelets" of the type specimens are found primarily in "northern" populations. More importantly, the single, large, rounded dorsal spot on most of the syntypes is a pattern definitely known only from the upper Río San Juan in the vicinity of Santa Cecilia (5°18′N, 76°13′W), present-day Department of Risaralda. It is an extraordinary color pattern even for a *Dendrobates*, a genus renown for inventive livery. This pattern—seen on the lectotype and four of the six paralectotypes—is well matched in selected variants from the Santa Cecilia region (compare first five specimens in fig. 4 with variation in fig. 5). An additional spot on the sacrum, possessed by the lost syntype

[10] In keeping with a previous study (Myers and Daly, 1976), a level of 0.01 was preselected for testing differences between sample means. Selecting the usual level of 0.05 would have meant rejecting the null hypothesis for males ($P = 0.02$) but not for females (0.06).

[11] Size differences between samples of dendrobatids, if not genetic based or due to random sampling, may also be related to interdeme differences in age structure (Myers and Daly, 1980: 13) or even to collector bias.

TABLE 2
Size and Proportions of *Phyllobates bicolor* Bibron, from Santa Cecilia Region, Upper Río San Juan[a]

Character	N	Mean ± 1 S.E.	SD	CV (%)	Range
Snout-vent length (SVL) in mm	26♂	36.05 ± 0.28	1.43	3.95	32.1–38.8
	22♀	38.92 ± 0.36	1.69	4.34	35.7–42.7
Tibia length/SVL	26♂	0.475 ± 0.003	0.014	3.04	0.45–0.51
	22♀	0.463 ± 0.003	0.014	2.93	0.44–0.49
Head width/SVL	26♂	0.350 ± 0.003	0.014	3.98	0.33–0.39
	22♀	0.349 ± 0.003	0.016	4.48	0.33–0.39
Eye length/tip of snout to eye	25♂	0.785 ± 0.013	0.065	8.25	0.67–0.91
	22♀	0.796 ± 0.014	0.064	8.08	0.68–0.93
Center naris to edge eye/lower edge tympanum to angle of jaws	26♂	2.582 ± 0.067	0.341	13.20	2.06–3.36
	22♀	2.587 ± 0.058	0.271	10.48	2.17–3.42
Width 3rd-finger disc/finger width below disc	23♂	1.562 ± 0.034	0.163	10.41	1.30–1.86
	21♀	1.565 ± 0.025	0.116	7.38	1.33–1.75

[a] Table corrected from Myers et al. (1978: 315), in which data for one female were inadvertently included under males.

(fig. 1) can also be seen as a variant in the Santa Cecilia sample (fig. 5). Thus, at least five of the original seven syntypes probably were drawn from a population such as the one at Santa Cecilia.

Except for a specimen with erroneous locality data (Cochran and Goin, 1970: pl. 4g–i; see Myers and Daly, 1976: 206 for comment), the pattern of a rounded dorsal spot and unmarked flanks has not been explicitly reported from anywhere other than the Santa Cecilia region. Although the distinctive pattern seems to be known from nowhere else, it cannot be said with absolute certainty that it is actually confined to populations of the immediate Santa Cecilia region. But, if not, it seems safe to predict that the geographic occurrence of the "Santa Cecilia pattern" must be restricted to the lower Pacific slopes of the Cordillera Occidental roughly between parallels 5 and 6° North—a region in which the upper San Juan is nearly central, in the expanse of Andean foothills between Cerro Tamaná and the uppermost drainage of the Río Atrato. A somewhat similar pattern occurs in a population of *histrionicus* slightly to the north (6°14′N) of this region, on which Myers and Daly (1976: 206) commented as follows: "Silverstone (1975) has likened a slightly different color pattern to Berthold's [illustrated] type specimen, but in these frogs (from the Río Arqui, upper Atrato drainage) the dorsal spot is situated on the head and there are large lateral spots . . ." Similar patterns of head spots plus lateral blotches also occur as intrapopulational variation in the Río San Juan drainage downstream from Santa Cecilia (Myers and Daly, 1976: figs. 8, 9, pl. 1B), but they are not to be confused with the Santa Cecilia pattern (op. cit.: fig. 7 and pl. 1A).

Two of the seven *histrionicus* syntypes differ in pattern from the others and seem likely to have come from different demes. One (fig. 5, row 2, third from left) has conspicuous paired dorsolateral spots, while the other one (fig. 5, row 2, fourth from left) has an unmarked back, with a vague head marking and an extension of the pale ventral blotch onto each side of the body. Neither of the last patterns was represented among the frogs obtained for skin toxins and as voucher specimens (AMNH 85159–85170, 98259–98277), at localities 2–3 km airline NE and about 7 km airline SE Santa Cecilia, although the one with the unmarked back is reminiscent of the aforementioned intrapopulation variation downstream from Santa Cecilia. The specimen with the pair of dorsolateral spots is similar to one in a color photograph in Polder (1975: 304) except that the photograph shows a frog with a lighter body (light gray, with vivid red dorsolateral spots, labial blotch, and bracelets). The frog

in Polder's photograph probably came from the Department of Risaralda not far from Santa Cecilia, inasmuch as suitable habitat does not occur very far to the east of Santa Cecilia—but the locality unfortunately was kept secret.[12]

In summary, based on color pattern, the lectotype and paralectotypes of *Dendrobates histrionicus* may well represent three local demes from somewhere in the upper Río San Juan drainage. The prevalent pattern, including that of the lectotype, is consistent with the Santa Cecilia regional population of *D. histrionicus*. The relatively small body sizes of the adult lectotype and paralectotypes are consistent with a sample of *D. histrionicus* from Santa Cecilia, where the frogs are significantly smaller than in populations at lower elevations on the Río San Juan (Myers and Daly, 1976: 202–204).

Phyllobates and *Dendrobates* in Sympatry

The species of *Phyllobates* occupy relatively small, disjunct ranges in lower Central America and western Colombia, with an especially broad distributional gap on the eastern half of the Isthmus of Panama (map in Maxson and Myers, 1985, and Myers and Daly, 1983). Members of the *histrionicus* species group of *Dendrobates* are more extensively distributed in Central America and northwestern South America (Nicaragua to NW Ecuador), but the group shares the same distributional break in Panama as *Phyllobates* and the two may have had a similar history (Myers et al., 1984: 19).

It has not been previously pointed out that *Phyllobates* spp. seem *always* to occur in sympatry with one or more members of the *histrionicus* group—one of which will nearly always be less secretive, more obvious, and more easily collected than the *Phyllobates*. Thus, collections of *Phyllobates* nearly always include a species of the *histrionicus* species group (but not vice versa); Colombian *Phyllobates* spp. always occur with one or more distinctive populations of *D. histrionicus* itself.

Berthold's dendrobatid syntypes are most similar to known populations of *Phyllobates bicolor* and *Dendrobates histrionicus* in the region of Santa Cecilia, upper Río San Juan. Based on current knowledge, we conclude that the type series of *Phyllobates melanorrhinus* (= *P. bicolor*) probably was collected in sympatry with some part of the type series of *Dendrobates histrionicus*, in the upper drainage of this river, in lower montane rain forest in the general region of Santa Cecilia. From here eastward, the old trail to the interior rises through open, relatively semiarid land of unsuitable habitat for these kinds of dendrobatids.

On Berthold's "Provinz Popayan" as Type Locality

Berthold's reports on the Degenhardt collection from "Provinz Popayan" count as his most successful herpetological work in one sense—all but one of the seven names proposed are still considered valid. His species epithets, as currently used, are:

Dendrobates histrionicus Berthold, 1845
Phyllobates melanorrhinus Berthold, 1845 = *Phyllobates bicolor* Bibron, 1840
Anolis latifrons Berthold, 1845
Polychrus gutturosus Berthold, 1845
Bothrops schlegelii (Berthold, 1845)
Stenorrhina degenhardtii (Berthold, 1845)
Urotheca lateristriga (Berthold, 1859), see fn. 5

Berthold's 1845 synopsis (which validates new species diagnosed therein) included a report on a collection made by a Mr. Degenhardt during a long stay in the Province of Popayán, New Granada. Berthold's longer report, appearing the following year, added geographic coordinates for the collection:

> eine Anzahl von Thieren in Spiritus . . . welche der Herr Degenhardt während eines längeren Aufenthalts in der Provinz Popayan, etwa 2° N. B. und 301° L., selbst gesammelt hatte.

Many authors have simply given "Provinz

[12] Polder's article shows several other specimens of *Dendrobates histrionicus* with interesting patterns, including ones of the Santa Cecilia type. Specimens of diverse pattern type were said to have been obtained by Herman Oostveen on four sides of a pyramidal-shaped hill, somewhere in "provincie Chocó."

A later article attributed to Oostveen (1976) admits the still-secret locality to be between 200 and 900 m elevation in the Río San Juan drainage, erroneously said to be south of the equator in a nonexistent "Pacific Department."

Popayan" as type locality for Berthold's 1845 and 1859 species, although some (e.g., Barbour, 1934: 136) have referenced it as "Popayan, Colombia," apparently meaning the highland city Popayán. Recent authors (e.g., Peters and Orejas-Miranda, 1970: 54; Myers, 1974: 187) have tended to adopt the last view because of the forceful conclusion of Dunn and Stuart (1951a: 56):

> the original description [of *Bothrops schlegelli*] gives not only "Provinz Popayan" but also a latitude and longitude which are those of the city of Popayan 2 degrees north latitude, and 301 degrees longitude, the latter being, of course, longitude east of Ferro in the Canaries, which was the zero meridian for hundreds of years and which corresponds to the present 77 degrees west of Greenwich. This affects not only this species but all the others in the early and important collection from Colombia made by Degenhardt and sent to Berthold in Göttingen. Recent specimens from Popayan have been seen.

Contrary to Dunn and Stuart, however, their conclusion does *not* apply to all the specimens obtained by Degenhardt—certainly not to the two dendrobatid frogs, as realized by Myers and Daly (1976: 199) and by the Colombian naturalist and Popayán resident Kjell von Sneidern, who wrote (*in* Silverstone, 1976: 24) that "I have never seen any colorful *Phyllobates* or *Dendrobates* near Popayán; they do not exist here."

Berthold, a reasonably careful writer, never mentioned the city of Popayán. His *Provinz Popayan, etwa 2° N. B. und 301° L.* may have been no more than a general locator for the Province itself. The city of Popayán was founded by Belacázar in 1536 and has been a stable geographical entity for over four centuries. A colonial province of the same name seems to have existed with variable borders from the middle of the 16th century to 1820, when Bolívar issued a decree from Bogotá changing the name of the province from Popayán to Cauca and moving its capital to Cali. Subsequently, the name Province of Popayán came to be restricted to one of the smaller political divisions of the Department of Cauca.

Various old maps show that the colonial Province of Popayán once included nearly all of what is now western Colombia, although other provinces, including Antioquía and Chocó, had been separated out of it by the time of Bolivár's liberation of New Granada (Henao and Arrubla, 1972). We know nothing about Degenhardt, who obtained the specimens described by Berthold in 1845—nothing about his profession, his travels, his sense of geography, what maps were available to him, or the approximate years of his stay in New Granada—not even the extent of his biological collections.[13] Nonetheless, the biological evidence provided by the dendrobatid frogs clearly shows that the coordinates given by Berthold are not relevant and that Degenhardt's "Provinz Popayan" should be viewed in the broadest sense to mean western Colombia.

The species named by Berthold all occur on the Pacific versant of Colombia, but there is no reason to conclude that all specimens originated from a single locality.

CONCLUSIONS

Type localities of the two lizards and two snakes named by Berthold in 1845, and a third snake in 1859, can at this time be clarified only to the following extent:

> "Provinz Popayan" = western Colombia, probably on the Pacific versant.

For the two dendrobatid frogs treated in this paper, however, the type locality may be stated as follows:

> "Provinz Popayan" = Pacific versant northwestern Colombia, probably upper Río San Juan drainage in the present-day Department of Risaralda.

It should be noted that we have only clarified the above type locality based on evidence provided by knowledge of geographic ranges and geographic variation. These are not spurious "restrictions." Although we differ with Dunn and Stuart's interpretation of Berthold (see above), we do agree with the major thrust of their arguments against restriction of type localities by fiat.

Dunn and Stuart (1951a, 1951b) specifically criticized the actions of Smith and Taylor (1950), who restricted numerous type localities "only to localities from which spec-

[13] But Degenhardt did collect things other than amphibians and reptiles. Berthold described three new species of scorpions obtained by Degenhardt "aus Popayan" (Nachr. Georg-Augusts Univ. und K. Ges. Wiss. Göttingen, 1846, no. 4: 56–64).

imens are known to have been taken, and/or to those at which there is a reasonable possibility the type or types may have been secured." But such conjecturing has value only in rare cases of neotype designation (Internatl. Commission, 1985: art. 75d5; recommendation 72Ha4).

With some exceptions (as in the case of species known to be confined to an island or mountain-top), restrictions are highly speculative and tend to obscure the meaning of type locality.

Every species whose name is tied to a single specimen (i.e., holotype, lectotype, or neotype) has a single type locality, *whether that locality is known or not.* Inadequate published localities should be clarified or corrected to the extent allowable by available data as recommended in the *International Code* (72H), but the unsanctioned concept of "restriction" as used by Smith and Taylor (1950) and other systematists should in our opinion be discarded as meaningless. The inventing or hypothesizing of a type locality is not binding nomenclaturally and therefore has no practical value.

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[14] *Bibliographic note:* We reference only Berthold's herpetological papers here. His publication outlets in zoology included the *Göttingische Gelehrte Anzeigen* (1840a) and the *Nachrichten von der Georg-Augusts-Universität und der Königl. Gesellschaft der Wissenschaften zu Göttingen* (1845 etc.). Papers published in the latter are sometimes seen referenced to the former. According to the *Union List of Serials*, the *Nachrichten*, for the first decade or so of its existence, was "issued with" the *Gelehrte Anzeigen*, evidently leading to the possibility of dual citation. See Berthold, 1850b, for another instance that allows for the possibility of different journal citations for a single paper.

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