An Arboreal Poison Frog (*Dendrobates*) from Western Panama

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ABSTRACT

Dendrobates arboreus, new species, is a small arboreal frog with a dorsal and ventral pattern of vivid yellow spots on a brown or black field. It is abundant at 1100–1300 m. above sea level on a low section of the continental divide in western Panama, where, in undisturbed cloud forest, virtually the entire population resides high aboveground on trees laden with bromeliads and other epiphytes. A few specimens also come from a locality in the adjacent Caribbean lowlands.

The pale-spotted color pattern of *Dendrobates arboreus* is similar to that of the enigmatic *D. maculatus,* also from western Panama, but these two species differ significantly in morphology and are not closely related. *Dendrobates arboreus* is assigned to the *histrionicus* species group, which includes two species occurring macrosympatrically with *arboreus, D. speciosus* (highlands) and *D. pumilio* (lowlands). The monophyly of the *histrionicus* group is indicated by very similar-sounding chirp calls—given as long trains of harsh notes that

differ among species in rate of note repetition, note duration, and dominant frequency. New spectrographic analysis of pulse rates compels a restatement of Myers and Daly's original distinction between chirp calls and buzz calls, two important classes of dendrobatid vocalizations.

Courtship and egg laying of *Dendrobates arboreus,* and cannibalism of eggs by an adult female, were observed in captivity. There is no amplexus during mating, although typical cephalic amplexus (primitive within the Dendrobatidae) is retained in the behavioral repertory, possibly in an aggressive context. Courtship includes tactile signals by both sexes prior to their assuming a vent-to-vent position for egg laying and fertilization. An instance of mate piracy was observed when a second male successfully intruded at a late stage of courtship, bypassing the preliminary tactile signaling of the original pair.

Defensive skin secretions of *Dendrobates arboreus* contained 14 piperidine alkaloids, includ-

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ing members of the pumiliotoxin-A class and its allopumiliotoxin-A subclass. Remaining alka- loids, including two new compounds, are left un- classified. Histrionicotoxins were not detected.

RESUMEN

Dendrobates arboreus, especie nueva, es una pequeña rana arborea con un patrón dorsal y ventral de manchas amarillas vívidas, sobre un fondo chocolate o negro. Es abundante entre los 1100 y 1300 metros sobre el nivel del mar, en una sección baja de la división continental al oeste de Panamá, en el bosque nublado inalterado, en donde virtualmente toda la población reside sobre árboles altos, poblados con bromelias y otras epífitas. Algunos especímenes se obtuvieron también, de una localidad adyacente en tierras bajas del Caribe.

El patrón de manchas pálidas en *Dendrobates arboreus* es similar al de la enigmática *D. maculatus,* también del oeste de Panamá; pero estas dos especies tienen significantes diferencias morfológicas y no están íntimamente relacionadas. *Dendrobates arboreus* pertenece al grupo *histrionicus* que incluye dos especies casi simpátricas con *arboreus, D. speciosus* (de las tierras altas) y *D. pumilio* (de las tierras bajas). La monofilia del grupo *histrionicus* está indicada por varios sonidos de chirrido muy similares, dados como cadenas largas de notas ásperas que, entre especies, difieren en la tasa de repetición, de duración, y la frecuencia dominante. Nuevos análisis espectrográficos sobre tasa de pulsaciones, obligan a una repetición

de la distinción original que Myers y Daly hicieron entre chirridos y zumbidos, como cantos que representan dos tipos importantes de vocalización en dendrobátidos.

En cautiverio se observó el cortejo y la puesta de huevos por *Dendrobates arboreus,* y también, canibalismo de huevos por una hembra adulta. No se observó amplexus durante el apareamiento, aunque el amplexus céfalico típico (primitivo entre los Dendrobatidae) se mantiene como parte del repertorio de comportamiento, posiblemente dentro del contexto de agresividad. El cortejo incluye señales táctiles por ambos sexos, antes de asumir la posición de juntar los extremos posteriores, para la postura y fertilización de los huevos. Se observó un caso de piratería en el cortejo, cuando un segundo macho se introdujo con éxito casi en la fase final del cortejo, al desviar la señal táctil preliminar, del par original.

Las secreciones defensivas en la piel de *Dendrobates arboreus* contienen 14 alcaloides tipo piperidina, incluyendo miembros de la clase pumiliotoxina-A y la subclase allopumiliotoxina-A. Otros alcaloides, incluyendo dos nuevos compuestos, han sido dejados sin clasificar. No se detectaron histrionicotoxinas.

INTRODUCTION

Several new species of dendrobatid frogs are in the process of being described from the Isthmus of Panama. One recently discovered species is the subject of the present paper. Among the interesting features of the new frog is its coloration, which is uniformly brown or black with small spots of bright yellow. This unusual color pattern is similar to that of the only known specimen of another small frog, *Dendrobates maculatus*—a "lost" species that was named more than a century ago from an unknown locality in western Panama (see Myers, 1982). But even though *D. maculatus* and the new species share a peculiar color pattern and small size, they are otherwise distinct and are not closely related.

The first specimens of the new spotted frog were collected by one of us (Martínez) in 1981, while traveling with a military contingent over the northern part of an oil-pipeline route

across western Panama.[4] Two specimens were taken from the base of a large tree in the Atlantic lowlands and eight others near a newly cleared helicopter pad in cloud forest on the continental divide. Two of us (Martínez and Myers) collected near the latter place for several days in July 1982, but failed to find additional specimens. For that reason, and in order to continue the faunal survey of

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[4] Construction of the 125-km. transisthmian pipeline was started in 1981 and completed in 1982. It runs from Puerto Armuelles on the Pacific side northeast to Chiriquí Grande on the Atlantic Coast, passing through cloud forest on a low section of the continental divide at about 1120 m. above sea level (type locality of the new species described herein). This route transects diverse types of climate and vegetation, and its fauna includes somewhat over half of the species of amphibians and reptiles known from Panama (unpubl. data).
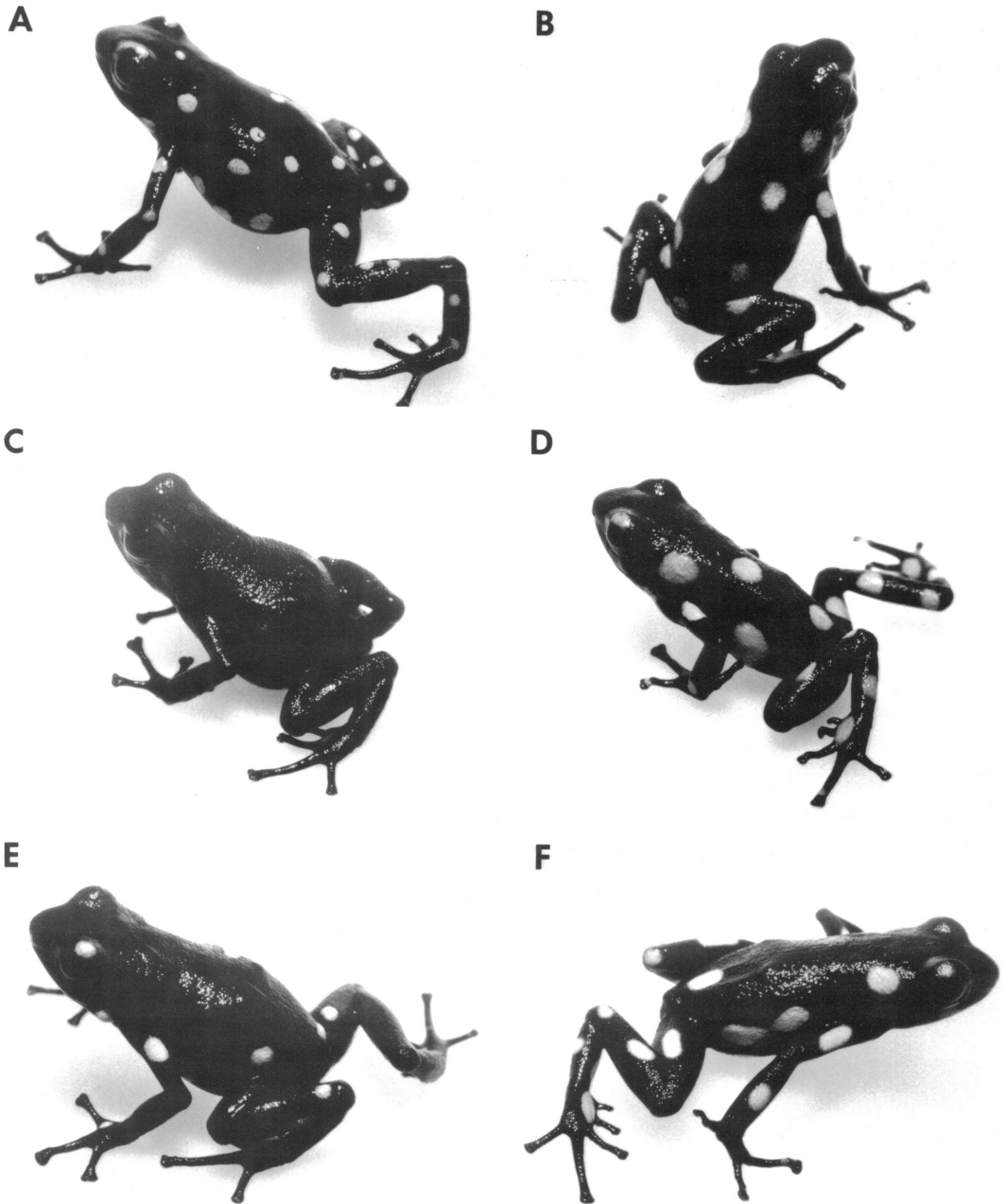
FIG. 1. *Dendrobates arboreus,* new species, showing variation in size and placement of the yellow spots; about 2.0–2.2 times life size. (AMNH catalogue nos. as follows: A, 116724 [holotype]; B, 116725; C, 116727; D, 116726; E, 116729; F, 116769.)

this newly accessible cloud forest, the three of us spent several weeks in the region in January 1983. We soon determined that the new frog occurs in a dense population along part of the continental divide. It proved, however, exceedingly difficult to collect in
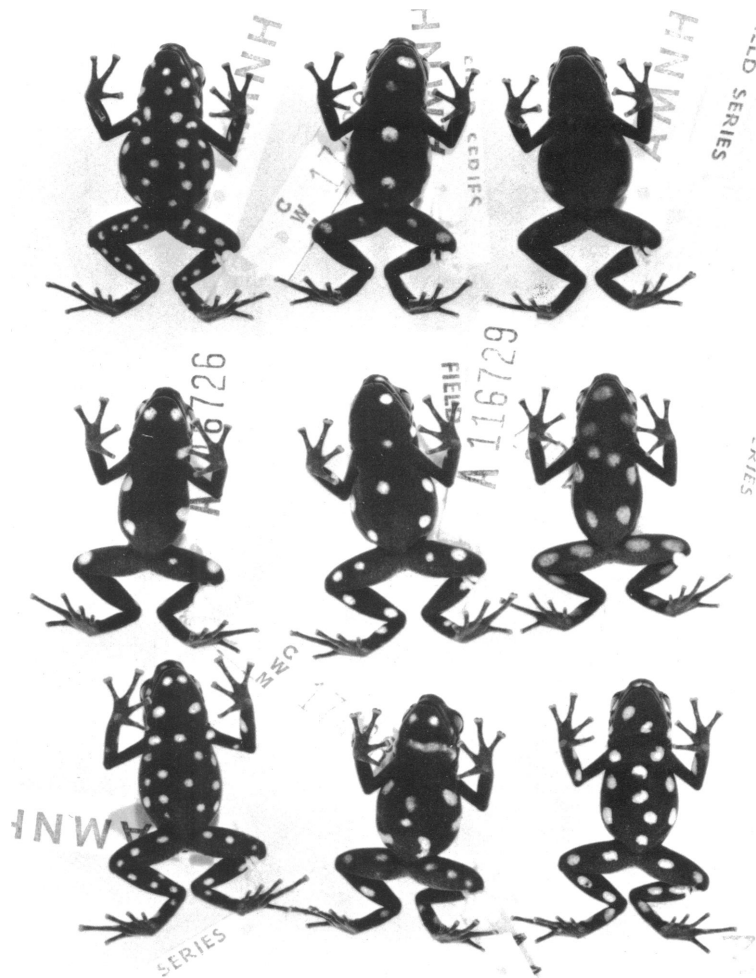
FIG. 2. *Dendrobates arboreus,* new species, showing variation in ventral spotting; 1.2 times life size. Holotype is in upper left corner. (Specimens from left to right in rows 1–2 are the same as frogs A–F in fig. 1. Specimens in row 3: AMNH 116734, 116739, 116747.)

undisturbed forest, since the population resides high aboveground in trees that are choked with epiphytic growth and therefore dangerously hard to climb. Fortunately, several dozen specimens were obtainable from trees felled along a new roadway, enabling us to characterize the morphology, vocalization, and skin toxins of this remarkably attractive little frog.

ACKNOWLEDGMENTS

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The 1981 fieldwork by Martínez was made possible by officers of the Guardia Nacional, especially Col. Roberto Díaz H. and Lieut. Luis Puleio.

Dendrobates arboreus, new species
Figures 1–3A, 4–7, 9–10A

HOLOTYPE: AMNH 116724 (field no. CWM 17486), an adult female obtained by John W. Daly, Víctor Martínez, and Charles W. Myers on January 21, 1983, in cloud forest at 1120 m. elevation on the continental divide above the upper Quebrada de Arena, at longitude 82°12′31″W, on the border between the provinces of Chiriquí and Bocas del Toro, western Panama.

PARATYPES: A total of 56 specimens, all from western Panama as follows: AMNH 116725–116748, 116749–116760 (skinned carcasses), 116761–116768 (cleared and stained), with same collecting data as holotype except that 116748 (recorded) was taken on January 24. AMNH 116769, 116770, from 1200–1300 m. elev. on continental divide above upper Quebrada de Arena, about 82°13′W, Chiriquí-Bocas del Toro border (Daly and Myers, January 16–18, 1983). AMNH 116771–116780, a geographically mixed series from two localities as follows: Two specimens from roughly 7 km. airline W Chiriquí Grande, about 20 m. elev., Bocas del Toro Province (Martínez, April 1981); eight specimens from continental divide, about 1100 m. elev., above upper Quebrada de Arena, Chiriquí-Bocas del Toro border (Martínez, June 1981).

ETYMOLOGY: The epithet arboreus is a Latin adjective relating to trees, in reference to the arboreal habits of this species.

DEFINITION AND DIAGNOSIS: A small to medium-sized dendrobatid having an adult snout to vent length of about 20–22 mm. Body and limbs overall brown or black, with usually vivid yellow spots dorsally and ventrally (figs. 1, 2). Teeth absent. Appressed first finger much shorter than second; discs of fingers 2–4 markedly expanded; third finger disc of adults about 1.6–2.0 times wider than finger. Vocalization a slow chirp call (3–4 notes/sec.) up to 1 min. long, at a dominant frequency of ~3800 Hz. Piperidine skin alkaloids present, including members of pumiliotoxin-A class (histrionicotoxins not detected). Strong arboreal tendencies.

In Central America, Dendrobates arboreus can be confused only with the somewhat similarly patterned and similar-sized D. maculatus, which differs in having the first finger longer than second, smaller finger discs, presence of vestigial webbing between toes 2–4, and presence of maxillary teeth (see fig. 3 for hand and foot differences).

Few other Dendrobates have pale spots on a dark ground, excepting some populations of Colombian-Ecuadorian D. histrionicus (much larger, adults 24–38 mm. SVL), Colombian D. occultator (yellow lateral spots below a red dorsum, adults to 27 mm.), some Panamanian-Colombian populations of D. auratus (green spots, adults >25 mm.), and several small South American species in western Amazonia. Of the latter, D. vanzolinii is distinguished by its reticulated limbs and blotched venter, D. captivus by smaller size and tendency for elongated dorsal spots and confluent ventral markings, and D. mysteriosus by spots of very irregular size.

MEASUREMENTS (IN MM.) OF HOLOTYPE: The female holotype (figs. 1A, 2 top-left) is an adult, with mature ovaries. Length from snout to vent 20.6; tibia length from heel to fold of skin on knee 8.5; greatest width of body 10.3; head width between angles of jaws and head width between outer edges upper eyelids both 6.6; approximate width of interorbital area 3.0; head length (oblique) from tip of snout to angle of jaw 6.3; tip of snout to center of naris (oblique) 1.0; center of naris to anterior edge of eye 2.0; distance between centers of nares 2.9; eye length from anterior to posterior edge 2.5; horizontal diameter of tympanum >1 (posteriorly concealed); corner of mouth to lower edge tympanic ring 0.7; hand length from proximal edge of large medial palmar tubercle to tip of longest (third) finger 6.3; width of disc of third finger 1.1; width of third finger (penultimate phalanx)

TABLE 1
Size and Proportions of Adult[a] *Dendrobates arboreus*, New Species, from Vicinity of Type Locality[b]

Character	N	Mean ± 1 S.E.	S.D.	C.V. (%)	Range
Snout–vent length	10♂	20.91 ± 0.11	0.36	1.74	20.3–21.6
(SVL) in mm.[a]	14♀	21.26 ± 0.14	0.53	2.49	20.4–22.2
Tibia length/SVL	10 ♂	0.402 ± 0.004	0.014	3.50	0.38–0.42
	14 ♀	0.402 ± 0.003	0.011	2.85	0.38–0.43
Head width/SVL	10 ♂	0.320 ± 0.002	0.007	2.10	0.31–0.33
	14 ♀	0.310 ± 0.002	0.007	2.23	0.30–0.32
Center naris to edge	10 ♂	0.732 ± 0.009	0.029	3.92	0.69–0.77
eye/eye length	14 ♀	0.756 ± 0.001	0.042	5.53	0.68–0.80
Width 3rd-finger disc/	10 ♂	1.883 ± 0.036	0.114	6.07	1.71–2.00
finger width below disc	14 ♀	1.843 ± 0.035	0.133	7.20	1.57–2.00
Hand length/SVL	10 ♂	0.300 ± 0.003	0.010	3.19	0.29–0.32
	14 ♀	0.299 ± 0.003	0.010	3.48	0.28–0.32
Hand length/head width	10 ♂	0.940 ± 0.008	0.025	2.63	0.91–0.98
	14 ♀	0.963 ± 0.006	0.023	2.41	0.91–1.01

[a] Three paratypic juvenile females (unenlarged ova) are 13.0–15.7 mm. SVL.

[b] Sample consists of standard museum specimens (excluding 20 paratypes skinned for alkaloid analysis) collected in January 1983; measured after five weeks in preservative.

below disc 0.7; width of disc of third toe 0.8; width of third toe below disc 0.6; width of disc of fourth toe 0.9; width of fourth toe below disc 0.7.

DESCRIPTION

A small to medium-sized *Dendrobates* (probably maturing at <20 mm. SVL) with an observed maximum of 22.2 mm. SVL; sexual dimorphism in size slight or absent (table 1). Head width between outer edges of upper eyelids equal to or only slightly less than width between jaw articulations. Head narrower than body; head width between angles of jaws averaging 74 percent of greatest body width in 10 adult males (range 64–85%), and 70 percent in 14 adult females (61–83%). Head width averaging about 31–32 percent of SVL in adults (table 1) and somewhat greater in juveniles ($\bar{x}$ = 34.9%, range 33–38% in three juvenile females 13.0–15.7 mm. SVL). Adult males with well-developed vocal slits on both sides; shallow, subgular vocal sac moderately distensible, tending to form (when collapsed) a pair of parallel folds on base of throat.

Dorsal skin weakly rugose or slightly granular, becoming nearly smooth in preservative; ventral skin also weakly rugose to granular on throat and chest, but coarsely granular on belly and undersides of thighs. On some individuals, the pale spots occupy raised glandular-like areas (fig. 4). 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 and from below but not from above. Canthus rostralis rounded; loreal region vertical and slightly concave (nearly flat). Interorbital area wider than upper eyelid. Eye shorter than snout length; distance from naris to eye = 68–80 percent of eye length in adults (table 1), 65–75 percent ($\bar{x}$ = 71%) in three juvenile females. Tympanum concealed posterodorsally, where it subcutaneously dips under anterior edge of m. depressor mandibulae; tympanum seen by dissection to be either circular or vertically elliptical, with an area greater than 50 percent of eye.

Hand large (fig. 3A), its length (proximal edge of metacarpal tubercle to tip of longest finger) averaging about 30 percent of SVL and about 95 percent of head width in adults (table 1); hand relatively smaller in juveniles ($\bar{x}$ = 28% [26–29%] of SVL, $\bar{x}$ = 79% [69–86%] of head width in three juvenile females). Relative length of appressed fingers 3 > 4 > 2 > 1; appressed first finger usually about
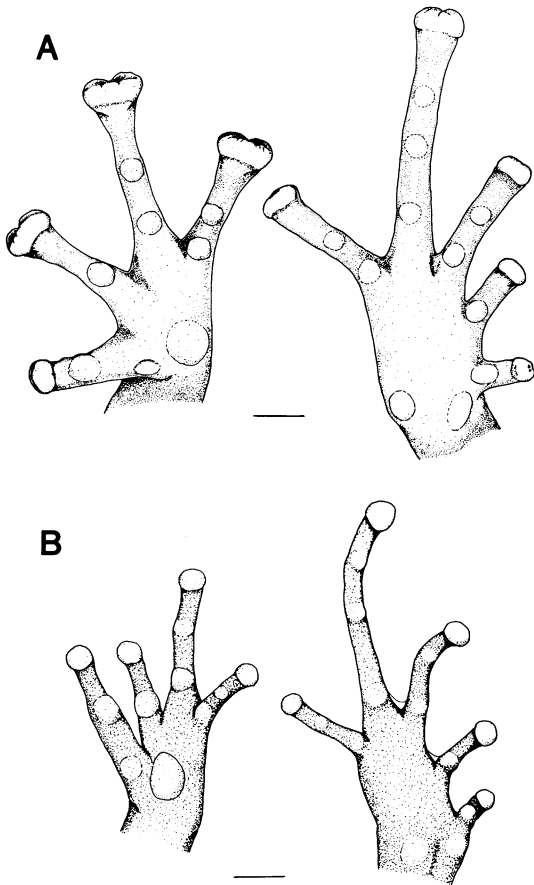
A

B

FIG. 3. Left hands and right feet of pale-spotted poison frogs in lower Central America, drawn to same scale (lines = 1 mm.). A. *Dendrobates arboreus,* new species (AMNH 116727 [paratopotype], the smallest adult ♀ 20.4 mm. SVL). B. *Dendrobates maculatus* W. Peters (ZMB 7817 [holotype], only known specimen, an adult ♀ 18.9 mm. SVL).

FIG. 4. Raised pigment spots ×40 on frog shown in figure 1E (AMNH 116729). The pale spots of many *Dendrobates arboreus* appear undifferentiated from surrounding skin except for containing a thin layer of bright pigment. Some specimens, however, have swollen, glandular-like bumps that seem to be active centers for synthesis or at least storage of yellow pigment.

three-fourths length of second and always failing to reach disc of second finger. Discs noticeably expanded on all except first finger. In adults, disc of third finger 1.57–2.00 times wider than distal end of adjacent phalanx, averaging little wider in males than in females (table 1); discs relatively less expanded in juveniles, the third finger disc being only 1.50–1.60 ($\bar{x} = 1.567$) times wider than finger in three females <16 mm. SVL. A large circular to elliptical outer metacarpal tubercle on median base of palm, a small, inconspicuous inner metacarpal tubercle on base of first fin-
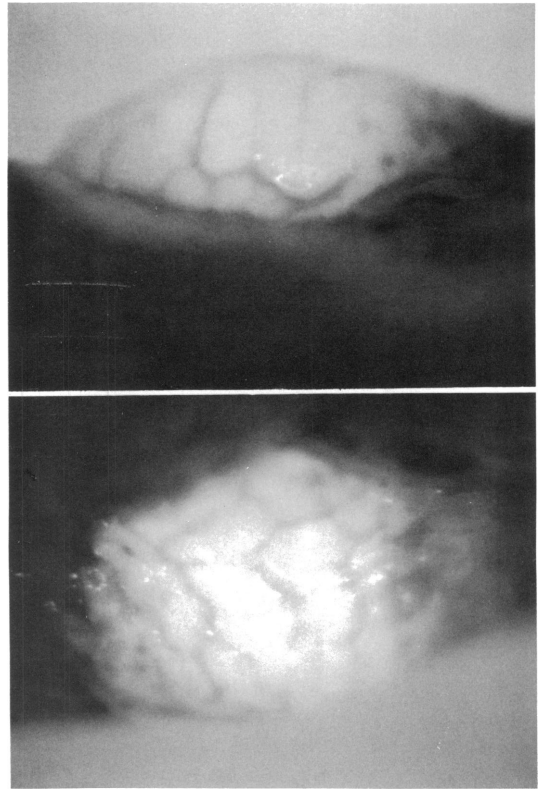
ger, and one or two subarticular tubercles on fingers (one each on fingers 1, 2, two each on fingers 3, 4); all tubercles low, with rounded surfaces.

Hind limbs rather short, with heel of appressed limb failing to reach eye but usually reaching tympanum; tibia 38–43 percent of SVL in adults, there being neither sexual dimorphism (table 1) nor ontogenetic differences (tibia 40–41% of SVL, $\bar{x} = 40.2\%$, in three juvenile females). Relative lengths of appressed toes 4 > 3 ≥ 5 > 2 > 1; first toe short but not exceptionally so, reaching at least to base of subarticular tubercle on second toe. First toe with unexpanded disc; other toes with distinct, slightly expanded discs

(smaller than those on fingers). Small inner and outer metatarsal tubercles usually about the same size but with the outer one being more protuberant. One to three nonprotuberant subarticular tubercles (one each on toes 1, 2, two each on 3 and 5, three on 4), often indistinct, especially on toes 4 and 5. A small, usually weak tubercle on inner side of tarsus; a weak tarsal ridge present or absent, when present extending from aforesaid tarsal tubercle to or toward inner metatarsal tubercle. Hands and feet lacking webbing, supernumerary tubercles, or lateral fringe (although normal keels are present on ventrolateral edges of digits).

In life (fig. 1), adult frogs are patterned dorsally and ventrally with bright yellow spots on a virtually uniform ground color of black, blackish brown, or, most commonly, brown with a slight bronzy tinge.[5] The usually round spots are normally smaller than the eye and tend to be well spaced. Positioning of the spots is variable (figs. 1, 2), although there is a tendency for them to be absent or sparse middorsally, with some individuals (e.g., fig. 1B) showing a linear dorsolateral alignment of the uppermost spots; the spots tend to be more numerous and widely distributed on the ventral surfaces of throat, belly, and limbs. A few individuals have spots that are noticeably raised (fig. 4); one individual is nearly spotless (fig. 1C). A few small juveniles differ from adults in having greenish bronze dorsa and black venters, with inconspicuous (not vivid) pale yellow spots; the smallest juvenile (13 mm. SVL) had an unspotted greenish bronze dorsum and pale *blue* ventral spots (blue pigmentation not seen on any other specimen). The iris is brown in life, with almost no contrast between it and the pupil in normal daylight, under which the eye appears uniformly black. In preservative, the specimens are blackish with the yellow spots fading to white.

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[5] Under a dissecting microscope, the bronzy tinge of living frogs is seen to be caused by suffusions of metallic bronze and (in some individuals) pale yellowish green, these colors being confined to epidermal depressions around the slightly raised, dark brown granulations. Such pigmentation may be more developed dorsally than ventrally, but in most adult specimens the dorsal ground color is no lighter than the dark ventral color.

MYOLOGY AND OSTEOLOGY

MYOLOGY: Dissection of jaw and thigh musculature was done on eight specimens before clearing and staining (AMNH 116761–116768). The following taxonomically important muscles showed constant patterns. A massive superficial slip of the m. depressor mandibulae originates from the dorsal fascia and conceals a smaller, deeper slip originating from the otic ramus of the squamosal bone; the latter slip also includes a comparatively few fibers that originate from the posterodorsal margin of the tympanic ring but do not themselves seem to form a discrete slip. The large superficial slip of the depressor mandibulae conceals the rear of the tympanum as is typical in dendrobatids. There is no m. adductor mandibulae externus. On the thigh, the distal tendon of the deep m. semitendinosus pierces the tendon of the mm. gracilis complex prior to insertion. The flesh of *Dendrobates arboreus* is heavily pigmented, appearing deep black in freshly skinned specimens.

OSTEOLOGY: Skull about as wide as long. Frontoparietals long, fused along their entire length, with median suture faint. Sphenethmoid large, closely encircling and fused with anterior end of frontoparietal pair and fused with nasal bones; a ventrolateral process from sphenethmoid extending either nearly to or (usually) well separated from facial lobe of maxillary. Nasal bones widely separated, posterolaterly failing to reach facial lobe of maxilla. Palatine bones absent. Vestigial prevomers toothless, small and widely separated, lying beneath lateral sides of nasal bones; each prevomer usually with a slender or threadlike posteroventral process extending toward lower edge of orbit. Maxillary and premaxillary teeth absent. Alary processes of premaxillae tipped slightly forward. Maxillary posteriorly shallow, anteriorly with a low facial lobe; with or without a small, anteriorly directed preorbital process on maxillary facial lobe. Eight presacral vertebrae, with some fusion in all eight specimens: vertebrae 2+3 fused dorsally and ventrally in all; vertebra 8 fused dorsally and ventrally with ninth (sacral) in seven of eight specimens; vertebra 1 (cervical) fused dorsally and ventrally with vertebrae 2+3 in one specimen, partially
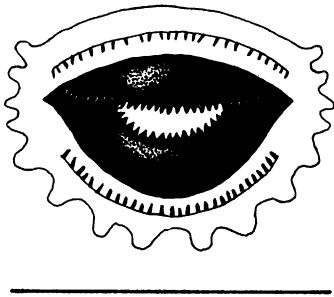
FIG. 5. Mouth of *Dendrobates arboreus* tadpole, stage 28–29 (semidiagrammatic, based on AMNH 117643). Line equals 1 mm.

fused in another. Neural spines of vertebrae somewhat irregularly flattened, sometimes with several being slightly expanded laterally, thus forming very narrow "shields" atop some vertebrae. Omosternum absent in two individuals, present in six others; cartilaginous when present and varying from a short to a relatively long style.

TADPOLES

Tadpoles were not found in the field despite a search of many bromeliads, but several larvae were hatched by placing captive-laid eggs in water (see Breeding Biology and Egg Cannibalism). One clutch hatched 14 days after laying. The larvae were not seen to feed although they were offered a variety of food (boiled lettuce, bits of fresh chicken heart, drops of both raw and cooked chicken-egg yolk, and eggs of their own species); growth apparently was due entirely or mainly to their own yolk reserves, and all those not preserved died before metamorphosis.

One tadpole preserved immediately after hatching is in stage 28 of the Gosner system (external gills absorbed, small limb buds as wide as long), with a total length of 9.6 mm. The largest tadpole had advanced only to stage 29 (limb buds 1.5 times longer than wide), although it had increased its length by about 80 percent, to 17.6 mm.; this larva was preserved after it had died, probably from starvation. The following description is based on the five larvae preserved (AMNH 117643) at the time of this writing.
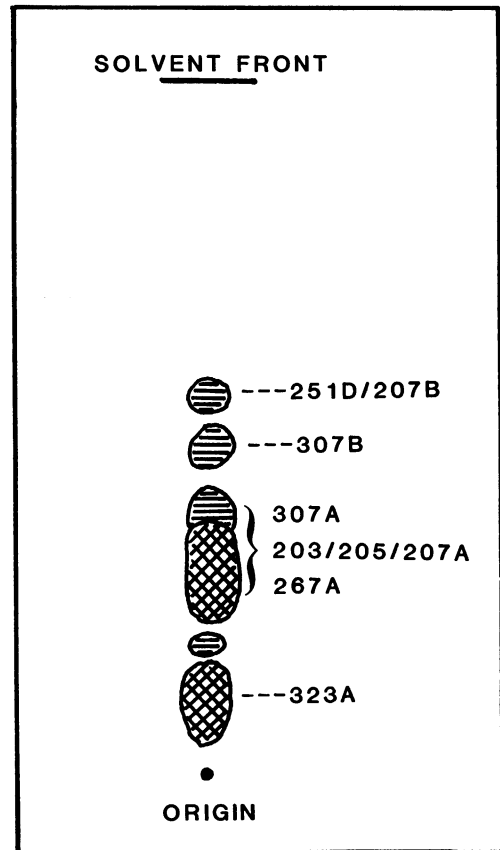
HABITUS, PROPORTIONS, AND MEASURE-

FIG. 6. Representation of a thin-layer chromatoplate of alkaloids from *Dendrobates arboreus*. A sample of 10 μl of methanolic alkaloids equivalent in amount to 10 mg. wet skin was applied at the origin and the silica gel GF plate (Analtech Co.) developed with 9:1 chloroform : methanol. Visualization, after chromatography and drying was by exposure to iodine vapor. Spot intensities depicted as follows: Cross-hatched pattern = large amounts; horizontal pattern = moderate amounts (reference standards are figs. 1–2 in Myers and Daly, 1976). The approximate positions of various alkaloids are indicated; alkaloids are designated by their molecular weights and, where necessary, with an added code letter.

MENTS: Viewed from above the head and body form an elongated ellipse rounded at both ends, with body width averaging 57.6 percent (53–60%) of head–body length. The head and body are depressed (width distinctly greater than depth), slightly convex above, concave below. Eyes and nostrils in a dorsal position,
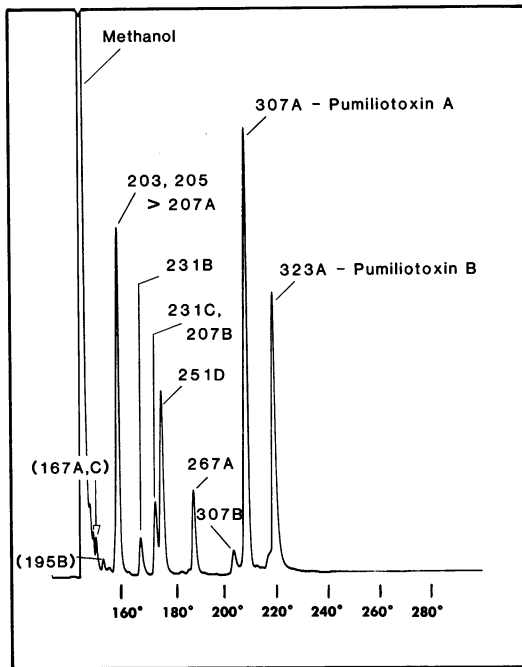
FIG. 7. Gas chromatogram of alkaloids from *Dendrobates arboreus*. A sample of 2 μl of methanolic alkaloids equivalent in amount to 2 mg. wet skin was injected at 150°C. onto a 1.5% OV-1 on Chromasorb G AW-DMCS (Applied Science Laboratories) column. After the maximum for the methanol solvent peak was passed the column was programmed at 10° per min. from the initial 150° to 280°C. Emergent temperatures differ somewhat with different batches of column packing. A flame ionization detector was used. Alkaloids identified by combined gas chromatography–mass spectrometry are designated by their molecular weights and, where necessary, with an added code letter; parentheses indicate trace compounds.

with eyes directed anterolaterally and nostrils dorsolaterally. The spiracle is sinistral and low, and the anus medial. The long, low-finned tail averages 66.6 percent (65–69%) of total length, and its greatest depth (nearly uniform throughout) is only 13.0 percent (11–15%) of total length. The dorsal fin reaches the body although it is somewhat indistinct at its anterior terminus; the end of the tail is rounded.

The following measurements, in millimeters, pertain to the smallest tadpole (new hatchling, stage 28), and the second largest

one (stage 28–29), respectively: Head–body length 3.0, 5.4; greatest body width 1.6, 3.2; total length 9.6, 16.2; greatest tail depth from upper edge dorsal fin to lower edge ventral fin 1.2, 2.4; width of oral disc 0.6, 1.0 (fig. 5).

PIGMENTATION: In preservative, the head and body are rather uniform grayish brown, with sparser pigmentation on the translucent venter. The tail is pale grayish brown, with scattered white flecks over the caudal musculature and on the fins, becoming transparent towards the end.

MOUTHPARTS: The mouth is directed anteroventrally. The toothrow formula is 1/1 (possibly 0/1 in one with damaged mouth), sometimes with an irregularly positioned gap in one or both rows. The beak is massive, with coarsely serrate cutting edges (fig. 5); it is incompletely keratinized in the smallest individuals, especially the new hatchling. The lower beak is rounded, not indented or V-shaped. The oral disc is not indented laterally. The anterior edge of the oral disc is nude, but its lateral and posterior edges bear a single row of about 12–17 large, rounded papillae.

The larval mouthparts of *Dendrobates arboreus* are very similar to those of the egg-eating tadpoles of *Dendrobates pumilio* and *D. histrionicus* (Weygoldt, 1980; Zimmermann and Zimmermann, 1981), as may be seen by comparing figure 5 with the illustrations in Silverstone (1975, figs. 18, 21).

SKIN ALKALOIDS AND TOXICITY

Analysis was carried out with two samples of 10 skins each from specimens collected at the type locality on January 21, 1983. Specimens were skinned and skins placed in methanol for transport at ambient temperature until eventual storage at −5°C. The blotted wet weight of each 10-skin sample was 0.9 g., for a calculated average wet weight of 90 mg. per frog. Alkaloid fractions were prepared from methanol extracts and analyzed by thin-layer chromatography (fig. 6) and by combined gas chromatography–mass spectrometry (fig. 7). Results obtained for the two 10-skin samples were identical.

ALKALOIDS: The extracts from *Dendrobates arboreus* contained 14 alkaloids (table

TABLE 2
Alkaloids from *Dendrobates arboreus,* New Species

Alkaloid[a]	Empirical Formula	Major Mass Spectral Ions (m/e)[b]	Exchangeable Hydrogen[c]	Perhydro- Derivative[d]	Occurrence in *D. arboreus*[e]
Pumiliotoxin-A Class					
1) **251D**	$C_{16}H_{29}NO$	166, 70	1	H_2	+ +
2) **307A**	$C_{19}H_{33}NO_2$	166, 70	2	H_4	+ + +
3) **307B**	$C_{19}H_{33}NO_2$	166, 70	1	H_2	+ +
4) **323A**	$C_{19}H_{33}NO_3$	166, 70	3	H_4	+ + +
Allopumiliotoxin-A Class					
5) **267A**	$C_{16}H_{29}NO_2$	182, 70	2	H_2	+ +
Unclassified					
6) **167A**	$C_{11}H_{21}N$	138	0	H_0	+
7) **167C**	$C_{11}H_{21}N$	166	1	H_0	+
8) **195B**	$C_{13}H_{25}N$	138	0	H_0	+
9) **203**	$C_{14}H_{21}N$	138	0	H_6	+ + +
10) **205**	$C_{14}H_{23}N$	138	0	H_4	+ + +
11) **207A**	$C_{14}H_{25}N$	138	0	H_2	+ +
12) **207B**	$C_{13}H_{21}NO$	166	1	H_2	+ +
13) **231B**	$C_{16}H_{23}N$	152	0	H_6	+ +
14) **231C**	$C_{16}H_{23}N$	138	0	H_6	+ +

[a] Alkaloids are designated by molecular weight in boldface type, followed where necessary by a code letter to distinguish from other dendrobatid alkaloids of the same weight.

[b] Major ions are for electron impact mass spectrometry.

[c] The exchangeable hydrogens were assessed by chemical ionization mass spectrometry with deuteroammonia.

[d] The degree of unsaturation was determined after perhydrogenation with palladium charcoal catalyst (H_0 = no addition of hydrogen).

[e] + + + = present as major compound; + + = minor compound; + = trace compound.

2). Four of these were of the pumiliotoxin-A class, typified by major mass spectral fragment ions at masses of 166 and 70. The structures of pumiliotoxins **251D**, **307A** (pumiliotoxin A) and **323B** (pumiliotoxin B) have been determined (Daly et al., 1980), whereas the structure of pumiliotoxin **307B** remains poorly defined. It is of interest that while **307B** has the same empirical formula as pumiliotoxin A, it contains one hydroxy group rather than two as based on the presence of only one exchangeable hydrogen. The other oxygen is probably present as an ether. In addition to the four pumiliotoxin-A class alkaloids, one member of the allopumiliotoxin-A subclass was present in *D. arboreus.* The allopumiliotoxins differ from other compounds of the pumiliotoxin-A class in having a 7-hydroxy substituent. Thus, allopumiliotoxin **267A** of *D. arboreus* is in fact the

7-hydroxy derivative of pumiliotoxin **251D**. Alkaloids of pumiliotoxin-A class and its allopumiliotoxin-A subclass occur commonly in many species of *Dendrobates.* The macrosympatric *Dendrobates speciosus* contains pumiliotoxins **251D**, **267A**, **307A**, and **323A**. Mainland populations of *D. pumilio* from the adjacent Atlantic lowlands (Río Guarumo Valley) contain **251D**, **267A**, **307A**, and **323B**. The mainland population of *D. auratus* from the same lowlands contains only **267A** of this alkaloid class, but other populations of this species contain a range of alkaloids from the pumiliotoxin-A class and the allopumiliotoxin-A subclass.

A recent new technique using deuteroammonia as the ionizing gas for chemical ionization mass spectrometry has revealed that many of the alkaloids previously tentatively assigned as secondary amines of the pumil-

iotoxin-C or hydroxypumiliotoxin-C classes of dendrobatid alkaloids (Daly et al., 1978) are actually tertiary amines. Until the structures of these tertiary amines (probably variously substituted pyrrolizidines, indolizidines, and quinolizidines) are better defined they have been placed among the "unclassified dendrobatid alkaloids" (Daly, 1982). The extracts from *D. arboreus* contain seven such tertiary amines (compounds 6, 8–11, and 13–14, in table 2), all of which lack an exchangeable hydrogen. Compound 7 (**167C**) does contain an exchangeable hydrogen and is thus a secondary amine, perhaps of the pumiliotoxin-C class. Compound 12 (**207B**) has an exchangeable hydrogen, but that is undoubtedly present on the oxygen (alcohol) function and this alkaloid thus represents another tertiary amine. There is insufficient data for more than speculation as to the structure of alkaloid **207B**; it seems possible that it is a member of the pumiliotoxin-A class.

Six of the tertiary amines, namely **167A**, **195B**, **203**, **205**, **207A**, and **231C** of *D. arboreus* are all closely related in structure, affording on electron-impact mass spectrometry a base peak at m/e 138 ($C_9H_{16}N^+$) which undoubtedly corresponds to a bicyclic ring system (quinolizidine or methylindolizidine). Thus, these six alkaloids differ only in the nature of the side chain as follows: **167A**, -C_2H_5; **195B**, -C_4H_9; **203**, -C_5H_5 (one double, one triple bond); **205**, -C_5H_7 (two double bonds or a triple bond); **207A**, -C_5H_9 (one double bond); **231C**, -C_7H_9 (one double, one triple bond). Alkaloids of this group (base peak m/e 138, no exchangeable hydrogens) are widely distributed among dendrobatid frogs. For example, **167A**, **195B**, and **207A** occur in the macrosympatric *D. speciosus*. The seventh simple tertiary amine, alkaloid **231B**, is a relatively common dendrobatid alkaloid, also occurring for example in macrosympatric *D. speciosus*. This alkaloid exhibits a base peak at m/e 152 ($C_{10}H_{18}N^+$); that is, the ring fragment contains one methylene group more than in the six alkaloids discussed immediately above. The side chain lost in **231B** is -C_6H_7 (one double, one triple bond).

Alkaloids **231C** and **207B** have not been detected in any species other than *Dendro-*

bates arboreus, while **167C**, which has not been previously documented, does occur in certain other dendrobatids (unpubl. data).

TOXICITY: Subcutaneous injection of methanolic extract equivalent to 100 mg. of wet skin (one skin ~90 mg.) led to the following results. After initial agitation, the mouse exhibited severe locomotor difficulties, thrusting extensor movements of the hind limbs, labored breathing, gagging, followed by convulsions and death within six minutes. *Dendrobates arboreus,* thus, is a relatively toxic dendrobatid as might be expected from the presence of pumiliotoxins A and B as major alkaloids.

DISTRIBUTION AND NATURAL HISTORY

DISTRIBUTION: *Dendrobates arboreus* occurs in western Panama, where it is only known from one site in the Atlantic lowlands and from adjacent mountains in the vicinity of the continental divide. The few localities are situated north of parallel 8°46'N, between meridians 82°10'–82°13'W. The species is abundant on the continental divide and also was heard calling in the Pacific drainage (Chiriquí Province) just south of the divide, at about 1050 m. elevation near the upper Quebrada de Arena. This stream drains into the highland valley (about 1000 m. elev.) of the upper Río Chiriquí. *Dendrobates arboreus* was not found during a faunal survey of the lower end of this high, wet valley (Myers and Duellman, 1973, p. 12), and we assume that its distribution is especially limited on the Pacific versant.

On the Atlantic versant, the elevational range of *Dendrobates arboreus* seems surprisingly great, suggesting that the species might have a considerably larger distribution than now known. The two lowland specimens from west of Chiriquí Grande are from an elevation no greater than 20 m., whereas the highland localities are 1050–1300 m. above sea level. But *D. arboreus* does not seem to be continuously distributed in the 18 km. between the highland and lowland sites, since we did not hear it calling in the intervening forest between 500–800 m. elevation in the upper Río Guabo drainage.

HABITAT AND BEHAVIOR: The two speci-

mens from the Atlantic lowlands were found by Martínez on the buttresses of a large tree in an area of low, rather swampy rain forest. The habitat on the continental divide is a much cooler cloud forest (fig. 8), which receives almost daily fog that is frequently accompanied by rain and mist. This cloud forest is a facies of high-canopied lower montane rain forest. Tree growth is very dense, and there is a frequently dense herbaceous and fern layer at ground level. There is a modest "moss layer" on the trunks of trees, which support a profusion of epiphytic growth, including bromeliads. There are few bromeliads near the ground, although they are common higher in the trees, especially above 10 m.

In nearly three weeks on the continental divide, we found only one adult and one juvenile *D. arboreus* on the ground in undisturbed forest. Nonetheless, it is an abundant species at least on that section of the continental divide from 82°12′31″ to about 82°13′W. This was evident from the frequency of calling that we heard in the ridge-top cloud forest, where, as near as we could judge, the frogs were calling from bromeliads or other epiphytes well above the 10-m. level. This was substantiated by cutting down an 18-m. tree isolated near the edge of a clearing (near site shown in fig. 8). Nine specimens of *D. arboreus* were taken from this tree, which was stripped of all vegetation after being felled; eight *Dendrobates* (some still in their bromeliads) were at the 13–16-m. level and one was on the trunk at the 5-m. level.[6] We confidently characterize the new *Dendrobates* as a highly arboreal species, with most of the population at the type locality existing at subcanopy heights in the cloud forest (estimated canopy height ∼ 18–20 m.). We suspect, however, that the vertical range of the frogs in any given tree depends primarily on bro-

[6] Other amphibians and reptiles inhabiting this tree, and their approximate heights aboveground, were as follows: one *Bolitoglossa* sp. (15 m.), one *Hyla uranochroa* (14 m.), five *Hyla zeteki* (13–16 m.), two *Eleutherodactylus diastema* (14–15 m.), three small *Eleutherodactylus* sp. (14–15 m.), three large *Eleutherodactylus* sp. (3–15 m.), one male and one female *Anolis insignis* (10–13 m.), and one *Leptodeira annulata* (16 m.).

meliad distribution rather than on height per se.

Despite the difficulty of collecting *Dendrobates arboreus* in undisturbed forest, specimens were easily obtained from bromeliads on trees that had been felled during road construction. The fallen trees were on a steep mountain side, where the original forest floor was buried under new earth pushed downslope from the construction area. The trees had been felled some months previously and were well isolated from one another by barren soil, which may have inhibited the frogs from migrating to nearby forest. *Dendrobates arboreus* appeared to occur mainly on those trees still supporting water-filled bromeliads, where all but a few of the frogs were found. When approached, they tended to back themselves down into the water in the base of the plant, but they seemed less averse to trying to leave their bromeliads than was the sympatric *Hyla zeteki*.

SEX RATIO: The 1983 sample of 47 specimens was obtained at the type locality primarily by searching bromeliads on fallen trees, where only a few males were caught by tracing their calls. Excluding three juvenile females, there are 27 females to 17 males (1.6:1.0) in the sample of 44 adults. This difference is not statistically significant at this sample size ($\chi^2 = 2.2727$, $P = 0.1317$).

BREEDING BIOLOGY AND EGG CANNIBALISM: Neither eggs nor larvae were found in the field. The tadpoles are probably carried to the water in bromeliads, but those plants searched on fallen trees contained none. Absence of larvae conceivably might have been due to cannibalism of eggs by adult frogs that probably were abnormally concentrated amongst the relatively few bromeliads that still contained water (the frogs were mostly absent from dry bromeliads). Clutches of four to eight eggs ($\bar{x} = 5.0$, $N = 9$) were laid in captivity, with the deposition sites being in exposed places on bromeliad leaves, 3–20 cm. out from the basal part of the leaf. If left in place, the eggs were cannibalized by adult (presumably nonparental) *D. arboreus*. One adult frog seen eating eggs was removed from the terrarium and was determined to be a female (vocal slits absent). Tadpoles were obtained for study by removing eggs and placing

FIG. 8.   Canopy of cloud forest at type locality of *Dendrobates arboreus*, which inhabits epiphytic growth high on the trees. Photographed January 26, 1983, looking north from 1120 m. elev. on continental divide (border between provinces of Chiriquí and Bocas del Toro), western Panama.

them in water; one such clutch hatched 14 days after laying.

Aggressive grappling among males has not been seen (although such behavior is commonplace in *D. pumilio* and often is performed by freshly caught frogs confined in plastic bags). A brief instance of typical cephalic "amplexus"[7] might have been aggressive behavior; the amplexing individual was a male but the sex of the other one was not determined. In any case, amplexus was ab-

[7] Stylized *cephalic* amplexus (Myers and Daly, 1983, p. 120) appears to be a synapomorphy of the Dendrobatidae and at the same time to be primitive within the family, since amplexus has been dropped from the mating behavior of some dendrobatids. In some species, grasping identical with that of cephalic amplexus seems to have been incorporated into the aggressive repertory (Myers, Daly, and Malkin, 1978, p. 324).

sent from a few observed matings of captive frogs.

The most completely observed bout of courtship and egg laying was complicated by an act of mate piracy by a late-arriving second male. The courtship apparently had just begun when a female was seen approaching a calling male who was sitting on the outer end of a bromeliad leaf, facing inward toward the base of the plant. The female crouched facing the sporadically calling male, retaining this position for ~5 min. while occasionally shifting her body slightly and briefly drumming her hind feet against the leaf. She finally moved a bit closer and with an appearance of deliberateness reached out several times with her right hand and softly touched the male's snout—which in retrospect seems to have signified her acceptance of the male.

After being patted on the snout, the male

jumped 12 cm. to the ground, immediately followed by the female. Both then climbed back onto the bromeliad, the female following the still-calling male who crawled out to the middle of a different leaf where oviposition was to occur. He quit calling and turned toward the center of the plant and the female again crouched with lowered head before him. Now, however, she began turning her body in circles, both clockwise and counterclockwise, slowly and irregularly, frequently moving her hands up and down and drumming the leaf with her hind feet. While turning in these little circles she often bumped against the waiting male. On such occasions he patted her hindquarters or flanks with one of his hands. This female-turning and male-patting behavior lasted more than 20 min., during which time the male was silent.

After about 15 min. of the above behavior, a second, silent male approached the courting frogs. He moved slowly up the leaf to within several cm. and watched intently from a frozen, crawling position. After several minutes he moved slightly closer, then again remained motionless in a crawling posture (a position never taken by the first male, which paid no apparent attention to the intruder). Finally, at a time when the female had her back turned to the first male, the intruding male moved forward and touched snouts with her. The female and second male thereupon immediately turned in half-circles and assumed vent-to-vent contact with each other. The original male meanwhile was moving alongside, and, being unable to make direct cloacal contact with the female, placed his hind quarters atop those of the female and second male, facing away from them at a right angle.

Almost as soon as the trio of frogs had assumed the position described, the female began laying eggs accompanied by muscular contractions of her flanks, and within seconds the original male had ejaculated a clear fluid over the lower backs of the female and second male. The "pirate" male presumably also ejaculated although this could not be seen; in any case he was clearly in a better position to flood the eggs with seminal fluid, whereas that of the first male was largely wasted on the others' backs.

The original male left a minute or so after ejaculation and the intruding male left a few minutes later. Having laid eight eggs, the female remained atop the clutch, occasionally shifting her body or turning in another direction; she left the clutch 35 min. after laying. The original male was lost sight of, but the pirate male concealed himself close by in the base of the bromeliad, where he called periodically. One hour after the female had left the eggs, the pirate male returned and sat for some minutes atop the clutch, which would seem to reinforce the probability that he had contributed sperm to the mating.

Considering the somewhat complicated courtship behavior, it seems extraordinary that another male—without having been involved in any of the tactile signals given by both sexes of the original pair—could successfully introduce himself into a late stage of the proceedings. It could not be determined whether the female signaled in some way that oviposition was imminent, but the snout-touching initiated by the second male appeared to be the stimulus for them to attain the most favorable position for fertilization, thus giving the advantage to the pirate male. But in another case the impetus for male fertilization seemed to be visual, after oviposition had commenced. A female was first observed drumming her feet and turning in circles, as described above, in the proximity of a silent male who occasionally patted her hindquarters and who crawled around her while watching intently. She started to lay without an immediately prior physical contact; the male watched the first egg being extruded and then assumed a vent-to-vent position. When this female began to lay the first of a total of four eggs, it could clearly be seen that it was she that voided also a quantity of water that wet the oviposition site. The male left the site within a minute after assuming the vent-to-vent position; fertilization had occurred in this brief period, as determined by microscopic examination that revealed the presence of sperm on the egg clutch.

Clearly there is some plasticity in the mating behavior, at least of males. Calling males also were seen hopping after apparently uninterested females, although in the first case described it was a female that approached a stationary calling male.

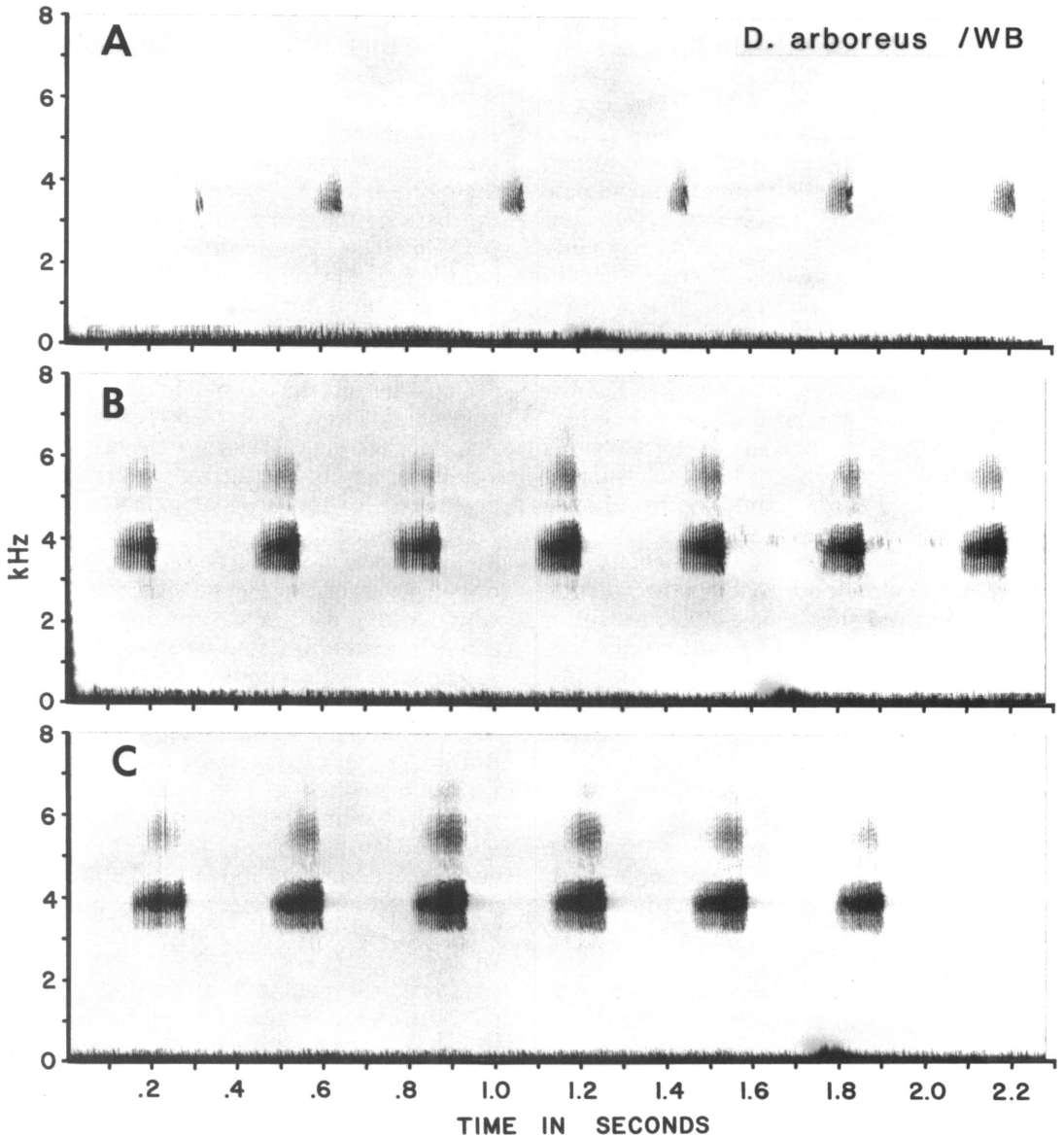VOCALIZATION: In the undisturbed cloud

FIG. 9.   Wide-band (300-Hz filter) sound spectrograms of beginning (A), middle (B), and end (C) of a 17-seconds-long chirp call of *Dendrobates arboreus,* new species, from 1120 m. elevation at type locality. Specimen calling by day in tangled vegetation on fallen tree, 20.0°C. at calling site, January 24, 1983 (AMNH 116748 on AMNH reel 245:3). See figure 10A for narrow-band equivalent of call segment B above.

forest males were heard calling only high aboveground. In recently cleared forest they were calling mainly from bromeliads on felled trees, although a few also were found calling within tangles of vegetation on the fallen

trunks. One individual was recorded in the field and numerous other recordings were obtained from freshly caught frogs confined in plastic bags.

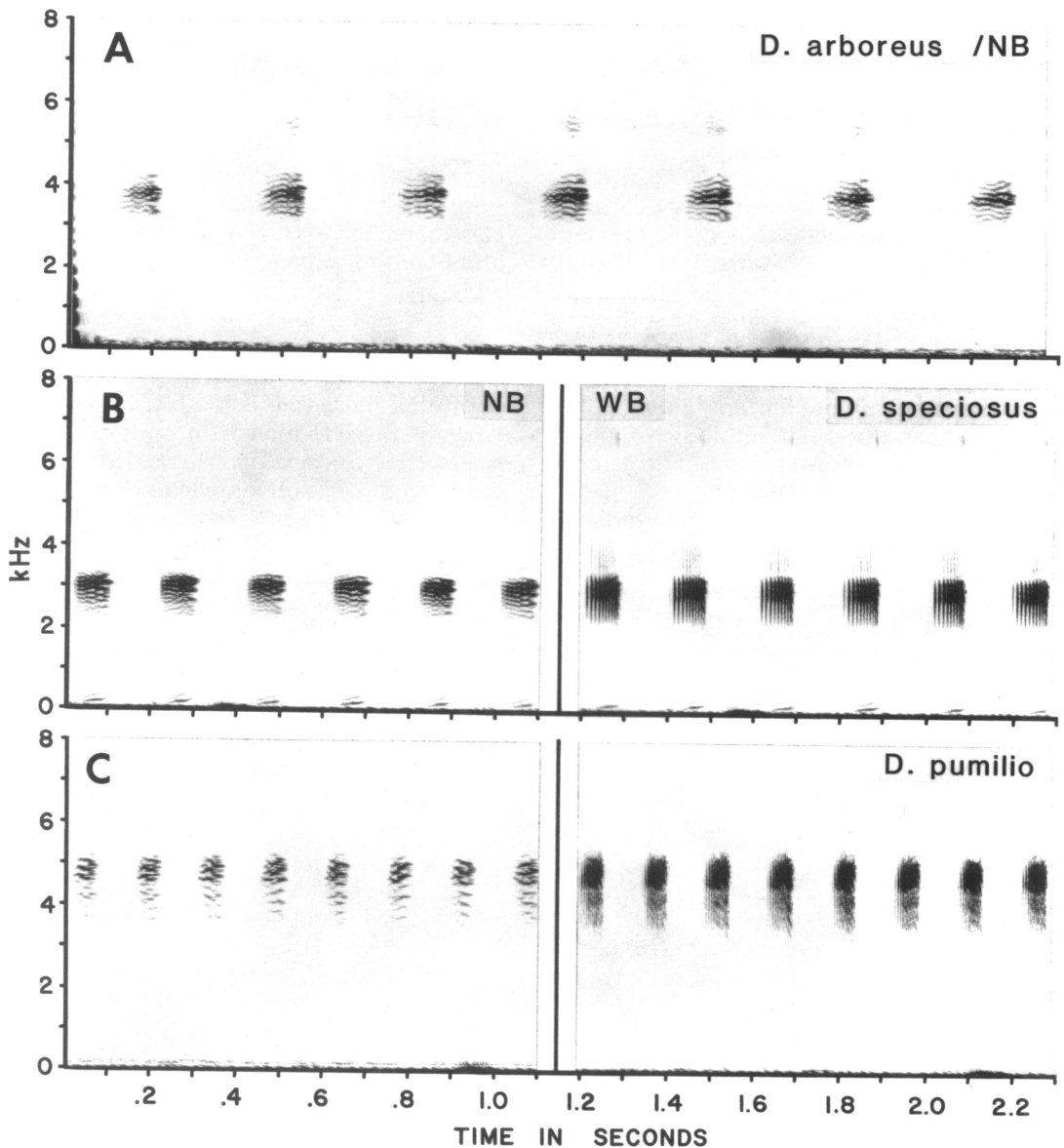In 22 recordings, the call is a short to mod-

FIG. 10.   Chirp calls of three species of *Dendrobates* in western Panama. The auditory quality of these calls is very similar, but notice the diagnostic species differences in rate of repetition of notes, in duration of individual notes, and in dominant frequency. Top spectrogram (A) graphed with narrow-band (45 Hz) filter (see fig. 8B for wide-band equivalent). Other two spectrograms (B, C) shown in narrow-band on left side, wide-band on right.

A. *Dendrobates arboreus,* new species, data as in figure 9 (20.0°C.). B. *Dendrobates speciosus* from 1300 m. elev. on continental divide at 82°13'40"W, Chiriquí-Bocas del Toro border; 17.8°C. at calling site (AMNH reel 246:4). C. *Dendrobates pumilio* from 7.5 km. WSW Chiriquí Grande, 10 m. elev., Bocas del Toro; 25.0°C. at calling site (AMNH reel 232:1).

erately long (7–60 sec., $\bar{x}$ = 26.7 sec.) train of harsh notes given at a rate of 3–4 notes per sec. Note duration is as short as 0.02–0.07 sec. at the start of some calls (fig. 9A), in-

creasing to about 0.10–0.15 sec. throughout most of the train (fig. 9B); in at least some calls the last note or so may be somewhat shorter than those preceding (fig. 9C). Sections show a dominant frequency peak usually at about 3800 Hz in a total range of about 3700–4000 Hz; the frequency appears to be fairly constant throughout a given train of notes, although one call started at a low of 3500 Hz before increasing to 3800 Hz.

One to several chirps sounding similar to those in the longer trains often are given intermittently. Spectrograms of several such notes show them to be shorter (4 notes, 0.07–0.10 sec.) than those in the middle of longer calls, and to have a lower dominant frequency at about 3300–3400 Hz.

Successive calls even of the same individual may vary considerably in length. A 2 min., 27 sec. field recording of one specimen contains a sequence of five calls of 22, 7, 17, 4, and 42 sec. duration (excluding intermittent chirping).

The rate at which notes are produced within a train, and the pulse rate, appear to be positively correlated with temperature. A specimen was recorded in the field (see above) at 20.0°C. at the calling site. Spectrograms from the beginning, middle, and end of each of five calls consistently contained 6–6.5 notes in 2-sec. intervals, for a rate of 3.0–3.25 notes/ sec. In contrast, spectrograms from the middle of 16 calls (of captives) at 22.1°C. had rates of 3.5–4 notes/sec. The pulses were individually discernible in wide-band spectrograms of calls recorded at the lower temperature (mean pulse rate = 174/sec., range = 142–192, in 24 notes from five calls). Only some of the pulses (usually in the first part of the note) can be counted on wide-band spectrograms of calls recorded at the higher temperature—partly because of recording-level "overload" but also partly because of increased pulse rate; several notes from these spectrograms, however, show rates of 200/ sec., which is approaching the apparent limit of resolution (~220/ sec.) of the 300-Hz filter on the sound spectrograph in use at the American Museum as of this writing. There is a slight modulation of the pulse rate at both temperatures, with pulsation being somewhat slower in the early part of the note as can be seen in figure 9.

The harsh, nonmusical notes of *Dendrobates arboreus* have much the same auditory quality as the vocalizations of species such as *D. histrionicus, D. pumilio,* and *D. speciosus.* All these species and certain others produce rather long trains of such notes. The vocalization of *D. arboreus* consequently is classifiable as a "chirp call." But the resolvability of individual pulses in chirp notes on wide-band spectrograms (figs. 9, 10B, C) requires a restatement of Myers and Daly's (1976, p. 228) original definition of this class of dendrobatid vocalizations. Their statement that pulse rate is too fast for resolving with the 300-Hz filter is in error because of misinterpretation of overloaded recordings. Lack of appreciation for machine-induced artifacts also can be seen in their spectrograms for *D. pumilio,* in which the frequency range of the notes is excessively extended from 0–8 kHz (compare their fig. 17 with fig. 10C herein).

Chirp calls with resolvable pulses on wide-band spectrograms visually resemble "buzz calls," but the latter group of dendrobatid calls have a definite beelike buzzing quality to the human ear, whereas chirp calls have a much harsher quality. The distinction seems to be only partly due to differences in the pulse rate. Dendrobatid buzz calls so far analyzed have rates of 75–134 pulses/sec., as determined by extrapolating rates from the total pulses counted in spectrograms of individual notes. In contrast, the mean rates of three to six notes from each of five chirp calls of *D. arboreus* ranged from 160–184 pulses/sec., with a grand mean of 174 pulses/sec. In the chirp notes of *D. speciosus,* however, pulse rates are slower and overlap those of the faster buzz calls (e.g., pulse rates in 21 notes from 2 *D. speciosus* = 122–180/sec., $\bar{x}$ = 130.8 and 145.3/sec.). Thus, there is no single breaking point in pulse rates that will distinguish sounds perceived as either buzzes or harsh chirps. As another example, the lowest rate in a single *D. arboreus* chirp note was 142 pulses/sec., a rate certainly exceeded in the short, definite buzzes of *D. reticulatus,* in which a portion of the pulses are repeated much too fast for spectrographic resolution (Myers, 1982, fig. 2). Waveform analysis of buzz calls and chirp calls may help elucidate

the differences that are so evident to the human ear, but this has yet to be done.

SYSTEMATICS

Dendrobates arboreus has a distinctive color pattern of small pale spots, a pattern which, although unusual in the Dendrobatidae, is paralleled in a few Amazonian species and in the enigmatic *D. maculatus* of western Panama. This general pattern has been separately derived in several lineages of small *Dendrobates* (Myers, 1982), with *D. arboreus* providing still another example. There seems to be no detailed correspondence between the pattern of *D. arboreus* and that of any other pale spotted *Dendrobates* (see Diagnosis for names). Also, the condition of noticeably raised spots (fig. 4), seen in some specimens of *D. arboreus,* has not so far been noted in any other dendrobatid.

At the present time, the best clue to the relationships of *Dendrobates arboreus* is its vocalization (figs. 9–10)—a chirp call similar to that which characterizes all species of the *pumilio* and *histrionicus* assemblages of *Dendrobates* (Myers and Daly, 1976, p. 238). The harsh, often continuously given chirp call is suggested to be a uniquely derived character (synapomorphy) that unites the Central American *pumilio* assemblage and the South American *histrionicus* assemblage as a monophyletic unit, to be known as the *histrionicus* species group. Incomplete data on larval mouthparts (see Tadpoles) are supportive of this arrangement. The *histrionicus* group as here defined includes the following species:

1) *D. arboreus* of this paper, western Panama
2) *D. granuliferus* Taylor, southwestern Costa Rica
3) *D. histrionicus* Berthold, western Colombia and northwestern Ecuador
4) *D. lehmanni* Myers and Daly, western Colombia
5) *D. occultator* Myers and Daly, western Colombia
6) *D. pumilio* O. Schmidt, Nicaragua to western Panama on Atlantic versant
7) *D. speciosus* O. Schmidt, highlands of western Panama
8) *D.* species (Myers and Daly, in manuscript), western Panama

The closest relative (sister species) of *Dendrobates arboreus* may be number 8 above, which is another highly arboreal species of western Panama. Comparisons with *arboreus* are being deferred until the formal description of this new species (Myers and Daly, in prep.). Meanwhile it is worth noting that the eastern half of the Isthmus of Panama forms a large gap in the distribution of the *histrionicus* group. The geographic distribution of the group is therefore remarkably similar to that of the genus *Phyllobates* (Myers and Daly, 1983, map). Immunological evidence indicates that species radiation in *Phyllobates* occurred within the last five million years and that the genus entered Central America sometime after uplift of the Isthmus of Panama *ca.* three million years ago (Maxson and Myers, MS). The *histrionicus* group of *Dendrobates* may have shared a similar history, and samples of serum albumin from six of the eight species have been obtained for a test of this hypothesis (Maxson, Myers, and Daly, in prep.). It is predicted that vicariant events in Costa Rica and western Panama occurred at an earlier time than the final distributional break in eastern Panama, with the latter possibly having been due to climatic-vegetational changes in the Pleistocene. In any case, assuming that dendrobatids did not penetrate lower Central America until after the availability of the Panamanian land bridge, a relatively recent event in the eastern half of the isthmus has had a markedly disruptive influence on some dendrobatid distributions. In addition to the large gap in the distribution of *Phyllobates* and the *histrionicus* group of *Dendrobates,* there are other anomalies to be explained. Central Panamanian populations of *Dendrobates fulguritus* and *D. minutus,* for example, are widely separated from conspecific populations in the Pacific lowlands of northwestern Colombia.

APPENDIX

The following three new dendrobatid alkaloids are to be added to those previously catalogued for species of *Dendrobates* (Daly et al., 1978; Daly, 1982). Alkaloids are designated by molecular weight with an added code letter where needed. The empirical formula is based on high resolution mass spectrometry. The R_f value, where shown, is for thin-layer chromatography on silica gel with

methanol : chloroform (9:1). The emergent temperature is for gas chromatography on a 1.5% OV-1 column programmed from 150° to 280°C. (see Daly et al., 1978). The electron impact mass spectrum is given in nominal masses followed for each ion by the intensity (in parentheses) relative to the base peak set equal to 100. The perhydro derivative (H_0 = no addition of hydrogen) was obtained by catalytic reduction. The number of exchangeable hydrogens (NH and/or OH) was based on exchange with deuteroammonia during chemical ionization mass spectrometry.

167C. $C_{11}H_{21}N$, ____, 152°, m/e 167 (100), 166 (30). H_0-derivative. One exchangeable hydrogen. Trace constituent in *D. arboreus*. Has also been detected as trace constituent in certain *D. pumilio* populations (unpubl. data).

"207" becomes **207A** because of the following addition.

207B. $C_{13}H_{21}NO$, 0.47, 170°, m/e 207 (10), 190 (15), 166 (100), 70 (80). H_2-derivative m/e 209, 70. One exchangeable hydrogen. Known only as a minor constituent in *D. arboreus*.

231C. $C_{16}H_{25}N$, ____, 171°, m/e 231 (3), 138 (100), H_6-derivative m/e 237, 138. No exchangeable hydrogen. Known only as a minor constituent in *D. arboreus*.

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