American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2372 MAY 12, 1969

Snakes of the Genus *Coniophanes* in Panama

By Charles W. Myers[1]

The present paper is an account of three species of *Coniophanes* as they occur in the Republic of Panama. *Coniophanes bipunctatus* is reported from Panama for the first time, thus extending its known range approximately 625 miles southward from northeastern Honduras. A second specimen of the recently described *C. joanae* provides new data on the distribution and variation of this rare, possibly endemic snake, and allows me to place its affinities with a South American species, *C. dromiciformis*. Some observations on the wide-ranging *C. fissidens* are given also.

The genus *Coniophanes* is comprised of small-sized to medium-sized snakes that have smooth dorsal scales in 17 to 25 anterior rows that undergo reduction on the posterior part of the body; the body scales lack apical pits; anal (supracloacal) ridges may be present, especially on adult males. The head is slightly distinct from the neck, head scutellation is generalized, and the pupil is round. The tail is of moderate length, and anal and subcaudal plates are divided. The hemipenis is calyculate, capitate or not, single or bifurcated, and has a forked sulcus spermaticus. The recurved maxillary teeth are followed by a gap and two enlarged, deeply grooved fangs. The groove varies from about one-half to four-fifths of the length of the fang, the tip of which is laterally compressed and knifelike, a characteristic that Laurence M. Hardy and I have checked for each species and which may be added to the definition of *Coniophanes* in Bailey (1939). Members of the genus have at least traces

[1]Assistant Curator, Department of Herpetology, the American Museum of Natural History; Associate in Herpetology, the University of Kansas Museum of Natural History, Lawrence.

of longitudinal body striping and may resemble the related snakes of the genus *Rhadinaea;* the combination of grooved fangs and reduction in posterior scale rows distinguishes *Coniophanes* from *Rhadinaea,* although either characteristic alone normally suffices. *Coniophanes* usually is placed in the family Colubridae, although, according to Underwood (1967), it belongs to the Natricidae.

The five species of *Coniophanes* in lower Central America and South America are separable by the following key. Two species in the key do not occur in Panama. *Coniophanes piceivittis* is not found south of Costa Rica and is not discussed in the following text. *Coniophanes dromiciformis,* of Ecuador and Peru, is illustrated (figs. 7C, 8C, 9C) and compared herein with *C. joanae.*

Key to the Southern Species of *Coniophanes*

1. Dorsal scales in 21 rows anteriorly; belly usually conspicuously spotted or speckled with dark pigment. 2
   Dorsal scales not in 21 rows anteriorly; belly immaculate or with only inconspicuous dark punctuations, or belly over-all darkened with diffused pigment and smudges. 3
2. Two rows of bold black spots on the venter, with little or no additional spotting or speckling; supralabials mottled black and white. . . . . *C. bipunctatus*
   Venter usually irregularly marked with black speckles and small spots that never can be described as "large and bold" but some of which may show a tendency to form a double row; supralabials spotted or speckled rather than mottled, in some cases with a white longitudinal line. . . . . *C. fissidens*
3. Dorsal scales in 23 or 25 rows on anterior half of body; two well-defined pale stripes on a black body; ventrals not tipped with dark pigment, lower two scale rows pale like belly. . . . . *C. piceivittis*
   Dorsal scales in 17 or 19 rows on anterior half of body; striping not so distinct (dark brown on medium brown); ventral plates tipped with dark pigment from lower scale rows. 4
4. Dorsal scales in a maximum of 17 rows; belly diffused with brown pigment and with a dark smudge across base of each ventral plate. . . . . *C. joanae*
   Dorsal scales in a maximum of 19 rows; belly pale, immaculate or with inconspicuous dark punctations. . . . . *C. dromiciformis*

Abbreviations

The following abbreviations designate the depositories of specimens to which reference is made:

A.M.N.H., the American Museum of Natural History
A.N.S.P., Academy of Natural Sciences of Philadelphia
C.A.S., California Academy of Sciences, San Francisco
F.M.N.H., Field Museum of Natural History, Chicago
G.M.L., Gorgas Memorial Laboratory, Panama City, Republic of Panama
H.C.-S.R.T., collection of Howard Campbell and Sam R. Telford, Jr.
K.U., the University of Kansas Museum of Natural History, Lawrence

M.C.Z., Museum of Comparative Zoology, Harvard University, Cambridge
U.M.M.Z., University of Michigan Museum of Zoology, Ann Arbor
U.S.N.M., United States National Museum, Smithsonian Institution, Washington

Coniophanes bipunctatus (Günther)

Figures 1–4A

Coronella bipunctata GÜNTHER, 1858, p. 36. Type locality unknown.

DISTRIBUTION AND HABITAT: According to published reports (Bailey, 1939; Stuart, 1963), *Coniophanes bipunctatus* ranges from Veracruz, Mexico, to northern Spanish Honduras. It was, therefore, with considerable surprise that I caught a specimen (K.U. No. 110289, fig. 1) on Isla Escudo de Veraguas, about 20 kilometers east of the Valiente Peninsula, northwestern coast of Panama (fig. 2). Isla Escudo is uninhabited by man and is situated slightly more than 1000 kilometers (about 625 miles) southeast of Tulóa ("Toloa" on my maps), northeastern Honduras, which is the previous southernmost record for this species.

The specimen was found an hour after dark, October 17, 1966, as it was moving across soggy ground in a swamp forest (fig. 3), behind the beach on the east end of the island. It made no attempt to bite. Bailey (1939, p. 26) hinted that *C. bipunctatus* may have semiaquatic habits; it is noteworthy that the present individual was found in a swamp forest and contained remains of a gymnotid eel in its stomach. Twenty-five species of amphibians and other reptiles that I collected on the island were found also on nearby mainland areas; the other snakes were *Drymarchon corais, Leptophis depressirostris, Oxybelis aeneus,* and *Bothrops schlegeli.*

COLOR AND PATTERN IN LIFE: The five middorsal scale rows are medium brown, on which is superimposed a darker, grayish brown, vertebral line that overlaps slightly onto the paravertebral rows. A dark grayish brown lateral stripe runs the length of the body on row 4 and adjacent edges of rows 3 and 5. The body is yellowish brown between the ventrals and lateral stripe, and between lateral stripe and dorsal dark area; this ground color is palest on rows 3 and 5 on each side of the dark lateral stripe, which is thus emphasized.

The top of the head is a rich, somewhat mottled brown, but this color is not sharply delineated from the body. There is a pair of poorly defined dark dots, one on each side of the anterior part of the interparietal suture. In front of the eye, on the upper part of the preocular and the edge of the prefrontal, is a short, black-edged, white line. This line continues behind the eye as a series of three or four dashes on the upper postocular, primary temporal, and the bottom temporal in row 2. A postocular white line, heavily black-bordered above, starts at the lower

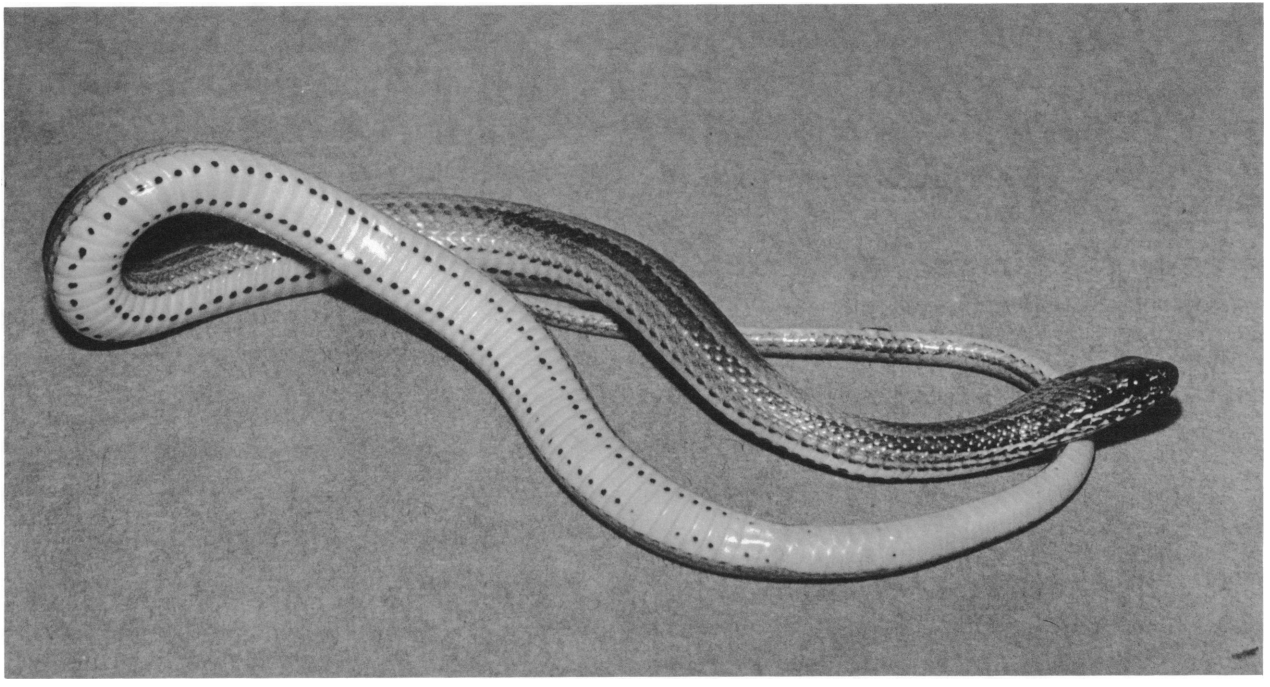

FIG. 1. *Coniophanes bipunctatus,* male, K.U. No. 110289, 380 mm. in total length. This specimen extends the known range of the species from northeastern Honduras to northwestern Panama.

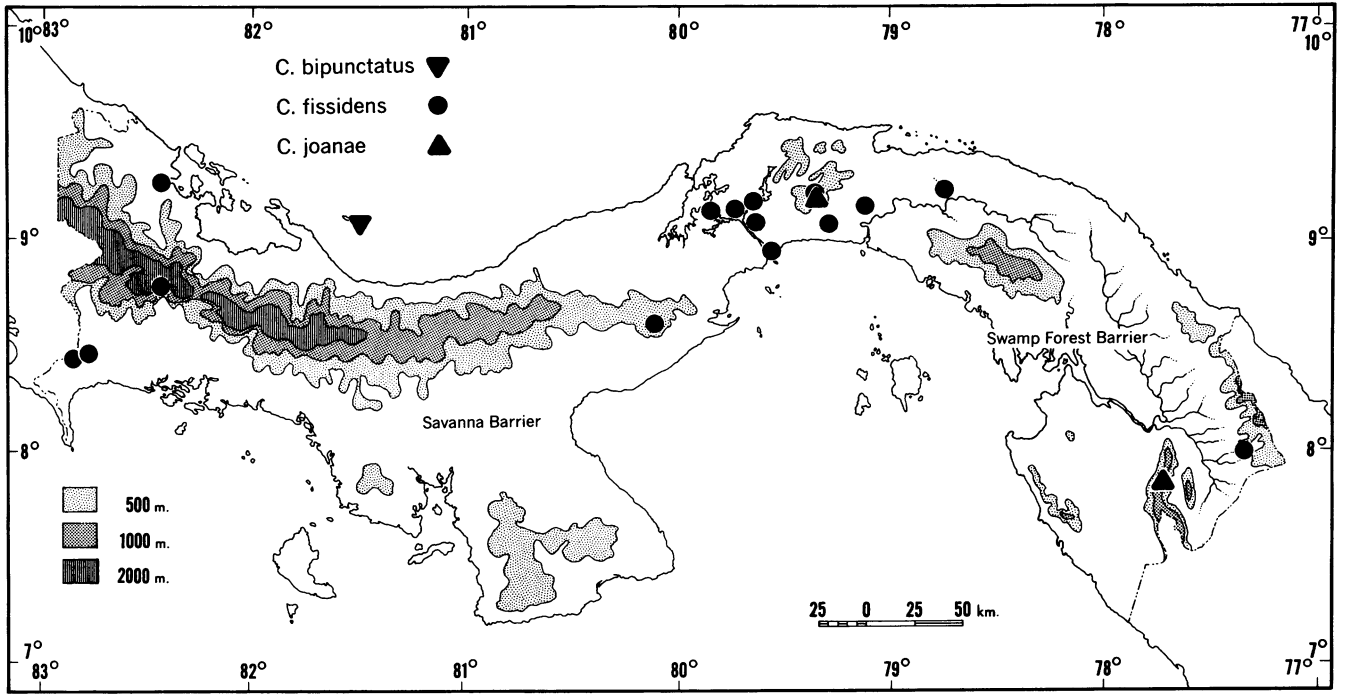

FIG. 2. Localities in Panama where species of *Coniophanes* have been collected. *Coniophanes bipunctatus* is to be expected in swamp forests on the mainland of northwestern Panama. The area of savanna is considered unsuitable habitat for *C. fissidens*. The term "swamp forest" is here meant also to include low-lying cuipo forest, obvious barriers to the distributions of *C. fissidens* and *C. joanae*. The range of *fissidens* is probably continuous along the Atlantic drainage, and *joanae* might likewise be distributed continuously along the continental divide in eastern Panama.

part of the eye and runs nearly horizontally across the last three supralabials to the corner of the mouth, there slanting slightly downward to continue caudad on the lower side of the nape on row 2, for a distance of seven scales.

The labials and under side of the head are heavily mottled black and brown on white. The venter is light yellow, turning pale orange near the edges of the ventrals, which are slightly tipped with dark brown from the sides of the body. There is a conspicuous, double row of bold black spots (fig. 1), each line of which is roughly halfway between the edges of the ventrals and the middle of the belly. These spots become tiny near the tail, the under side of which is marked with scattered dark specks.

The iris is rust brown. The tongue is brightly colored. The stalk of the tongue is black with orange mottling on the basal four-fifths, and pure white distally. The forks of the tongue are bright orange on their basal thirds, and gray on the distal two-thirds.

SIZE AND SCUTELLATION: The specimen is a moderately robust male 380 mm. in total length (preserved), of which the tail is 137 mm. or 36.1 per cent of the total. Dorsal scales are in 21-21-19 rows, and anal ridges are present. There are 127 ventrals, 101 pairs of subcaudals, one preocular, two postoculars, and 1+3 temporals. There are eight supralabials, the second to third touch the loreal, the fourth to fifth in contact with the eye. Infralabials are 10, the first five touch the anterior genials, the fifth to sixth touching the posterior genials.

MAXILLARY DENTITION: There are 13+2 teeth on the right maxilla. The prediastemal teeth slightly increase in size from front to rear; the fangs are less than one and one-half times larger than the posteriormost prediastemal teeth.

HEMIPENIS: I was able to evert the hemipenes only halfway when I preserved the specimen in the field, but both organs were removed in the laboratory and the one on the left side was relaxed and successfully everted with hot paraffin, although possibly it is not so bulbous as it should be (fig. 4A). The extended organ reaches approximately to the end of subcaudal six if pressed against the tail. The distal one-fourth of the organ is capitate, the capitulum being slightly bifurcate[1] and calyculate. The calyces bear tiny papillae, which are longest around the

[1] This is not an artifact of preparation, because I can detect partial divisions of the organs *in situ* of a specimen from Guatemala (K.U. No. 57158). Curiously, the indication of bilobation of the hemipenis and retractor muscle *in situ* is present only on the medial wall, in which a narrow slit or crevice is nearly concealed by the covering mesentery and is hard to detect, which probably explains why Bailey (1939, pp. 4, 25) regarded the hemipenis of *C. bipunctatus* as being single, although the possibility of variation within the species is not ruled out.

FIG. 3. Swamp forest habitat of *Coniophanes bipunctatus,* photographed October 20, 1966, on eastern end of Isla Escudo de Veraguas, northwestern Panama. The substratum is deep muck, but numerous tiny roots provide enough support to allow the traveler to penetrate the swamp in places such as shown here.

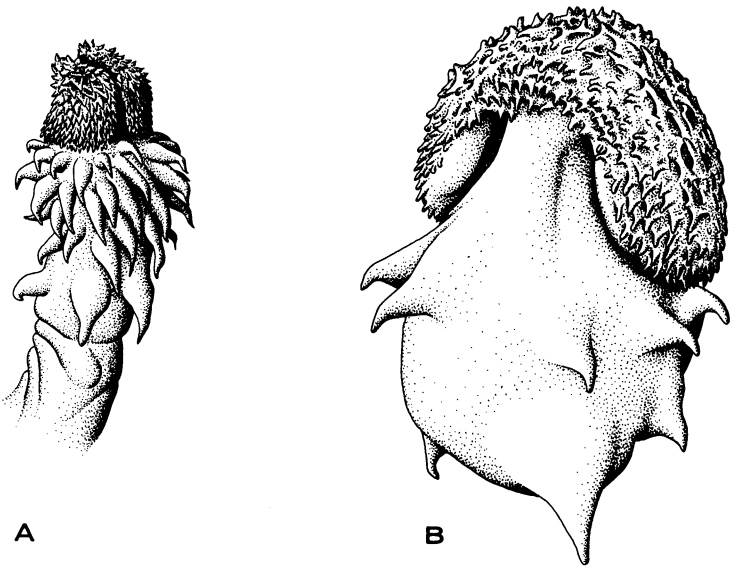

FIG. 4. Everted hemipenes viewed from asulcate sides. A. Left organ of *Coniophanes bipunctatus,* snout-to-vent length 243 mm., K.U. No. 110289 (fully extended but perhaps not completely expanded; see text). B. Right organ of *Coniophanes fissidens,* snout-to-vent length, 318 mm., K.U. No. 110284. ×7.

edge of the capitulum. There is an encircling band of approximately 60 spines below the capitulum. These are small near the sulcus and medium-sized on the asulcate side (fig. 4A). The capitulum plus the band of spines occupy the distal half of the hemipenis. There are four additional spines situated around the organ, slightly below the spinose band mentioned above. There are some spinules on each side of the sulcus spermaticus, which bifurcates a little below the capitulum, the branches extending onto the capitulum but not all the way to the tip.

REMARKS: *Coniophanes bipunctatus* resembles some specimens of *C. fissidens* in dorsal color pattern, habitus, and scutellation. The double row of bold, black ventral spots (fig. 1), however, immediately gives *bipunctatus* an entirely different aspect. Even when in well-defined rows these spots are not so large and conspicuous in *fissidens* which, in lower Central America at least, usually has a profusion of tiny spots and speckles. *Coniophanes bipunctatus* evidently has a greater number of subcaudals (101 in the Panamanian specimen) than does *fissidens* (57–74 in 15 specimens from Costa Rica and Panama). A comparison of the preceding data with those given by Bailey (1939, pp. 20, 26) suggests that *fissidens* and *bipunctatus* may have opposing clines in numbers of subcaudals. In *fissidens* there is a geographic increase in numbers of

subcaudals from south to north, whereas the reverse seems indicated for *bipunctatus*. A most significant difference between these species is in the nature of the hemipenes (fig. 4). There are few spines on the hemipenis of *fissidens,* and the unbifurcated capitulum comprises a large part of the organ. In *bipunctatus* there are more spines, and the capitulum is small and slightly bilobated. The copulatory organ of *bipunctatus* is closest to that of *C. dromiciformis* and that of *C. joanae* (*q. v.*).

Quite probably there is at least a partial habitat separation between *C. bipunctatus* and *C. fissidens,* as the latter occurs on well-drained terrain (compare figs. 3 and 6) and is unknown from swamp forest in Panama.

Coniophanes fissidens (Günther)

Figures 2, 4B–6

Coronella fissidens GÜNTHER, 1858, p. 36. Type locality: Mexico.

DISTRIBUTION AND HABITATS: *Coniophanes fissidens* is the most widely distributed member of the genus, with a range from Veracruz, Mexico, to northwestern Ecuador. In Panama, its distribution can be estimated from sparse records (fig. 2) and, because it is a litter snake, it occurs principally in well-drained mesic forest (e.g., fig. 6) below 1000 meters in elevation. Such forest is virtually continuous along the north (Atlantic) coast of Panama, and extends south to the Pacific coast in two areas, in the region of the Canal Zone and along the Colombian border. *Coniophanes fissidens* probably occurs throughout this forest, which climatically (and physiognomically) varies from *Af,* tropical wet climate (rain forest, fig. 6) to *Am,* tropical monsoon climate (monsoonal rain forest). The species must be presumed absent from the extensive cuipo forests (*Cavanillesia platanifolia*) and intermingled swamp forests that occur on great expanses of nearly base-level terrain in the Chucunaque and Bayano drainages of eastern Panama. It was not among more than 3000 snakes collected in the lower Chucunaque-Tuira basins during the Panamanian snake census (Dunn, 1949), nor has more recent work uncovered it there. Specimens are available from the Río Silugandí, a tributary of the Bayano, but, according to Heatwole and Sexton (1966, p. 47), the forest there is on rolling, hence well-drained, ground.

Coniophanes fissidens occurs in rather open country in extreme southwestern Panama near the Costa Rican border. I picked up a dead individual on the Inter-American Highway, in a region from which all but small groves of the forest had been cleared for some years and the land turned to pasture (*Am* climate). *Coniophanes fissidens* has been found at an elevation of approximately 1000 meters in the vicinity of Boquete in southwestern Panama (Slevin, 1942), but it seems absent from the

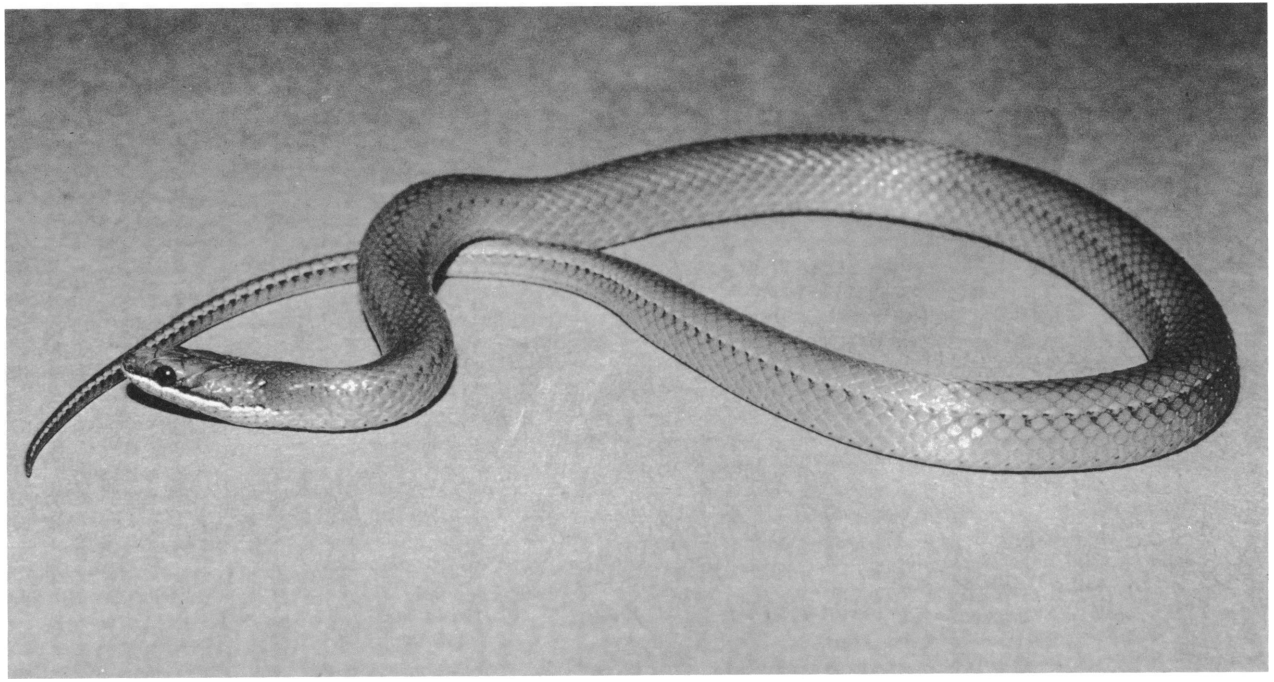

FIG. 5. *Coniophanes fissidens,* female, A.M.N.H. No. 102326, 364 mm. in total length; from the vicinity of Gamboa, Canal Zone, Panama.

FIG. 6. Tropical rain-forest habitat of *Coniophanes fissidens,* photographed October 7, 1966, approximately 5 kilometers west of Almirante, 30–40 meters in elevation, northwestern Panama. K.U. No. 110283 was found on the forest floor in November, 1964.

relatively well-known snake fauna above Boquete at Finca Lérida, at an elevation of about 1600 meters (Dunn, 1947).

Coniophanes fissidens almost certainly is absent from the extensive savanna (tropical wet and dry climate, *Aw*) that stretches eastward across the base of the Azuero Peninsula and nearly to the Canal Zone, but it does occur in mesic hill forest to the north. The species was not represented in a collection of some 1200 snakes from the savanna in Coclé and Herrera provinces (Dunn, 1949). *Coniophanes fissidens* has been taken in a much restricted savanna area east of Panama City, but habitat data do not accompany the specimens, and it is not known whether they came from the grassland proper or from gallery forest along the rivers, although the last possibility seems most probable.

BEHAVIOR: Limited observation indicates that *C. fissidens* is mainly a diurnal snake; I have seen individuals prowling in leaf litter in the middle of the day, near Almirante and on Barro Colorado Island. Native collectors for the Gorgas Memorial Laboratory encountered a few by day (e.g., K.U. No. 75673) on forest trails near the upper Río Tacarcuna in the Serranía del Darién, near the Colombian border. I found one at

El Valle, as it was crossing a road shortly after dark. This individual, which had a freshly injured tail, attempted to bite after it had been handled, but others have been docile.

One snake from the Canal Zone was kept alive for several months in the United States. It spent most of each day lying with its head held an inch or more above the substratum. Quite probably such a pose would be advantageous for a small snake resting in leaf litter, as it could watch the environment for food or predators yet remain largely concealed. The head and nape markings (see below) possibly function as disruptive coloration at such times.

The aforementioned individual in captivity accepted young lizards (*Eumeces fasciatus*) and baby snakes (*Diadophis punctatus*). It displayed the characteristic chewing motions by which rear-fanged snakes embed the enlarged posterior teeth, then hold the prey for a few minutes until it is motionless or dead. A juvenile of *fissidens* from near Almirante contained a diurnal ground gecko (*Lepidoblepharis xanthostigma*), and another juvenile from Barro Colorado Island had eaten a small diurnal frog (*Colostethus nubicola*).

COLOR AND PATTERN: The body is orangish brown to brown, weakly and somewhat variably striped or lined with dark brown or black. Usually there is a vertebral dark line or row of dots (one on each scale apex in the vertebral row) and, in addition, the median three or seven scale rows may be darker brown than the ground color on each side. Most Panamanian specimens that I have seen have a dark lateral stripe that lies principally on rows 4 and 5 and the lower edge of row 6, posteriorly dropping one row lower. The bottom side of this stripe tends to be ill defined, and in one individual the entire lower sides are darkened, as is frequent in specimens from Costa Rica. In part, this variation may be due to ontogenetic changes, as suggested by C. B. Fisher (*in litt.*). The upper margin of the lateral stripe is usually distinct because of a greater accumulation of dark pigment, and some individuals have only this dark line as a remnant of the broader stripe, which possibly is being lost in some populations. The upper margin of the lateral stripe, or line, usually is further emphasized by a series of small, white or pale tan dashes lying immediately above. These dashes are most distinct on the posterior part of the body, usually showing no traces elsewhere except on the neck, on which there is a short, white line several scales in length. Also on the neck is a pair of tiny, black-bordered white ocelli. Each ocellus is no larger than one or two scales and is situated between the posterior temporal plates and the anterior end of the short, white line on the sixth scale row.

The top of the head is brown, usually with an inconspicuous pair of black dots, one on each side of the anterior part of the interparietal suture. In some cases there is a fine, white line or series of dots extending from the upper margin of the eye a short distance back toward the white ocellus on the side of the nape. The upper edges of the anterior supralabials, from the snout to the eye, may be black-bordered or not, but all available specimens have a black postocular line that extends obliquely down from the eye and across the corner of the mouth to the lower side of the neck. Adjacent to the lower edge of the postocular black line there may be an enamel-white line that, on a few specimens, skirts the lower edge of the eye and continues uninterrupted to the snout. Below the white line the supralabials are grayish white and usually intensely speckled with black. The white lip marking may be partly an attribute of age, as it is obvious on six adults but reduced or absent from four juveniles, in which the black specking is likewise reduced or absent. The under side of the head is speckled with black in most specimens. There is a black dot near the tip of each ventral plate, and the number of black specks and little spots varies over the rest of the light venter. Although the ventral spotting is largely irregular, there often is a tendency for some markings to form two rows, each about a fourth to a third of the width of a ventral from the edge of the belly.

COLOR IN LIFE: Slevin (1942) stated that two specimens from Boquete were light brown, with a pinkish tinge, in life. At least some individuals from central Panama have the body strongly tinged with orange. The white ocelli on the nape and, when present, the white labial line and the dorsal, white postocular line (or row of dots), are enamel-white and very conspicuous in a hand-held specimen, although on the forest floor these markings possibly serve as disruptive (hence concealing) coloration. The under side of the head was white in four specimens for which I recorded data, but W. E. Duellman (field notes for K.U. No. 75672) noted one in which the chin was pale orange. Two Canal Zone specimens and one from El Valle had a pale to medium orange suffusion on the sides of the belly, with a reduced median part of the ventrals and most of the subcaudals light yellow. Another individual from El Valle had a yellowish white venter. The iris color of specimens from central Panama has been noted as reddish orange (two), reddish brown (one), and rich brown (one). The tongue is brown or reddish brown, with the distal end of the stalk and the forks black.

SIZE AND SCUTELLATION: *Coniophanes fissidens* is a moderately robust snake. The largest measurable Panamanian specimen is a female 466 mm. in total length (preserved), of which the tail is 120 mm. The tail

varies from 33.1 to 41.3 per cent of the total length in three males (including two juveniles) and from 25.8 to 38.5 per cent in six females (including two juveniles). Any possible ontogenetic variability in the tail length proportion is not obvious, because the extremes in the series of females are for two adults.

The dorsal scales are smooth, except for anal ridges that are present on some females as well as males, and usually are in 21-21-17 rows, although there may be reduction to 19 by midbody and to 15 immediately in front of the cloaca. Ventrals range from 110 to 121 (mean 114.5) in four males, and 116 to 124 (mean 119.2) in six females. Subcaudals are 63 to 70 (mean 66.3) in three males, and 57 to 66 (mean 61.3) in six females. There is one, or in some cases two, preoculars and two postoculars. The general temporal formula is 1+2, although there may be some asymmetry or other disarrangement of the basic pattern. Supralabials are eight per side, with the second and third touching the loreal and the fourth and fifth in contact with the eye. Infralabials are 10, or in some cases nine, with the first five (or first four if there are only nine plates) touching the anterior genials and the fifth to sixth (or fourth to fifth) touching the posterior genials.

MAXILLARY DENTITION: A single maxilla from each of six specimens bears 14+2 teeth. The fangs are about one and one-half times larger than the prediastemal teeth, which are subequal.

HEMIPENIS: The right everted organ of K.U. No. 110284 is a short and bulbous, unbilobated structure that extends to the end of the fourth subcaudal when pressed against the tail. Nearly the distal half is capitate and calyculate. The calyces bear papillae on the distal and sulcate surfaces of the capitulum, but spinules on the asulcate side. There is a row of nine small spines immediately below the edge of the capitulum on the sulcate side, which is very similar in appearance to the illustration given by Bailey (1939, pl. 3, fig. 1). There are eight moderate-sized spines on the asulcate side (fig. 4B). There are some spinules on each side of the sulcus spermaticus, which forks at the edge of the capitulum. The branches of the sulcus seem to extend only a short distance onto the head of the organ.

REMARKS: Any geographical trends in Panama are not detectable in the small sample (12 specimens) at hand. In fact, three specimens from a single locality (K.U. Nos. 110284–110286, El Valle) exhibit among themselves a large part of the variation in the description above.

I have compared the Panamanian material with 13 Costa Rican specimens in the University of Kansas collections, consisting of 10 from Turrialba, Cartago Province (including the five paratypes of *C. f.*

obsoletus), and one each from Guanacaste, Limón, and Puntarenas provinces. Some of the Turrialba individuals have more intensely speckled venters than any individuals from Panama. A short line of white dots extending posteriorly from the upper part of each eye is prevalent in the Costa Rican material, and shows (as a coalesced line) in a few Panamanian specimens. The bottom edge of the lateral stripe is obliterated to a greater extent in most of the Costa Rican specimens, in which the entire lower side tends to be dark, but a juvenile (K.U. No. 35654) from Turrialba has the lateral stripe distinct and in the same scale-row relationship as is usual in specimens from Panama. One from Limón Province (K.U. No. 86579) has a pair of tiny white dots superimposed on the usual dark parietal dots. Seven of 10 individuals from Turrialba have two preoculars (rather than one) on at least one side of the head, a situation that occurs in two of 11 from Panama (both from El Valle). The Costa Rican specimens have on the average a few more subcaudal plates.

In summary, then, interpopulational variation of *C. fissidens* in Costa Rica and Panama seems relatively slight. Thus, if one wanted to apply a subspecific epithet to the Panamanian snakes (which I do not), the name *Coniophanes fissidens obsoletus* Minton and Smith (type locality in Cartago Province, Costa Rica) is available. Whether this name really represents a population easily distinguishable from all those farther north remains to be seen. Minton and Smith (1960) gave several diagnostic characters for *obsoletus,* but at least two characters are of dubious value. *Coniophanes f. obsoletus* was said to lack a white dorsolateral streak on the nape, but all the paratypes have the same short, white, neck line that I describe above for the Panamanian snakes. This marking was not mentioned by Minton and Smith, and whether some northern populations of *fissidens* have an additional white "streak," to which they refer, I do not know. Minton and Smith also characterized *obsoletus* as lacking a "prominent row of relatively large dark spots at the ends of the ventrals." Such a statement should not be construed as an absolute difference. The spots are there but are simply smaller than the small spots found in some more northern populations of *fissidens,* and the rows tend to be inconspicuous partly because of additional speckles and little spots. Some other diagnostic characters were given but are not very convincing when one realizes that Minton and Smith were comparing quite distant populations. It is not evident by what logic the possibility of clinal variation is excluded in such cases.

I have indicated elsewhere (1966a) the need for a new variational study of *Coniophanes fissidens*. Such a study is now being undertaken by

Clyde B. Fisher, Northwestern State College of Louisiana.

LOCALITY RECORDS: The distribution map (fig. 2) of *C. fissidens* in Panama is based on the specimens listed below, but only those marked by an asterisk have been examined by me. Fisher has confirmed identifications of the other specimens, which he is studying. *Bocas del Toro Province:* Approximately 5 kilometers west of Almirante, 40 meters, K.U. No. *110283. *Canal Zone:* Ancon, K.U. No. *110287; Barro Colorado Island, K.U. No. *75672, M.C.Z. No. 18817, U.M.M.Z. No. 63702; *ca.* 5 kilometers northeast of Gamboa, A.M.N.H. No. *102326; Madden Dam, M.C.Z. No. 38230; Madden Forest Preserve, *H.C.-S.R.T. *Chiriquí Province:* Boquete, U.M.M.Z. Nos. 57959, 57961–57964; vicinity north of Boquete, C.A.S. Nos. 79015, 79016; 7 kilometers east-southeast of Paso Canoas, 100 meters, A.M.N.H. No. *102621; Progreso, U.M.M.Z. Nos. 57960, 57965. *Coclé Province:* El Valle, 550 meters, K.U. Nos. *110284–*110286. *Colón Province:* Aqua Clara, near Chagras River, A.N.S.P. No. 22272, M.C.Z. No. 45382. *Darién Province:* Laguna, 820 meters, K.U. No. *75673. *Panamá Province:* Cerro Jefe region. K.U. No. *110288; Chepo, A.N.S.P. No. 24699; Río Silugandí, U.M.M.Z. Nos. 124137, 124142; *sabanas,* M.C.Z. No. 45339; *sabanas*-Pacora area, M.C.Z. Nos. 39759, 39760. *No specific data* ("Panama"): F.M.N.H. No. 31190, U.S.N.M. No. 13569.

Coniophanes joanae Myers

Figures 2, 7A, B, 8A, B, 9A, B, 10

Coniophanes joanae MYERS, 1966a, p. 665. Type locality: Panama: Darién Province: Serranía de Pirre, southeastern slope Cerro Pirre (=Mount Pirri, Cerro Cana), 1440 meters in elevation.

The second known specimen of this diminutive species, and the first male, was caught by a field assistant of the Gorgas Memorial Laboratory a few months prior to my finding of the holotype. I was unaware of this "second" specimen until shortly before publication of the description of *C. joanae,* when my colleague Eustorgio Mendéz handed it to me for identification.

DISTRIBUTION AND HABITATS: The holotype (K.U. No. 93502) was found in cloud forest at an elevation of 1440 meters on Cerro Pirre, in extreme eastern Panama. The second specimen comes from the vicinity of Altos de Pacora, near Cerro Jefe, in Panamá Province; this locality is about 30 kilometers northeast of Panama City and approximately 235 kilometers northwest of the type locality (fig. 2). Precise data are not available, but the specimen comes from a region of mesic hill forest and probably was caught at an elevation between 500 and 800 meters. Cerro

Jefe, at about 980 meters in elevation, is the highest peak of the Río Chagras watershed. Altos de Pacora is a rural community at 820 meters in elevation, on the mud road about 7 kilometers northeastward from Cerro Jefe.

It seems unlikely that *Coniophanes joanae* inhabits the extensive lowlands that intervene between the two known localities, for it was not found during the Panamanian snake census (Dunn, 1949), but it might be expected in the isolated and biologically unexplored Serranía de Cañazas (fig. 2). A nearly continuous distribution between the known localities might be possible, by way of the mountains and low hills that form the continental divide close along the Atlantic coast and on the Colombian border. A similar continuous distribution was suggested for the frog *Cerathyla panamensis* in eastern Panama (Myers, 1966b), based on essentially the same information. This suggestion was partially substantiated in 1967, when I collected *Cerathyla* in the northern end of the Serranía del Darién, on the low continental divide between San Blas and Darién provinces. Most of the aforementioned terrain lies below the 500-meter contour, hence is not indicated in figure 2, but the hills and ridges are sufficiently high to cause mist and orographic rainfall from the Northeast Trades, and mesic conditions prevail even in the dry season (Myers, MS).

Color and Pattern: The two specimens are alike in having brown venters, which are somewhat clouded and on which the brown pigment tends to be concentrated along the bases of the ventral and subcaudal plates, forming dark transverse streaks (fig. 7A, B). Also, the ground color of the supralabials is brown. In these characteristics, *C. joanae* differs from all of its congeners, which have basically pale labials and venters (white in preservative). Both individuals have a black-bordered, pale, postocular stripe (actually a series of several coalesced dashes), which starts on the lower postocular, slants down and back across the fifth to seventh supralabials, and stops on the lower side of the neck (on the third scale row in the holotype, and overlapping slightly onto the second row in the Gorgas specimen).

The brown dorsal surfaces of the two specimens are strikingly different, and no one would hesitate to pronounce these snakes as different species on the basis of a cursory glance. The holotype has a dark middorsal streak on the median three scale rows (fig. 7A), and this becomes a definite, blackish-edged stripe near the end of the body and on the tail (Myers, 1966a, fig. 1). But the Gorgas specimen has three dorsal, longitudinal, dark markings (fig. 7B) that are conspicuous throughout the length of the body, although on the tail they merge to form a single

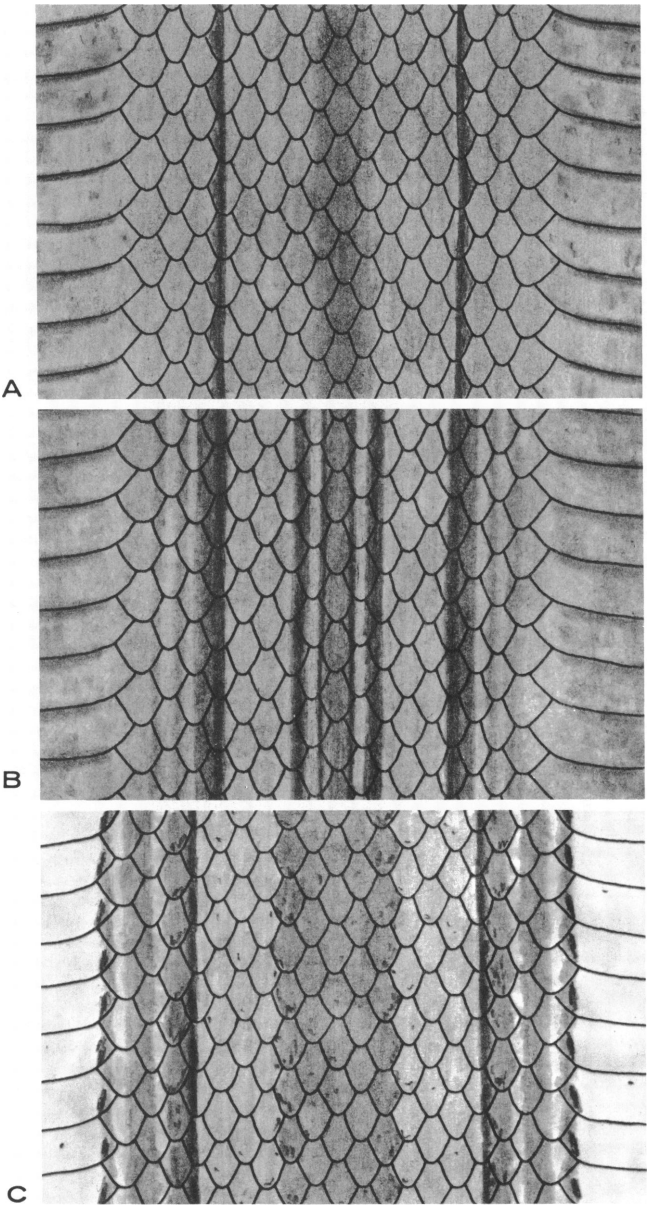

FIG. 7. Midbody patterns of *Coniophanes joanae* (17 scale rows) and *C. dromiciformis* (19 rows), drawn on generalized scale patterns. A, B. *C. joanae*. (A. Holotype. B. Gorgas Memorial Laboratory specimen.) C. *C. dromiciformis*, U.S.N.M. No. 165757, Río Macul near Balzar, Guayas Province, Ecuador.

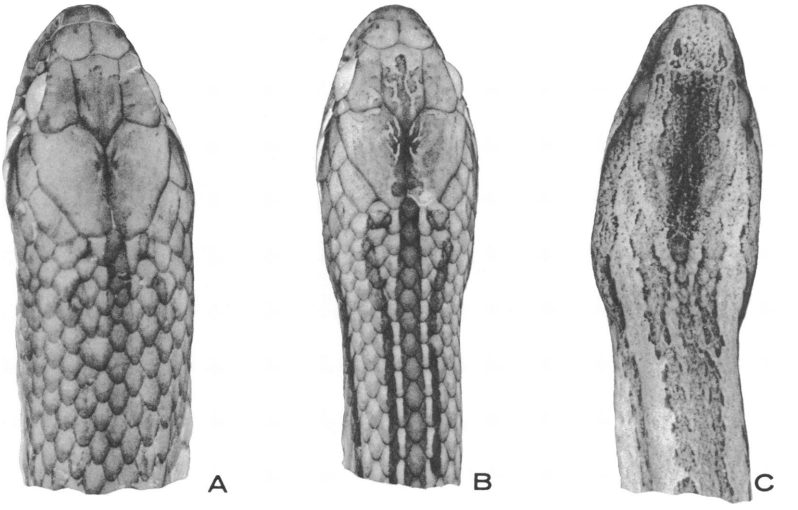

FIG. 8. Head and neck patterns. A, B. *Coniophanes joanae.* (A. Holotype. The thickness of the neck is due to over-inflation with preservative. B. Gorgas Memorial Laboratory specimen.) C. *C. dromiciformis,* U.S.N.M. No. 165758, El Milagro, Guayas Province, Ecuador. Approximately ×2.5–3.

stripe like that of the holotype. The median marking is a dark-edged stripe that covers the vertebral scale row and overlaps slightly onto the paravertebral (eighth) rows. On each side is a broad, blackish brown line on the edges of the seventh and eighth rows. That these middorsal differences are but variations on a basic pattern is revealed by the tail stripe and by the head and nape markings (fig. 8A, B). On the nape of the holotype, the broad, poorly defined, middorsal streak splits into a narrower vertebral stripe and two very faint accessory lines, all of which match the trunk markings of the Gorgas snake. The vertebral stripe extends forward onto the head where it disintegrates into barely discernible markings that match the darker vermiculations on the head of the Gorgas specimen. Thus, the dorsal markings, which differ so much on the trunks, become identical on the tails and heads and napes of the two specimens, although anteriorly they differ greatly in intensity.

The holotype has a blackish brown lateral line along the bottom of the fourth scale row (fig. 7A). The Gorgas individual has an identical marking which, however, blends with dark brown pigment below to form a broader lateral stripe, the whole occupying adjacent parts of rows 3 and 4 (fig. 7B). In both specimens the lateral stripe, or line, is continuous anteriorly with a pale brown stripe on the side of the head, above the

TABLE 1

SCALE COUNTS, SIZES (IN MILLIMETERS), AND PROPORTIONS OF KNOWN SPECIMENS OF *Coniophanes joanae*

Character	Male Gorgas Memorial Laboratory	Female Holotype, K.U. No. 93502
Dorsal scale rows	17–17–15	17–17–15
Paravertebral rows lost opposite ventral numbers	90/92	81/79
Ventrals	132	131
Subcaudals	53	47[a]
Supralabials	7/7	7/7
Infralabials	9/9	8/8
Preoculars	1/1	1/1
Postoculars	2/2	2/2
Temporals (each side)	1+2	1+2
Total length	290	369
Tail length	69	81[a]
Tail/total length	0.238	0.219
Head length[b]	12.0	11.5
Head width[c]	7.0	8.0
Head width/head length	0.583	0.696

[a] Terminal spine missing, including possibly one or two pairs of subcaudals.

[b] Snout to posterior end of mandible (postarticular process), a different standard from that used in the original description (Myers, 1966a, p. 665). Measurements are to nearest half millimeter.

[c] Greatest width (between sixth pair of supralabials in both specimens), to nearest half millimeter.

postocular pale stripe and behind the eye; in both specimens the lateral marking extends to the tip of the tail. The Gorgas specimen has faint dark streaks on rows 1 and 2 which are not present on the holotype.

The colors of the holotype in life are given in detail in the original description and are repeated here in abbreviated form. The dorsal ground color was medium brown and the venter orangish brown. The postocular light stripe was pale orange. The iris was pale orangish tan, which on each side of the pupil was darkened by reddish pigment.

SIZE AND SCUTELLATION: Pertinent data comparing the two known specimens are set down in table 1, where it can be seen that the differences are minor. The Gorgas Memorial Laboratory specimen has some additional minor differences from the published description (*q.v.*) of the holotype as follows: the rostral is slightly more than twice as broad as high; the frontal is twice as long as the distance from its anterior edge

to the tip of the snout (this proportion appears different in fig. 8B because of parallax); there is no groove on the nasal; one loreal plate is quadrangular in shape and the other is slightly pentagonal; the lower postocular is less than one-half of the size of the upper; the first four infralabials are in contact with an anterior genial on both sides, and the fourth and fifth labials touch the posterior genials; and the posterior genials are only about one and one-fourth times longer than the anterior ones. The eyes of the Gorgas specimen seem relatively larger, in that their diameters go less than one and one-half times into the length of the snout and they are visible from a ventral aspect.

MAXILLARY DENTITION: The maxillary formulas for the holotype are 14+2 (left) and 13+2 (right), and for the Gorgas specimen 15+2 on both sides. The prediastemal teeth increase slightly from front to rear in the holotype but are subequal in the Gorgas Memorial Laboratory specimen; the ultimate prediastemal socket lies well anterior to the ectopterygoid process. The left maxilla of the holotype is illustrated as figure 9A, and, as can be seen, the diastema is broad, being about four times the length of a prediastemal socket, rather than the lower number that I gave in the original description. The shape of the maxillaries of the Gorgas specimen are different from those of the holotype, especially in that the posterior dip on the dorsal surface is longer and smoothly curved and lacks the angular process seen in the holotype (compare fig. 9A with fig. 9B).

HEMIPENIS: The following description is of the left inverted organ, which first was examined *in situ* and then removed for illustration (fig. 10) and detailed study. The hemipenis is slightly bilobate, bifurcating opposite the end of the seventh subcaudal and with the lobes extending to the base of the ninth subcaudal. The two slips of the retractor muscle merge opposite the end of subcaudal 9, and the muscle inserts at the level of the twenty-fifth subcaudal. The sulcus spermaticus lies on the ventrolateral wall and forks at the end of the fifth caudal, one branch disappearing into the dorsal lobe (not opened) and the other running to the tip of the ventral lobe.

The extreme base of the organ is nude; 1 mm. above the base there is an ornamentation of spinules, which are most numerous and developed in the region of the sulcus. Four large, straight spines arise, equally spaced, across the middle of the hemipenis, and their points extend well onto the basal half of the organ, which otherwise is nude except for the small clusters of spinules already mentioned. Above the bases of the large spines and below the lobes is a thickly spinose area, which contains in excess of 50 small to medium-sized, straight or slightly recurved spines.

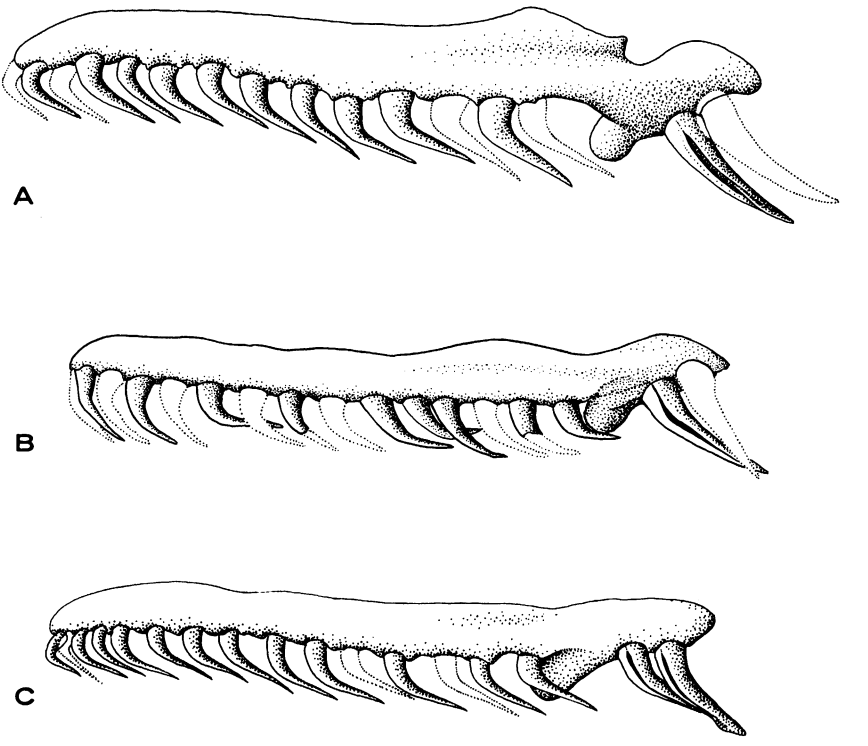

FIG. 9. Maxillae. A. From holotype of *Coniophanes joanae* left side. B. From *C. joanae,* Gorgas Memorial Laboratory specimen, right side (drawing reversed). C. *C. dromiciformis,* U.S.N.M. No. 165758, El Milagro, Guayas Province, Ecuador, right side (drawing reversed). ×15.

Many spinules are scattered among the basalmost of these spines, which are not in regular rows. The lobes and the space between the branches of the sulcus are covered with papillate calyces. There is a small cluster of slender, longer papillae on the asulcate side of the lobes. The bilobation is not extensive; the lobes occupy only about the distal one-seventh of the organ. A slight capitation seems to be discernible across the base of the exposed lobe, on its asulcate side, but an everted hemipenis is needed to verify this.

REMARKS: Taxonomic decisions often are subjective, as is my conclusion that the snake from Panamá Province is conspecific with the holotype of *Coniophanes joanae* from Darién. It can hardly be disputed that these specimens come from closely related populations. Not only are they similar in scutellation and proportions, but their ventral and

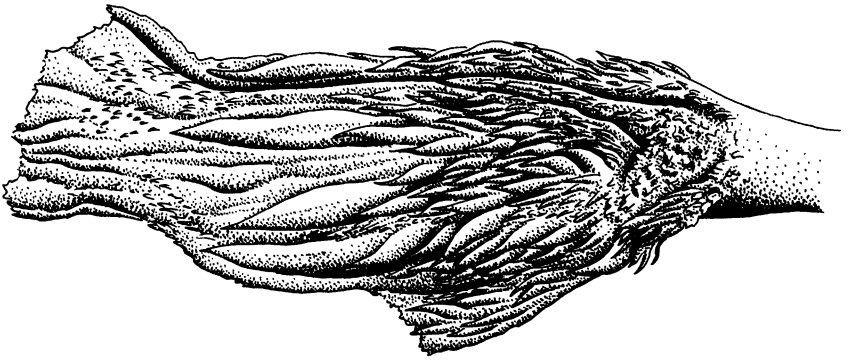

FIG. 10. Left inverted hemipenis of *Coniophanes joanae* (Gorgas Memorial Laboratory specimen), opened by midventral incision. ×8.7.

labial colorations are unique in *Coniophanes,* and the occurrence of only 17 anterior rows of dorsal scales is known elsewhere in the genus only for *C. meridanus,* a snake of very different aspect which lives on the Yucatan Peninsula. Nevertheless, the dorsal patterns and shapes of the maxillae differ so strikingly that some workers might justifiably conclude that two different, albeit related, species were involved. My own viewpoint is influenced by the totality of resemblances, including the fact that the two different trunk patterns become virtually identical on the heads and tails of the two specimens. Of course, neither viewpoint can be "proved" without additional data, particularly concerning intrapopulational variation in maxillary shape and trunk pattern.

Perhaps I should now answer a charge that may be made, namely, that the two specimens should at least be considered representatives of different subspecies. In the first place, subspecies is not an obligate taxonomic category, and I prefer not to use it. More to the point, the naming of subspecies without a prior understanding of variation is an all-too-common practice and a violation of scientific method, in that speculation is carried beyond all reason. Such guesswork has led to an undue proliferation of names that must be stored in synonymy. Although the two known specimens of *C. joanae* are quite different in appearance, there is no evidence that the differences are the reflection of discordant geographic variation instead of intrapopulational variation or clinal variation. I shall elsewhere demonstrate at least one case, in the related genus *Rhadinaea,* in which the sampling of a single population can produce individuals as strikingly different as these two individuals of *Coniophanes.*

I found significant resemblances when comparing both specimens of *Coniophanes joanae* with four of *C. dromiciformis,* from Ecuador (U.S.N.M. Nos. 165757–165759) and Peru (M.C.Z. No. 12426). The Ecuadoran specimens of *dromiciformis* have a grayish brown middorsal stripe on the median five scale rows (fig. 7C). In the Peruvian specimen this stripe narrows to the median three scale rows plus one-half row on each side, and there is a series of pale dashes on each paravertebral row, which gives this individual an appearance closest to the male specimen of *joanae* (fig. 7B). In all four specimens of *dromiciformis* the dorsal marking splits into three discrete parts on the nape (fig. 8C), with the median stripe extending onto the head, where it, in turn, may split into vague parallel markings (in three of four specimens). Postocular dark and light stripes are in the same relative positions as in *C. joanae,* and the dark one is continuous with a lateral stripe on the body; this lateral stripe is on the same scale rows in *joanae* and *dromiciformis,* despite the greater number of scale rows on the anterior part of the trunk of the latter (fig. 7B, C). There may be a heavy suffusion of brown pigment on the labials of *dromiciformis,* but these plates are not so darkened as in *joanae*. The maxilla of one of the *dromiciformis* is illustrated as figure 9C, but in our present state of knowledge nothing can be made of either similarities or differences in this bone.

The hemipenis of *C. joanae* comes out closest to that of *dromiciformis* in Bailey's key (1939, pp. 4, 5) in being slightly bilobated, in having enlarged spines below a band of smaller ones, and in seeming to have at least a trace of capitation. Direct comparison of the left hemipenis of *dromiciformis* (M.C.Z. No. 12426) with that of *joanae* reveals great similarity. Both have four large spines equally spaced across the middle of the organ and a dense spinose area between these and the calyculate lobes, which are only about one-seventh of the total length of the organ. Neither specimen has a well-defined capitulum, but the calyces form a slight overhang on the asulcate side of the lobe; this is best developed in *dromiciformis*. The differences between the two organs are several, but do not detract from the over-all similarity. In *dromiciformis* the papillae on the calyces are all about equal, whereas in *joanae* there are some long, slender papillae on the asulcate side of the lobe. There are fewer small- and medium-sized spines in the specimen of *dromiciformis,* and probably for that reason the spines seem to form more regular rows. I counted about three dozen spines (excluding the four large ones) in *dromiciformis* and more than 50 in *joanae*. The spinules on the base of the hemipenis of *dromiciformis* are rather uniformly distributed and not clustered as in *joanae*.

Coniophanes dromiciformis stands alone in Bailey's (1939, p. 12) arrangement of the genus. Because of the above-mentioned similarities in pattern and hemipenis, I suggest that *dromiciformis* and *joanae* are closer to each other than to any other congener and that they may be regarded as forming a natural species group. Bailey (*loc. cit.*) speculated that *dromiciformis* arose from an *imperialis* stock of *Coniophanes*. New data in the present paper on the hemipenis and distribution of *bipunctatus* must, however, be taken into consideration. As in the *dromiciformis* group, the hemipenis of *bipunctatus* has a small, slightly bilobated capitulum and four large spines spaced around the middle of the organ, with a dense area of smaller spines above. The hemipenis in the *imperialis* group is so different as to "possibly make this group deserving of generic rank" (Bailey, *loc. cit.*). It might be argued that the hemipenial similarity of the *dromiciformis* and *bipunctatus* groups is of greater importance than the low number of scale rows and lack of anal ridges characteristic of both the *dromiciformis* and *imperialis* groups. The absence of spines and other peculiarities of the hemipenes of *imperialis* and *meridanus* (Bailey, 1939, p. 5) lead me to believe that these species are far removed from the ancestors of the *dromiciformis* group and that no great importance can be attached to similarities in the low number of scale rows and absence of anal ridges. Contrary to other views (Bailey, 1939, pp. 8, 9), it seems logical to me that ancestral *Coniophanes* might have had 21 rows of scales and that populations characterized by fewer rows might have arisen on several occasions. Whatever happened, Bailey's thesis seems weakened by his stress on the importance of "19 scale rows and higher ventral counts" in the nominal *C. brevifrons* and *C. fissidens andresensis. Coniophanes brevifrons* is now regarded as having been probably erroneously described from "Ecuador" and a synonym of *andresensis,* from San Andrés Island off the coast of Nicaragua (Dunn and Saxe, 1950). Insular populations of snakes generally have high numbers of ventrals (and subcaudals), as indicated by Mertens (1934, p. 77) and Zweifel (1960, p. 114). Anal ridges have not often proved to be a useful taxonomic character. Not only are these structures in some cases subject to great ontogenetic, sexual, and uncorrelated variation (Myers, 1965, p. 83; 1967, pp. 72, 73), but they also may occur commonly in one species but not in another of the same group (e.g., in the *lachrymans-godmani* group of *Rhadinaea*).

Because of the range extension of *Coniophanes bipunctatus* into Panama, and the discovery of *C. joanae,* the distribution of *C. dromiciformis* no longer seems as anomalous as it did to Bailey (1939, p. 12). *Coniophanes dromiciformis* is known only from "Peru" and from elevations below 100 meters near the Gulf of Guayaquil in southern Ecuador. In addition to an old

record for Guayaquil (cited by Bailey, 1939), I know of the following localities, all in Guayas Province: vicinity of Babahoyo (Steindachner, 1902, p. 107); El Milagro (U.S.N.M. Nos. 165758, 165759); and Río Macul near Balzar, 50 meters (U.S.N.M. No. 165757). *Coniophanes dromiciformis* thus occupies lower and drier habitat than the hill forests of eastern Panama, in which *C. joanae* lives. Nothing is known of the natural history of either species, except that a specimen (U.S.N.M. No. 165758) of *dromiciformis* had a small frog of the genus *Leptodactylus* in its stomach. The similarities between *C. dromiciformis* and *C. joanae* evidently cannot be explained by convergent adaptation to comparable habitat, and they seem too close to have arisen independently from any other kind of *Coniophanes* now extant. Consequently, they must be regarded as southern remnants of an ancestral stock that at one time was more widespread.

ACKNOWLEDGMENTS

The field work (1964–1967) that provided most of the material for this report was supported by Grant GM-12020 from the National Institutes of Health to the University of Kansas. My tenure as a Visiting Scientist with the Gorgas Memorial Laboratory (Panama City) was most pleasant, and I owe a large debt of gratitude to Dr. Martin D. Young (Director), Mr. Pedro Galindo, Mr. Eustorgio Mendéz, Dr. Carl M. Johnson, Mr. José Antonio Tarté, and others of the staff for facilitating my work. Mr. Mendéz lent the second known specimen of *Coniophanes joanae* and other interesting material. Mr. Kenneth T. Nemuras sent me a living specimen of *C. fissidens* after my return to the United States, and an additional preserved specimen was provided by Drs. Howard Campbell and Sam R. Telford, Jr. Dr. James A. Peters of the United States National Museum, Smithsonian Institution and Dr. Ernest E. Williams of the Museum of Comparative Zoology provided several examples of *C. dromiciformis* for comparisons. Mr. David M. Dennis executed figures 4, 9A, 9C, and 10, and Mrs. Ellen E. Bowler drew figure 9B. The manuscript benefited from a reading by Dr. Richard G. Zweifel, and the section on *C. fissidens* was reviewed by Mr. Clyde B. Fisher.

Little snakes of the forest floor are uncommon in much of Panama, and I remember details of most encounters, including the companionship of Dr. William E. Duellman and Mr. Tómas Quintero, with whom I shared in some captures of *C. fissidens*. For encouragement and help in many ways, I am grateful most of all to my wife, to whom the species *Coniophanes joanae* is dedicated.

LITERATURE CITED

BAILEY, JOSEPH R.
1939. A systematic revision of the snakes of the genus *Coniophanes*. Papers Michigan Acad. Sci., Arts and Letters, vol. 24, pp. 1–48, pls. 1–3.

DUNN, EMMETT REID
1947. Snakes of the Lérida Farm (Chiriqui Volcano, western Panamá). Copeia, pp. 153–157.
1949. Relative abundance of some Panamanian snakes. Ecology, vol. 30, pp. 39–57.

DUNN, EMMETT REID, AND L. H. SAXE, JR.
1950. Results of the Catherwood-Chaplin West Indies Expedition, 1948. Part V. Amphibians and reptiles of San Andrés and Providencia. Proc. Acad. Nat. Sci. Philadelphia, vol. 102, pp. 141–165.

GÜNTHER, ALBERT
1858. Catalogue of colubrine snakes in the collection of the British Museum. London, xvi+281 pp.

HEATWOLE, HAROLD, AND OWEN J. SEXTON
1966. Herpetofaunal comparisons between two climatic zones in Panama. Amer. Midland Nat., vol. 75, pp. 45–60.

MERTENS, ROBERT
1934. Die Insel-Reptilien, ihre Ausbreitung, Variation und Artbildung. Zoologica, Stuttgart, no. 84, [iv]+209 pp., pls. 1–6.

MINTON, SHERMAN A., AND HOBART M. SMITH
1960. A new subspecies of *Coniophanes fissidens* and notes on Central American amphibians and reptiles. Herpetologica, vol. 16, pp. 103–111.

MYERS, CHARLES W.
1965. Biology of the ringneck snake, *Diadophis punctatus,* in Florida. Bull. Florida State Mus., Biol. Sci., vol. 10, pp. 43–90.
1966a. A new species of colubrid snake, genus *Coniophanes,* from Darién, Panama. Copeia, pp. 665–668.
1966b. The distribution and behavior of a tropical horned frog, *Cerathyla panamensis* Stejneger. Herpetologica, vol. 22, pp. 68–71.
1967. The pine woods snake, *Rhadinaea flavilata* (Cope). Bull. Florida State Mus., Biol. Sci., vol. 11, pp. 47–97.
[MS.] The ecological geography of cloud forest in Panama.

SLEVIN, JOSEPH R.
1942. Notes on a collection of reptiles from Boquete, Panama, with the description of a new species of *Hydromorphus*. Proc. California Acad. Sci., vol. 23, pp. 463–480, pls. 39–42.

STEINDACHNER, FRANZ
1902. Herpetologische und Ichthyologische Ergebnisse einer Reise nach Südamerika. Denkschr. K. Akad. Wiss., Math.-Naturwiss. CL., Vienna, vol. 72, pp. 89–112, pls. 1–5.

STUART, L. C.
1963. A checklist of the herpetofauna of Guatemala. Misc. Publ. Mus. Zool., Univ. Michigan, no. 122, pp. 1–150.

UNDERWOOD, GARTH
1967. A contribution to the classification of snakes. Publ. Brit. Mus. (Nat. Hist.), no. 653, x+179 pp.

ZWEIFEL, RICHARD G.
1960. Results of the Puritan-American Museum of Natural History expedition to western Mexico 9. Herpetology of the Tres Marías Islands. Bull. Amer. Mus. Nat. Hist., vol. 119, pp. 77–128, pls. 41–44.