



**Rare Snakes—Five New Species from Eastern Panama:
Reviews of Northern Atractus and Southern Geophis
(Colubridae: Dipsadinae)**

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Rare Snakes—Five New Species from Eastern Panama: Reviews of Northern *Atractus* and Southern *Geophis* (Colubridae: Dipsadinae)

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ABSTRACT

The South American genus *Atractus* barely enters political North America on the eastern half of the Isthmus of Panama, where it is extraordinarily rare. Collected over a period of 39 years, the five Panamanian specimens of *Atractus* known to the author represent five species! Four new species are described: *A. darienensis*, *A. hostilitractus*, *A. imperfectus*, and *A. depressiocellus*. The fifth species is *A. clarki* Dunn and Bailey, for which a second specimen is reported from the Colombia Chocó. The noncapitate hemipenis of *A. clarki* may be primitive in being calyculate and deeply bilobed.

The morphologically convergent *Geophis* is primarily a Middle American genus—Mexico to western Panama, with two or three outlying species in the western Andes of Colombia (*G. betaniensis*, *G. nigroalbus*, and probably *G. hoffmanni*). The genus is unrecorded from eastern Panama, and a few old records for central Panama seem to have been based on erroneous specimen data. Nonetheless, the genus does occur in east-central Panama, based on two specimens of *G. hoffmanni* (W. Peters) and on a specimen each of *Geophis bellus*, new species, and *G. brachycephalus* (Cope)—the latter representing a disjunct population separated by about 340 km from those in the Boquete area of western Panama.

Geophis bellus is a tiny snake differing from sympatric *G. brachycephalus* and South American *G. nigroalbus* in characters of size, color, and hemipenis. *Geophis brachycephalus* may be a composite species in western Panama. Unicolored specimens from the Atlantic versant seem to differ from those in the polymorphic Boquete population in hemipenial and other characters, and they are set aside as a *species inquirenda*. The first specimen of *Geophis hoffmanni* is reported from Colombia, but it lacks precise data.

Atractus depressiocellus, *A. imperfectus*, *Geophis bellus*, *G. brachycephalus*, and *G. hoffmanni* are at least broadly sympatric on the “Piedras-Pacora Ridge”—the continental divide—between the upper drainages of the Río Chagres and Río Pacora, some 30 km northeast of Panama City. This relatively low upland likely is a premontane forest refuge, where some very rare snakes may be making a last stand prior to extinction.

RESUMEN

El género *Atractus* esta ampliamente distribuido en Sudamérica y tiene su límite norte en la región oriental del Istmo de Panamá, adonde es extraordinariamente raro. ¡Los 5 únicos ejemplares panameños conocidos y estudiados por el autor, colectados a lo largo de 39 años, corresponden a 5 especies! Cuatro son especies nuevas que se describen en este trabajo: *A. darienensis*, *A. hostilitractus*, *A. imperfectus*, y *A. depressiocellus*. La quinta especie es *A. clarki* Dunn & Bailey, de la cual se reporta un segundo ejemplar del Chocó colombiano. Los hemipenes no capitados de *A. clarki* podrían ser primitivos por ser caliculados y profundamente bilobulados.

Geophis, que es morfológicamente convergente con *Atractus*, es primariamente un género mesoamericano—se distribuye desde México hasta el oeste de Panamá, con dos o tres especies aisladas en los Andes occidentales de Colombia (*G. betaniensis*, *G. nigroalbus*, y probablemente *G. hoffmanni*). *Geophis* no ha sido registrado hasta ahora en el este de Panamá, y unos pocos registros viejos del centro de Panamá parecen haber sido basados en especímenes de procedencia incierta. Sin embargo, el género ocurre en el centro-este de Panamá, como lo indican dos especímenes de *Geophis hoffmanni* (W. Peters), un espécimen de *G. bellus* (especie nueva), y un espécimen de *G. brachycephalus*. Este último representa una población disyunta, distante aproximadamente 340 km de las poblaciones más cercanas en el oeste de Panamá.

Geophis bellus es una pequeña culebra que se diferencia de la especie simpátrida *brachycephalus* y de la sudamericana *nigroalbus* en caracteres de tamaño, coloración y hemipenes. La especie polimórfica *G. brachycephalus* podría ser una especie compuesta en el oeste de Panamá. Ejemplares monocrómáticos de la pendiente atlántica parecen diferir en características de los hemipenes y de otros caracteres, y son mantenidos como *especie inquirenda*. Se reporta el primer espécimen de *Geophis hoffmanni* de Colombia, aunque faltan datos precisos.

Atractus depressiocellus, *A. imperfectus*, *Geophis bellus*, *G. brachycephalus*, y *G. hoffmanni* son ampliamente simpátridas en la “cresta Piedras-Pacora”, la divisoria de los altos drenajes de los ríos Chagres y Pacora, unos 30 km al nordeste de la ciudad de Panamá. Esta serranía

baja es probablemente un refugio de bosque montano, adonde algunas serpientes muy raras podrían presentar una última resistencia a la extinción.

INTRODUCTION

This paper is about some rare snakes on the eastern half of the Isthmus of Panama. Biologists familiar with the great diversity of serpents in tropical rain forests know that rarity or the appearance of rarity is compounded by several factors, including: (1) many, indeed most, wet-forest snakes seem to have low population densities relative to temperate species; (2) many are hard to find because of secretive habits; and (3) some are less likely to be encountered because of small geographic ranges and/or specialized microhabitats.

With time, however, sufficient specimens accumulate to allow approximation of geographic and ecologic distributions and assessment of morphological variation. But there are exceptions to this generalization—there are snakes seemingly rare in an absolute sense, so rare as to resist *verifiable* explanation of their rareness. For example, the little *Tantilla albiceps* is known to science only from a single specimen that was found in central Panama three-quarters of a century ago (Barbour, 1925)²; the type locality of *T.*

albiceps is Barro Colorado Island, which supports one of the world's best known tropical herpetofaunas (Myers and Rand, 1969; Rand and Myers, 1990). Perhaps *Tantilla albiceps* is extinct, at least on Barro Colorado Island. Perhaps biologists on the island have failed to differentiate an occasional specimen from the more common and similar appearing *Enuliophis sclateri*. Such explanations are unverifiable and unsatisfactory.

Five or six species in the two genera of concern in this paper seem to be, like the example above, *really* rare, although to be sure they come from less well-trodden ground. The terrestrial or semifossorial snakes of the genus *Atractus* reach the northern limits of the generic range in east-central Panama. To my knowledge, only five Panamanian specimens of *Atractus* have been collected—in the years 1936, 1938, 1966, 1967, 1974—with each specimen a different species, of which one was named in 1939 and the other four are described herein.

The second genus of concern, the semifossorial *Geophis*, ranges throughout much of Middle America and occurs also in the western Andes of northern South America. *Geophis* is well known from Costa Rica and western Panama, but published records for central Panama are based on erroneous locality data and the genus has not been documented from the eastern half of the isthmus. I am still unaware of specimens from extreme eastern Panama, but four snakes representing three species of *Geophis* were collected in east-central Panama in the 1950s and 1960s. Two specimens represent a simple range extension of the widely distributed *G. hoffmanni*, whereas a third specimen provides a widely disjunctive eastward extension of *G. brachycephalus*. The fourth specimen is of an undescribed species that is named herein.

Apparent rarity often implies insufficient collecting, and certainly the survey of the rich Panamanian herpetofauna is not (and may never be) complete. Nonetheless, Panamanian snakes have been better collected than in most tropical countries. My claims of

² Pérez-Santos and Martínez (1997: 451) erroneously reported *Tantilla albiceps* from Isla Coiba off the Pacific coast of western Panama; this record is based on a specimen of the widespread *Enulus flavitorques*. The collector, Ignacio De la Riva, kindly provided photographs of the specimen in life, showing a smooth-scaled, long-tailed small snake, dark brown above, grayish white on the lower few scale rows. The dark dorsal coloring is conspicuously broken by a yellowish nuchal collar crossing the rear halves of the parietals; the collar is interrupted by a small irregular brown blotch posteriorly on the interparietal suture. The left side of the head in profile shows a prominent rostral, a longer-than-high loreal plate entering the eye (no preocular), two postoculars, and 1 + 2 temporals. All these characters match well with *E. flavitorques*.

According to J.M. Savage (personal commun.), the unpublished notes of E.R. Dunn contain reference to a second specimen of *Tantilla albiceps* from Barro Colorado obtained in 1952, but no one else seems to have been aware of the specimen, and its whereabouts is unknown (there is no second specimen of *T. albiceps* entered in the electronic databases of ANSP, FMNH, or MCZ—the main depositories for Panamanian specimens examined by Dunn in the early 1950s). No other specimens have been reported (Ibáñez et al., “1995” [1997]: 153, 156).

unusual rarity for some of the snakes in hand can be put in perspective by consideration of the activities of the Gorgas Memorial Laboratory (GML), which operated out of Panama City from its opening in 1929 until its unfortunate demise in 1991. (GML's parent corporation in Washington, D.C.—the Gorgas Memorial Institute of Tropical and Preventive Medicine, Inc.—subsequently was reorganized in name under the Ministry of Health in Panama, but GML had been dependent on a permanent annual contribution from the U.S. Congress for its core support.)

GORGAS MEMORIAL LABORATORY (GML)
AND THE PANAMANIAN SNAKE CENSUS

Dr. Herbert C. Clark (1877–1960), first Director of the Gorgas Memorial Laboratory, initiated a snake census in Panama and conducted it at varying levels of intensity from January 1929 through 1953 (he retired in 1954). Not a new concept, the census was started as an extension of a then ongoing Central American snake census that used the labor forces on plantations of the United Fruit Company. Clark had earlier supervised the snake census in Tela, Honduras, but, with the resources of GML, Clark expanded the census in Panama well beyond the plantations and continued it for a quarter of a century.

Clark's primary aim was to learn the venomous species in Panama and to assess their relative medical importance (Clark, 1942). Bounties were paid for killed snakes (mostly heads), which were accumulated in formalin in central locations around the country. The GML snake census was initiated in cooperation with the old Antivenin Institute of America, one of whose founders was Thomas Barbour. In 1932, Barbour involved the Museum of Comparative Zoology (MCZ) of Harvard University, which "became actively interested in the studies and supported them in part" (Wright, 1970: 269). Early shipments were sent to the MCZ (e.g., Clark, 1937: 12), from where Barbour turned over the identification and study of the collection to his former student E.R. Dunn, who identified most of the material. Dunn eventually took over the study and reported on the results (Dunn, 1933, 1942, 1949a, 1949b;

Dunn and Bailey, 1939).³ Dunn obtained background information on the census methods during his visits to GML starting in 1939, and his 1949a paper is the most complete and easily accessible summary of Clark's GML snake census.

Dunn's 1949a account, however, did not include the census collections from most of western Panama nor from the limited uplands of eastern Panama (see below). But new species, new country records, and other noteworthy specimens from those areas were reported elsewhere (Dunn, 1942; Dunn and Bailey, 1939). Unfortunately, over 90% of the GML specimens were apparently discarded after Dunn's study, except for whole specimens and selected heads especially of rare species that were placed in major museums. Fewer than 1000 specimens with data were saved from the Panama snake census, which spanned a quarter of a century.⁴

A total of 13,745 snakes, mostly heads only, were accumulated in the overall period 1929–1953 (Wright, 1970: 269). Dunn

³ In describing one of the heads as a new species (*Dipsas nicholsi* [see Cadle and Myers, 2003]), Dunn (1933) acknowledged "the authorities of the Museum of Comparative Zoology for permission to examine the collection" (Dunn, 1933: 193). Later, however, it seems curiously inappropriate for Dunn (1949a: 39, 55) to have stated that the specimens were sent directly to him "during the years 1933 to 1945 inclusive, by Dr. H. C. Clark"—without mention of the MCZ or, especially, without acknowledgment to the late Thomas Barbour (died in 1946), who funded Dunn's early fieldwork in the Neotropics (Adler, 1989: 93). According to the GML annual reports, yearly shipments of snakes were sent to the MCZ at least through 1938 and 1939, and the MCZ continued to be mentioned as a cooperating institution through 1943; Dunn's identification services were acknowledged starting in the report for 1939, and the MCZ is not mentioned after 1943.

⁴ The following counts are derived from collection databases: Clark sent the early material to the MCZ, including 411 specimens from the Panama census and some 300 from his prior Honduran census. E.R. Dunn subsequently presented 273 of Clark's Panamanian specimens to the ANSP, starting with a few specimens in 1939 and with the bulk being given during the early 1940s. Finally, with Clark's approval, Dunn and GML staff member H. Trapido (see footnote 20) saw to it that 256 specimens from the Panama census went to the FMNH after Dunn's examination (Clark, 1952: 20). A jar of uncataloged heads without data is also at FMNH (Alan Resetar, personal commun.). In Panama, a small number of specimens were kept for identification purposes at least at GML and at Barro Colorado Island (Myers and Rand, 1969: 5).

(1949a: 39, 55) reported on nearly 80% of the collection, that is on “10,960”⁵ specimens from the lowlands of central Panama (“Chagres collection”) and from the Pacific lowlands of west-central and eastern Panama (combined collections from “Coclé-Herrera”, “Sabanas”, “Darién”). Excluding 1073 museum specimens, savanna collections, and those collections from west of the Panama Canal, Dunn’s (1949a; table 7) list of 70 species includes 2500 snakes from forested lowlands in the Chagres drainage of central Panama and 3044 snakes from areas of mixed banana plantations and forest in the Darién of eastern Panama.

Neither *Atractus* nor *Geophis* is included in the nearly 11,000 lowland specimens obtained by the GML snake census and reported in Dunn’s (1949a) summary paper. The absence of *Atractus* and *Geophis* from the large lowland collections seems surprising at first blush, inasmuch as there are many *Atractus* occurring in the South American lowlands and a specimen of *Geophis hoffmanni* was collected not far from the Panama Canal in 1968. Recent sampling in the central Panamanian lowlands has yielded neither *Atractus* nor additional specimens of *Geophis* (Ibáñez et al., “1995” [1997]).

Clark also pursued collections of snakes from upland areas, which are of limited extent in central and eastern Panama. Dunn and Bailey (1939: 3) reported on “268 snakes from the uplands of eastern Panama gathered in 1936 to 1938 through the initiative of Dr. H. C. Clark”. There are no *Geophis* in this collection, which, however, provided the first two specimens of *Atractus* from Central America.

There are eight species to be reported in the following pages (maps 1, 2). These eight species are represented by a total of nine central and eastern Panamanian specimens—five specimens of *Atractus* and four of *Geophis*. One *Atractus* was named in 1939; four specimens of *Atractus* and one of *Geophis* represent five “new” species that are named

⁵ Apparently a minor error, repeated later (Dunn, 1949b). Adding the column totals in Dunn’s (1949a) table 7 gives a grand total of 10,693 specimens. His count of 1073 museum specimens on page 55 agrees with the column totals in the table.

herein; the other *Geophis* specimens represent two species named in the 19th century.

The first two of the aforesaid nine specimens were obtained by the GML census in 1936 and 1938. I collected another two while resident Visiting Scientist at GML during 1964–1967. And five experienced field men (several earlier trained as collectors at GML) each caught one of the other five specimens in the 23-year period 1952–1974.

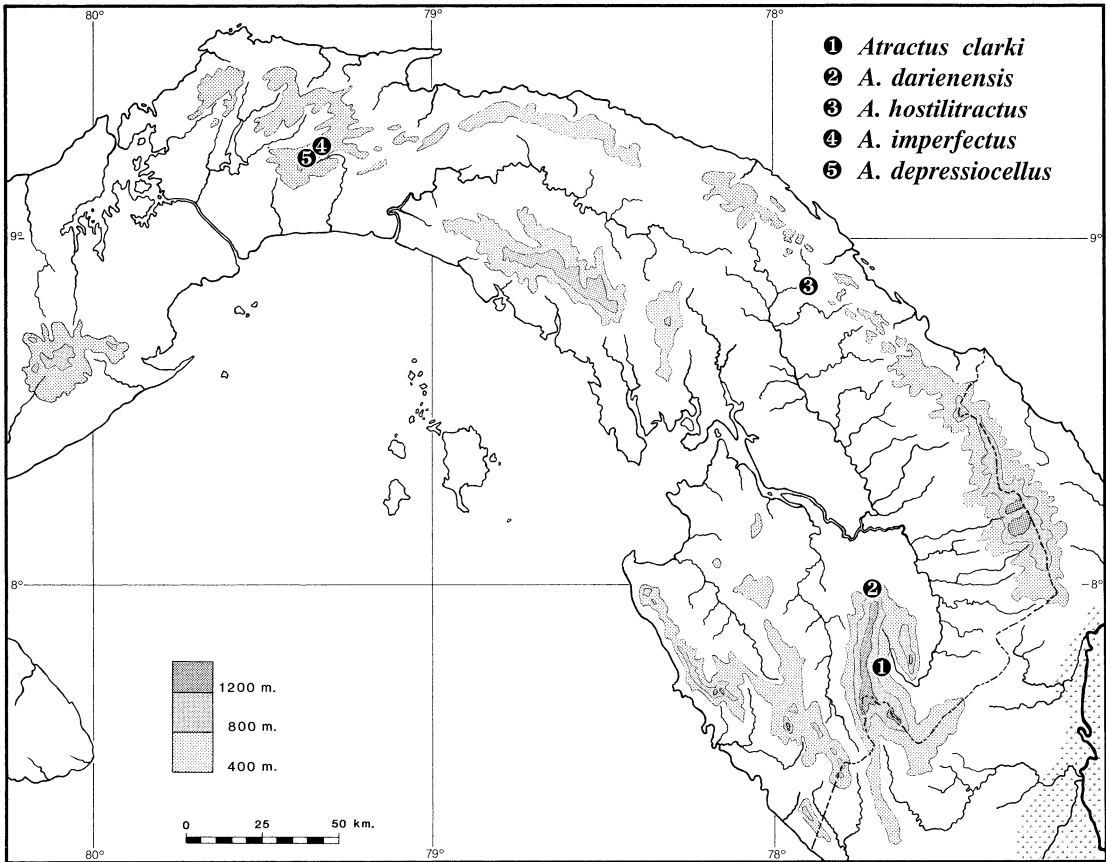
As a further indication of rarity, it may be noted that five of the eight species (*A. depressiocellus*, *A. imperfectus*, *G. bellus*, *G. brachycephalus*, *G. hoffmanni*) are from the region of the Piedras-Pacora Ridge, only about 30 km northeast of Panama City. The Piedras-Pacora Ridge—a section of the continental divide—delimits part of the southeastern side of the Madden Lake⁶ watershed, and is now included in the Parque Nacional Chagres. A team of Panamanian herpetologists (Ibáñez et al., “1994” [1995]) surveyed the herpetofauna of the Piedras-Pacora Ridge in 1990–1995; they invested 1253 man-hours of collecting in both wet and dry seasons (including 166 man-hours at night in the wet season). Their list is extensive, totaling 131 species of amphibians and reptiles, including 37 species of snakes. Among the small snakes collected was the third known specimen of *Coniophanes joanae*, but no new specimens of the still elusive *Atractus* or *Geophis*.

The Piedras-Pacora Ridge may be a pre-montane forest refuge for some small part of the fauna that is barely surviving the climatic-vegetational vicissitudes of the Pleistocene. The mingling of several very rare species in one place, including three species known *only* from that place, leads me to fear that it may be their “last stand” on the way to extinction. Should this be so, their Latin names may be their only epitaphs.

METHODS OF STUDY

Total length and tail length were determined by moderately stretching preserved specimens along a metric rule. Head and snout lengths, eye length, and head plates and their sutures were measured to the near-

⁶ Madden Lake is shown as Lago Alajuela on recent maps.



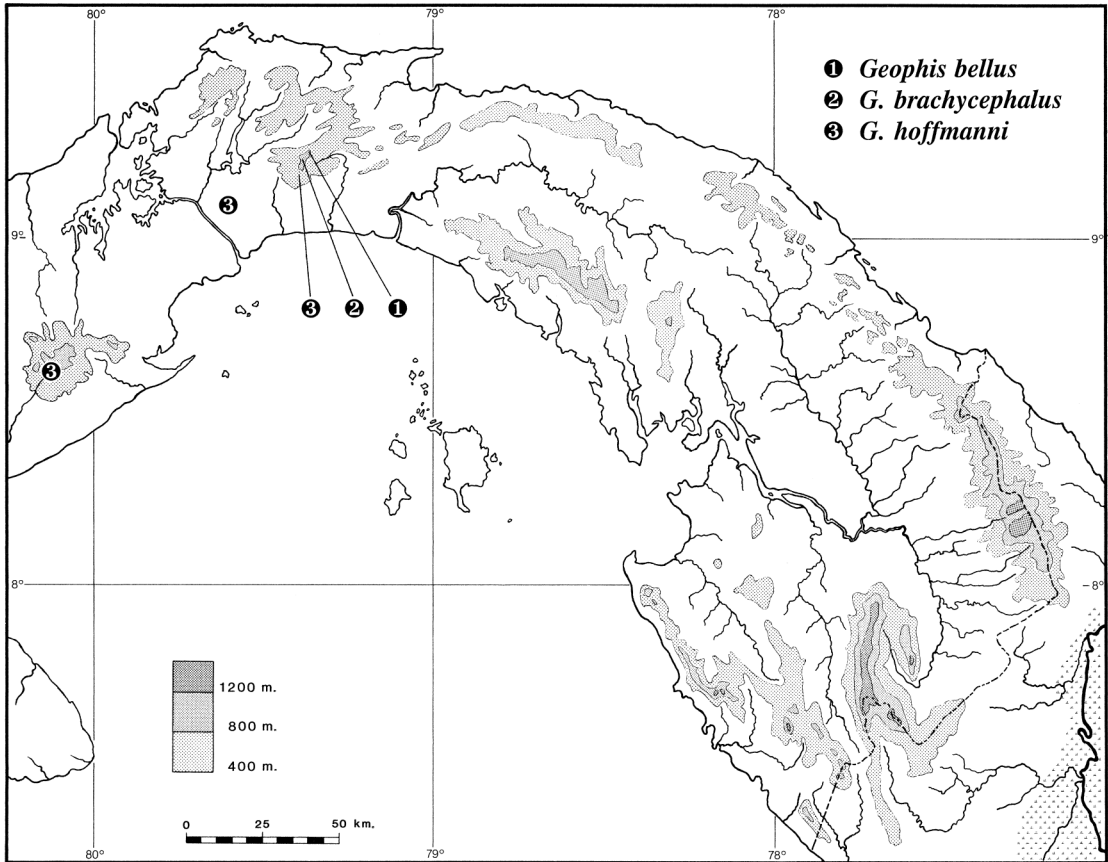
Map 1. Eastern Panama, showing locality records for the five Central American species of *Atractus*. One species (*A. clarki*) is also known from a specimen of indefinite locality in the Colombian Chocó, the others are known only from the Panamanian holotypes. Type localities: (1) Santa Cruz de Cana, an old gold mine; (2) north end of the Serranía de Pirre; (3) "Morti Hydro", a temporary helipad near the Río Mortí; (4) Piedras-Pacora Ridge; (5) Cerro Jefe on the Piedras-Pacora Ridge.

est 0.1 mm with an ocular micrometer in a dissecting microscope. Some measurements are used for comparisons, but most were converted to proportions for purposes of descriptions. It bears emphasizing that snout length (tip of snout to eye) was not measured on the oblique angle but on the sagittal plane by ocular micrometer, whereas head plates and the distance from eye to lip were determined along the plane of the greatest dimension, meaning that the head had to be differently inclined for different measurements. Therefore anyone comparing the descriptions with the drawings will have to be alert to the usual problems of parallax: In no case, for example, will a proportion such as nasal plate/loreal plate be retrievable from the figures,

whereas one such as eye length/eye-to-lip may or may not match a figure, depending on perspective of the drawing (e.g., dorso-lateral or lateral) and degree to which the lip is flared.

The drawings are my own, made with the aid of a camera lucida fitted to a Wild dissecting microscope. I photographed specimens positioned under glass on a raised plastic platform to eliminate shadows, and under alcohol to reduce glare from reflective surfaces of scales.

Ventral plates were counted by the Dowling (1951) method, starting with the first plate bordered on each side by the first dorsal scale rows; gular plates anterior to this, if wider than long, were termed preventrals



Map 2. Locality records for three species of *Geophis* known to occur in eastern Panama. The easternmost localities indicate broad sympatry on the Piedras-Pacora Ridge in Panamá Province.

(Myers, 1974: 37) for purposes of comparing type specimens with old original descriptions in which these plates were included in ventral counts.

Dowling's method has the advantage of giving a standard starting place for ventral counts that was said to correspond (in some snakes) in position with the atlas-axis articulation of the vertebral column. But the first ventral is not always quickly ascertained in the case of small, poorly preserved snakes with shiny scales, and I am sorry to have adopted this method some years ago. I seldom notice more than a few "preventrals", but comparisons with older literature are less accurate if these are not counted and added to the total. Therefore, I would not be critical of anyone refusing to adopt the Dowling

method over the older one summarized by Schmidt and Davis (1941: 26):

The ventrals and caudals of snakes correspond (with some variation) to the number of vertebrae. It is customary to count their number beginning beneath the chin *with the first one distinctly wider than long* [emphasis added], and excluding the anal plate . . . The first caudal, when they are in two rows, is the first one that meets one of the opposite side. It is customary to count them on only one side, and to include the terminal single scale [however, most workers nowadays do *not* count the terminal spine as a sub-caudal].

Downs (1967: 23) may have found a reasonable compromise between the above and Dowling's sometimes tedious method of determining the first ventral:

The ventrals were counted from the first scale clearly twice as broad as long . . . this system does not fol-

low the suggestion of Dowling (1951), but in practice is identical or nearly identical with it.

The practical reason for the above digression is to be seen in this paper in footnote 19. As a further aside, only a few workers (e.g., Peters, 1960: 10–12) have mentioned the occasional divided or “half-ventrals”, which may occur anywhere but are most common in some snakes just anterior to the anal plate. These correspond to anomalous vertebral duplications (King, 1959) and are not counted, although it may be useful to mention their occurrence in holotypes.

Except when a dentigerous bone was dissected out for illustrating, maxillary teeth were counted *in situ* (Myers, 1974: 27); the once common practice of excising maxillae from rare snakes for the sole reason of counting teeth is neither necessary nor justified.

Hemipenes were treated as described in Myers (1974), except that everted organs were inflated with carmine-dyed petroleum jelly (rather than wax or latex). A few hemipenes in preserved specimens were manually everted from either the retracted state (fig. 17) or from partially everted organs (figs. 14, 20B), after they were dissected out and then soaked first in glycerin and finally in a saturated solution of trisodium phosphate to restore elasticity. Although hemipenial eversions made from preserved specimens may be fully everted with all structures showing, some such organs may be less completely inflated (i.e., less robust) than fresh preparations. Techniques are reviewed by Myers and Cadle (MS).

All specimens were collected long before the availability of Global Positioning System (GPS) satellite receivers. The detailed 1:50,000 map series of Panama is still incomplete and, with one exception (see *Atractus hostilitractus*), topographic maps of this scale are still unavailable for the type localities in this paper. Therefore, approximate geographic coordinates were determined mainly from the maps *Canal Zone and Vicinity 1:100,000* (1957 edition, U.S. Army Map Service, Washington, DC) and the 12-sheet *Mapa General de la República de Panamá 1:250,000* (1st ed., circa 1966–1967, Dirección de Cartografía, Panama City). Some coordinates differ slightly from those

in Fairchild and Handley (1966), whose important gazetteer of GML and other collecting stations was based on an earlier 3-sheet 1:500,000 map of the Republic.

GENUS *ATRACTUS*

Atractus is a large South American genus whose range is now known to include the eastern half of Panama (map 1), where it seems to be exceedingly rare. The four whole specimens (figs. 1, 2) and the one head (fig. 10) known to me represent five species! Two of these specimens come from the low uplands east of the Canal Zone and three are from Darién; all localities are in well-drained (100 to >500 m) monsoon rain forest (Myers, 1969).

I have been unable to match any of the Panamanian specimens with previously named South American species. But identifying *Atractus* is often difficult owing to the many inadequate, poorly illustrated descriptions that usually emphasize characters present in a majority of species. A major review of the genus is needed. There have been good taxonomic and variational studies for Ecuador (Savage, 1960), Venezuela (Roze, 1961, 1966), Surinam (Hoogmoed, 1980), and eastern and central Amazonia (Cunha and Nascimento, 1983; Martins and Oliveira, 1993)—but the situation is less good for Colombia, which has a rich *Atractus* fauna of several dozen named species, whose variation and relationships are virtually unknown (lists of nominal species in Daniel, 1949; Peters and Orejas-Miranda, 1970; Sanchez-C. et al., 1987; Pérez-Santos and Moreno, 1988). Although a majority of Colombian *Atractus* are Andean, it would not be surprising if an older Colombian (or other South American) name were eventually found to be applicable to one of the purportedly new species herein described as Panamanian endemics. To ease the burden of workers who may have to decide this point without ready access to all holotypes, the five Panamanian specimens are described and illustrated in some detail. I additionally discuss and illustrate a Colombian specimen of *Atractus clarki* Dunn and Bailey, a species heretofore reported only from the Panamanian holotype.

This genus has been confused with *Geo-*

phis, but, in Panama, known *Atractus* are easily distinguished by the generic characteristic of a single pair of genials (two pairs in southern *Geophis*) and 17 rows of smooth scales (15 rows of scales, smooth or posteriorly keeled in southern *Geophis*); also, the southern *Geophis* have a usually diamond-shaped or rhomboidal frontal plate that is strongly angular anteriorly (as in fig. 12), whereas Panamanian *Atractus* have a more normal colubrid frontal that is roughly triangular or pentagonal, with only a small anterior apex at the prefrontal suture (fig. 3).

Unfortunately, the four whole specimens of Panamanian *Atractus* are all females and furnish no data on male genitalia, although opportunity is taken to describe and illustrate a hemipenis from the Colombian specimen of *A. clarki*. Hemipenial differences mentioned by Savage (1960: 30) have since broken down with further study of *Geophis* (see Downs, 1967: 184, and discussion herein under *Geophis bellus*), and the distinction is further blurred by the hemipenis of *Atractus clarki* (q.v.). Cadle (1984) considered *Atractus* a South American member of a mainly Central American xenodontine clade—now recognized as the subfamily Dipsadinae—for which the most diagnostic of several derived hemipenial features is the distal division of the sulcus spermaticus (Myers and Cadle, 1994: 27; Zaher, 1999: 33). The sulcus spermaticus in the Dipsadinae usually divides close to or within the capitulum; the hemipenis of *A. clarki* is noncapitate and the sulcus divides slightly below the midpoint of the organ (at least in the retracted condition)—somewhat lower than in most dipsadines but still higher than the basal bifurcation in the great majority of Xenodontinae (in which the sulcate bifurcation may rarely approach the midpoint of the organ, e.g., see Zaher, 1999: fig. 64, upper).

Atractus and *Geophis* have been often compared, but the closeness of their relationship is questionable and they are probably convergent to a similar life-style. On the basis of immunological comparisons, Cadle (1984) saw a closer relationship for *Geophis* with *Ninia* and other Middle American dipsadines than with Peruvian *Atractus elaps* and *A. major*. Zaher (1999: 33) suggested, on the basis of a muscle character, an espe-

cially close relationship between *Atractus* and the Middle American *Adelphicos*.

Panamanian *Atractus* share a number of features⁷ that are possessed by a majority of species in the genus (e.g., see data matrix in Peters and Orejas-Miranda, 1970: 24–26). They have 17 dorsal scale rows, large prefrontals that are in contact with the eye, usually two postoculars (2/3 in one), no preocular, an elongated loreal plate, seven supralabials, first pair of infralabials in contact behind the mental, and a basically cross-banded or blotched color pattern. The five Panamanian specimens/species are identifiable by the following key (see also comparative figures, diagnoses, and table 1):

KEY TO PANAMANIAN *ATRACTUS*

1. Venter black or clouded with dark pigment; no pale dashes on lower scale rows; eye length less than or scarcely greater than distance from its lower edge to lip 2
- Venter pale (fig. 2A); lower scale rows with pale centers; eye length noticeably greater than distance to lip (fig. 3A) *A. clarki*
2. Neck black with pale rings, or with black bands several times wider than those posteriorly on body; eye moderate, going less than 2.5 times into loreal; total length less than 500 mm (<400 mm in two females) 3
- Neck brown like body, with black transverse lines not greatly wider than on rest of body (fig. 1C); eye very small (fig. 3E), contained about three times in loreal plate; size large (one female 750 mm total length) *A. depressiocellus*
3. Snout bluntly pointed in profile (fig. 9A, C); loreal well separated from internasal; labials mostly white 4
- Snout in profile rounded like a coral snake (fig. 9B); anterior corner of loreal approaching or touching corner of internasal; labials mostly black; neck black with several pale rings, changing posteriorly to light reddish brown ground color (red in life?)

⁷ A peculiarity shared by four of the five Panamanian specimens, and some others I have seen, is that the asymmetrical suture between the prefrontal plates is noticeably dextral to the internasal suture (fig. 3). The dextral orientation also is seen in seven of eight species figured by Hoogmoed (1980). Some *Atractus* have the two sutures aligned in the normal colubrid manner.

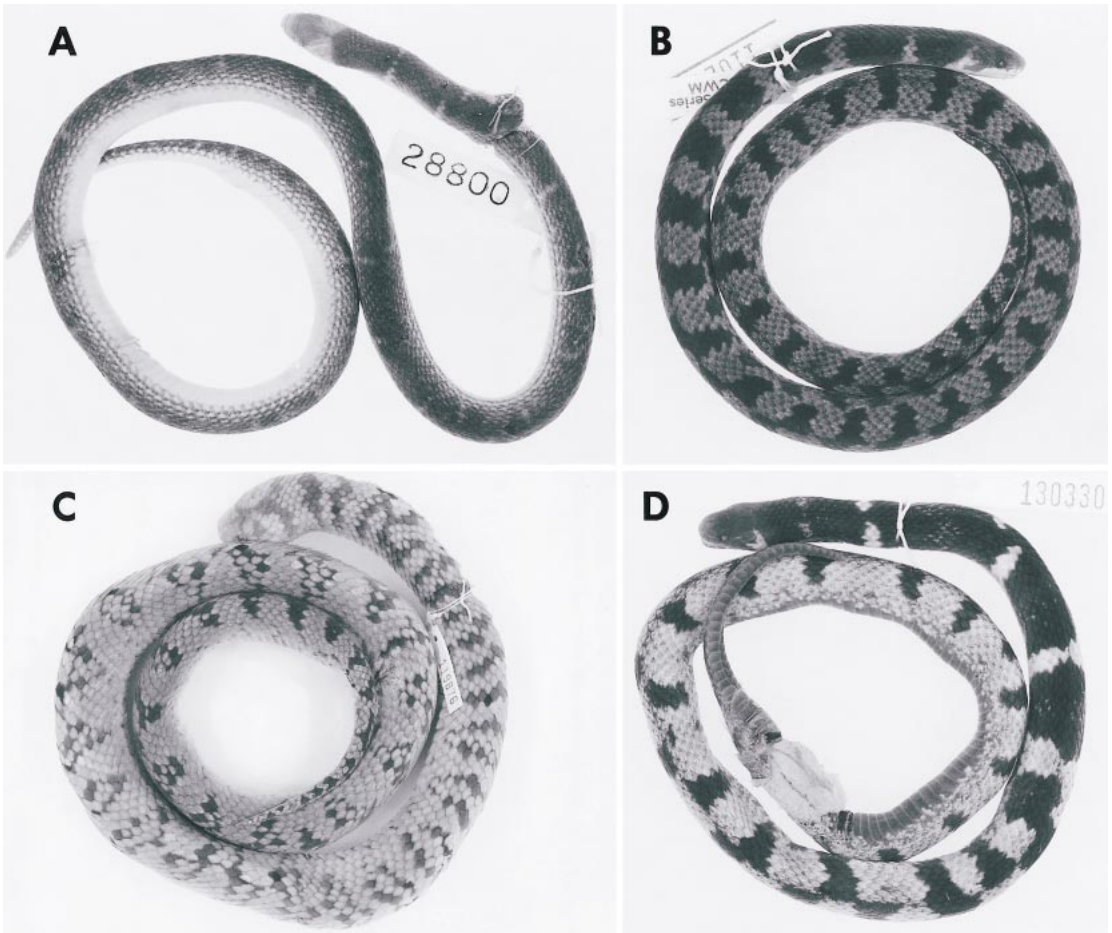


Fig. 1. Panamanian *Atractus*: Holotypes in dorsal view. **A.** *A. clarki* Dunn and Bailey (MCZ 28800), $\times 1.0$. **B.** *A. darienensis*, new species (KU 110274), $\times 0.8$. **C.** *A. depressiocellus*, new species (AMNH 119876), $\times 0.4$. **D.** *A. hostilitractus*, new species (AMNH 130330), $\times 0.8$. See figure 10 for a fifth Panamanian species (*Atractus imperfectus*, new species).

- with black bars (fig. 1D) *A. hostilitractus*
- 4. Neck with black saddles (fig. 1B [obscure in life]) several times wider than posterior black bars, but narrow interspaces between anterior saddles brown like rest of ground color, not whitish (or red or yellow); rostral narrowly visible in dorsal view; eye length less than 90% of distance to lip *A. darienensis*
- Neck black with pale bars or ringlike markings (fig. 10 [posterior pattern unknown]); rostral plate well visible in dorsal view; eye length about equal or slightly larger than distance to lip *Atractus imperfectus*

Atractus clarki Dunn and Bailey
 Figures 1A, 2A, 3A, 4, 5; map 1

Atractus clarki Dunn and Bailey, 1939: 8–9 (holotype: MCZ 28800, an adult female collected by native worker in 1938, at Mine at Santa Cruz de Cana [approx. 7°46'N, 77°41'W, 500 m], Province of Darién, eastern Panama).

DIAGNOSIS: *Atractus clarki* is readily distinguished from other Panamanian species in having a uniformly pale venter, narrow pale dorsal bars, pale dashes on the lower scale rows, and in having a relatively large eye whose length is noticeably greater than its

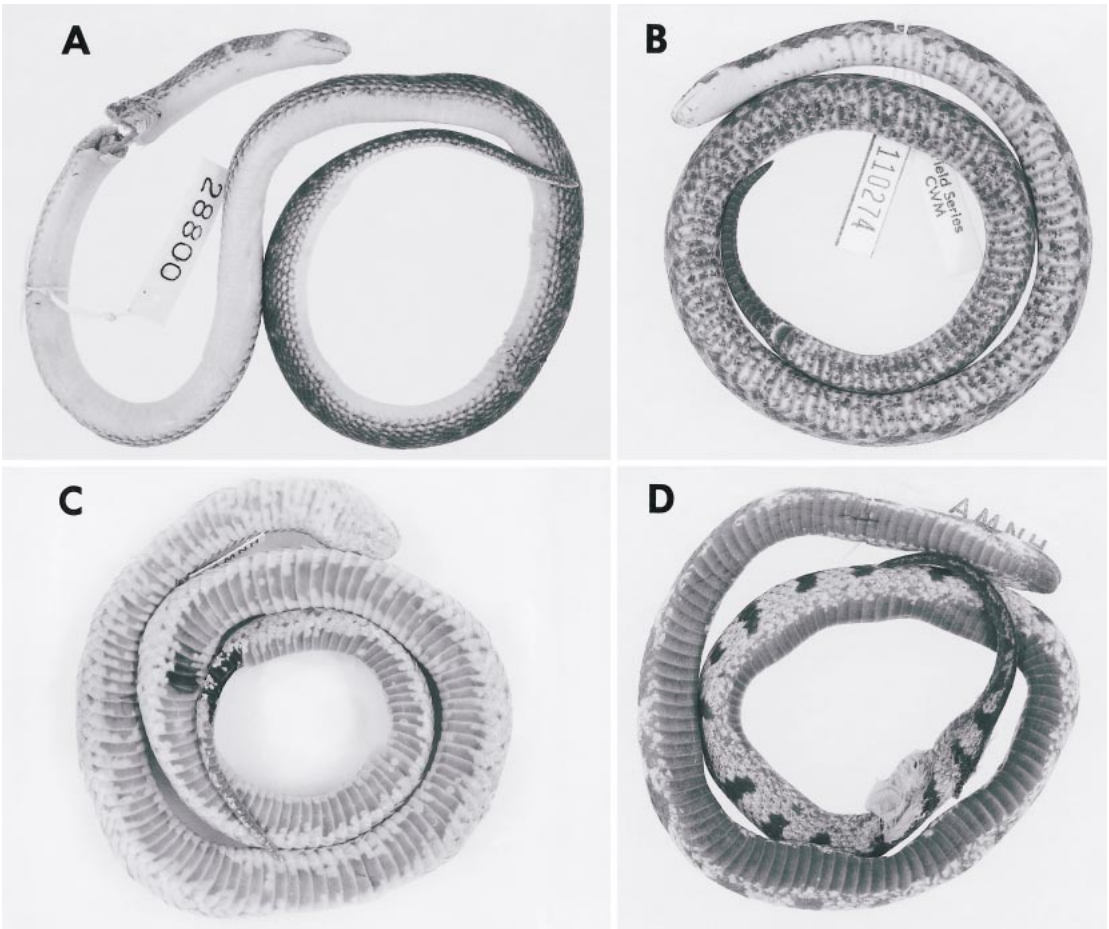


Fig. 2. Panamanian *Atractus*: Holotypes in ventral view. **A.** *A. clarki*. **B.** *A. darienensis*. **C.** *A. depressiocellus*. **D.** *A. hostilitractus*. Specimens shown $\times 0.4$ – 1.0 as given individually in figure 1. See figure 10 for the fifth Panamanian species (*Atractus imperfectus*).

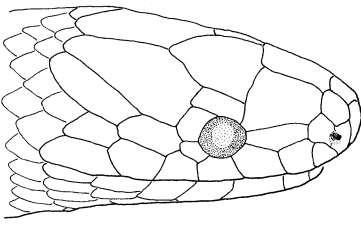
distance to lip and which is contained less than two times in length of the loreal plate.

Dunn and Bailey compared the species with Colombian *A. pamplonensis* and Ecuadorian-Peruvian *A. collaris*. Their nonillustrated original description is inadequate, particularly in omitting mention of pale bars in the dorsal pattern and in not clearly stating the presence of a well-defined nuchal collar.

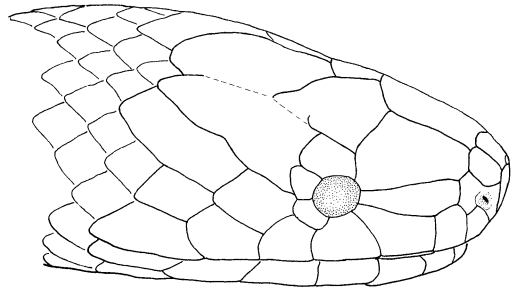
REDESCRIPTION OF HOLOTYPE

The specimen is a female, shown to be adult by condition of the oviducts, which are large and convoluted. The neck was nearly severed from the body by the collector, but otherwise it is in good condition.

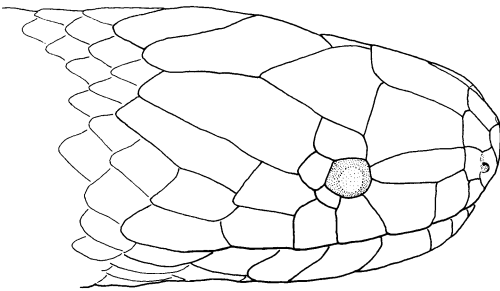
PROPORTIONS AND SCUTELLATION: Total length 310 mm, tail length 36 mm (11.6% of total). Slender, body rounded ventrolaterally; body anteriorly slightly wider than high, but scarcely wider than head; body posteriorly becomes laterally compressed and higher than wide (about 6 mm high \times 5 mm wide near end of body); greatest head width 64.3% of head length from snout to end of parietals, about 2.0% of SVL; greatest body width about 2.0% of SVL. Dorsal scales smooth, lacking apical pits, in 17–17–17 rows. Ventrals about 181 (the estimated “185” in original description would have included three large gulars or preventrals), anal plate undivided, subcaudals in 33 pairs.



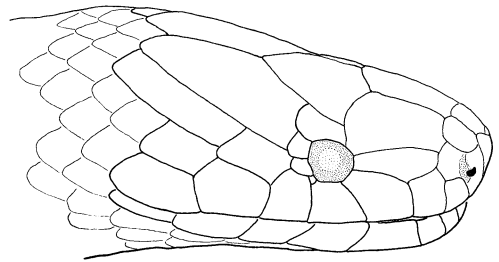
A: *Atractus clarki* × 5



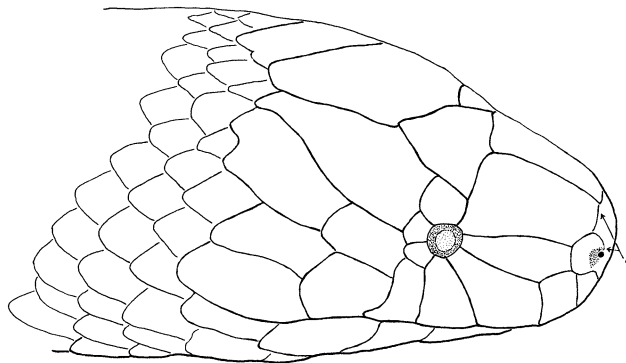
B: *A. darienensis* × 5



C: *A. hostilitractus* × 5



D: *A. imperfectus* × 5



E: *A. depressiocellus* × 2.7

Fig. 3. Heads of Panamanian *Atractus*; holotypes shown ×5, except ×2.7 for one large species. **A.** *A. clarki* Dunn and Bailey (MCZ 28800). **B.** *A. darienensis*, new species (KU 110274). **C.** *A. hostilitractus*, new species (AMNH 130330). **D.** *A. imperfectus*, new species (MCZ 50213). **E.** *A. depressiocellus*, new species (AMNH 119876).

TABLE 1
Standard Characters and Measurements (in mm) of Holotypes of Five Species of Panamanian *Atractus*

| | A.cla. adult ♀ | A.dar. adult ♀ | A.dep. adult ♀ | A.hos. adult ♀ | A.imp. ^a ? ^b |
|--------------------------------|-------------------|-------------------|-------------------|-------------------|---------------------------------------|
| Ventrals | ~181 | 159 | 167 | ~160 | — ^b |
| Subcaudals | 33 | 25 | 30 | 27 | — ^b |
| Maxillary teeth | 6 | 7 | 7 | 7 | 7 |
| Total length | 310 | 346 | 750 | 374 | — ^b |
| Tail length | 36 | 33 | 77 | 40 | — ^b |
| Tail/total length × 100 | 11.6% | 9.5% | 10.3% | 10.7% | — ^b |
| Head length ^c | 8.4 | 9.5 | 19.0 | 9.9 | 9.9 |
| Greatest head width | 5.4 | 7.5 | 19.7 | 7.7 | 7.3 |
| Greatest body width | ~5.5 | 8.7 | ~19 | ~8.5 | — ^b |
| Eye to snout tip (sagittal) | 3.2 | 4.0 | 8.0 | 3.7 | 3.6 |
| Eye length | 1.2 | 1.2 | 1.8 | 1.2 | 1.3 |
| Lower edge eye to lip | 0.9 | 1.4 | 3.7 | 1.4 | 1.2 |
| Nasal length | 1.4 | 1.4 | — ^d | 1.5 | 1.6 |
| Loreal length | 1.7 | 2.6 | 6.0 | 2.7 | 2.3 |
| Greatest length of internasal | 0.9 | 1.0 | — ^e | 1.1 | 1.1 |
| Greatest width of internasal | 1.0 | 1.0 | — ^e | 1.1 | 1.1 |
| Length of internasal suture | 0.5 | 0.8 | — ^e | 0.7 | 0.8 |
| Greatest length of prefrontal | 2.0 | 2.3 | 7 | 2.9 | 2.8 |
| Greatest width of prefrontal | 1.8 | 3.0 | 4.7 | 2.5 | 2.3 |
| Length of prefrontal suture | 1.7 | 2.3 | 6.0 | 2.3 | 2.1 |
| Frontal length | 2.6 | 3.1 | 5.1 | 3.3 | 3.0 |
| Greatest length of parietal | 4.1 | 4.4 | 9.6 | 5.0 | 4.8 |
| Length of interparietal suture | 2.2 | 2.3 | 6.2 | 2.5 | 2.5 |

^a A.cla. (*Atractus clarki*), A.dar. (*A. darienensis*), A.dep. (*A. depressiocellus*), A.hos. (*A. hostilitractus*), A.imp. (*A. imperfectus*). See text for museum numbers of holotypes.

^b *Atractus imperfectus* is an incomplete specimen, represented by 38 mm of head and neck.

^c Head length from tip of snout to ends of parietals.

^d Tip of snout damaged.

^e Missing internasals very small if originally present, possibly fused with large prefrontal plates (fig. 3E).

Head barely distinct from neck; snout bluntly rounded in dorsal view, bluntly pointed in profile; rostral wider than high, well visible from above; internasals small, slightly wider than long, about half (53%) of length of suture between prefrontals; prefrontals large and nearly as wide as long (greatest prefrontal width 90% of greatest length); prefrontal suture 63% length of frontal plate; supraoculars more than twice as long as broad; frontal as long as broad, roughly pentagonal in shape; interparietal suture 81% of frontal length.

Eye moderate, contained 1.4 times in loreal length, 2.7 times into snout length; eye length 25% larger than its distance to lip; eye protuberant beyond edge of lip so that it is slightly visible in ventral view. Nasal divided above and below near rear edge of naris, its

greatest length 82% of loreal length; loreal long, 2.4 times longer than greatest height, well separated from internasal, entering eye; no preoculars; supralabials 7, third and fourth touching eye, fourth wider than high; two postoculars, the uppermost largest; temporals 1 + 2, the upper one in row 2 elongated, reaching slightly past ends of parietals.

Infralabials 7, first pair in contact behind mental, first three on each side in contact with genials; single pair of large genials, about three times longer than wide; three large median gulars or preventrals between genials and first ventral. Head plate tubercles tiny, sparse and inconspicuous.

COLOR PATTERN: Dull blackish brown above, with about 25 narrow (about one scale wide) whitish bars, extending from the vertebral region down to the third or fourth scale

row; these pale dorsal bars are mostly alternating on each side, but there are a few scattered pairs that medially connect and give appearance of a pale ring in dorsal view (e.g., first pair on neck, fig. 1A). The pale bars are vague but tend to be bordered by almost uniformly dark areas about 1–2 scales wide, which add a little emphasis. Most intervening dorsal scales have pale centers, as do all lateral scales in rows 1–3, resulting in a nearly continuous white line on the second row. The whitish line continues well onto the tail, which dorsally has vague indications of the pale body bars.

The snout is gray, from its tip to the middle of the prefrontals above and to the eyes laterally. The top of the head is darker brown back to the middle of the parietals, with this color extending ventrad to include the postoculars and circling narrowly under the eyes. The supralabials are mostly white. An ill-defined black bar extends obliquely from the front edge of the primary temporal onto supralabial 6, with a small isolated spot matching up with it below the mouth, on the anterior end of the last infralabial. Dorsally an orange-brown band crosses the rear of the head, being narrowed medially and slightly broken by brown pigment along the interparietal suture; laterally this pale orangish band is confluent with, but distinct from, the white areas of the primary temporal and posterior labials. Except for the small vague dark spot on the last infralabial, the underside of the head is immaculate pale yellow. The ventrals and subcaudals are slightly edged with the dark body color and there is a weak, irregular median line of brown pigment under the tail. The venter otherwise is immaculate pale yellow.

MAXILLO-PALATO-PTERYGOID ARCH: Examined in situ on right side. Maxilla arched, extending anteriorly nearly to suture between rostral and first supralabial, with 6 well-spaced recurved teeth, decreasing in size posteriorly. First tooth springs from anterior tip of maxilla; first four teeth large, with noticeable gaps (not sockets) between 2 and 4, followed by a larger gap and two small teeth, the ultimate noticeably smaller than penultimate; teeth distally angular in cross section, with a lateral edge. Maxilla extending posteriorly past small teeth as a short toothless



Fig. 4. The second known specimen of *Atractus clarki* (MCZ 13301♂), from an unspecified locality in the Colombian Chocó, $\times 1.2$.

process. An expanded flange on maxilla extending medially and ventrad adjacent to the two small posterior teeth. Ectopterygoid forked, with one branch (apparently an expanded flange) tightly bound against the expanded maxillary flange. Maxillary process of palatine absent.

A SECOND SPECIMEN OF *ATRACTUS CLARKI*

A Colombian specimen (MCZ 13301) from the Chocó, without further locality data, has for many decades been misidentified as *Atractus multicinctus*, which is a better known Chocoan species. This “new” specimen (fig. 4) is a male, judged adult because the hemipenial spines are calcified. It was collected by M.V. Campbell in 1919.

PROPORTIONS AND SCUTELLATION: MCZ 13301 is 278 mm in total length, 43 mm tail

length (15.5% of total), with 159 ventrals and 40 pairs of subcaudals. Compared with the female holotype it has 22 fewer ventrals, 7 more caudals, and a relatively longer tail, with these differences being in the direction of expected sexual dimorphism. Other scale counts are identical to the holotype, and head plate proportions are similar. This specimen has a relatively wider head (71.6% of length vs. 64.3% in holotype), with the snout appearing more pointed in dorsal view. The eye is contained 1.25 times (1.4 times in holotype) in the loreal, which is 2.1 (vs. 2.4) times longer than greatest height, and contained 2.8 (2.7) times in the snout length. Eye length is 25% larger than distance to lip (identical to holotype), but the eyes are not quite visible from below as they are in the holotype, possibly due to the relatively wider head. As in the female holotype, the body anteriorly is slightly wider than high but posteriorly becomes laterally compressed and higher than wide.

COLOR PATTERN: The color pattern of the Colombian specimen (fig. 4) is bolder than on the Panamanian holotype (fig. 1A) but is essentially the same: There are about 28 vertical white bars on the left side, mostly alternating but sometimes aligned with those on the right; none of these are medially fused and most do not reach the vertebral scale row; there is an aberrant longitudinal patch of white on the right side of neck in place of the usual bars. As on the holotype the lateral white bars are vaguely set in areas of uniformly pigmented scales, which otherwise contain pale dashes. The lower several scale rows are strongly dashed with white.

The pale nuchal collar includes the dorsal scales immediately behind the parietals and upper secondary temporals, and the collar is thus wider than on the holotype. The snout seems to have been gray as in the type. The ill-defined black postocular bar described for the holotype is lacking, being represented on this specimen only by a few isolated small pigment spots. There is a smudge of dark pigment on the tip of the chin and a rare dark speck on ventrals and subcaudals, but otherwise the ventral surfaces are uniformly pale.

HEMIPENIS: The left retracted hemipenis bifurcated at the level of subcaudal 8 and terminated at the end of subcaudal 10, with the



Fig. 5. Hemipenis of *Atractus clarki* (MCZ 13301♂). Uneverted left organ opened midventrally, $\times 10$.

two slips of retractor muscle merging at the end of subcaudal 11. The organ was cut open along its midventral line, removed, and pinned flat for illustration (fig. 5).

The distal third of the organ is bilobed and calyculate, with the well-defined calyces bearing blunt to slightly pointed soft papillae. The calyculate region is continuous from lobe to lobe at the medial side of the crotch; the area within the fork of the sulcus is spinose. The sulcus spermaticus divides less than halfway (about 45%) up the organ, and its branches extend to the tips of the lobes in a centrifugal orientation—one branch lying on the ventral wall of the ventral lobe (this branch cut across when lobe opened midven-

trally, fig. 5) and the other lying on the dorsal wall of the dorsal lobe (determined by medial incision of this lobe, concealed in the figure); I am uncertain whether the centrifugal orientation of the branches would be maintained on the everted organ. The midsection of the hemipenis is densely spinose, with a few dozen medium-sized spines; most of these spines are arranged in V-shaped rows broken by the sulcus spermaticus, but smaller spines lateral and basal to the aforesaid are nearly arranged in transverse rows. There is no evidence of capitulation or semicapitulation between the spinose midsection and calyculate lobes. The extreme base of the organ is nude, with longitudinal expansion folds. Above the nude part are a few spinules and, most conspicuously, a cluster of small spines atop a heavy longitudinal fold on the dorsal wall. There is a heavy, nearly nude transverse fold of tissue adjacent to the spinose cluster; this fold proximally overlays a small cavity containing a few concealed spines (indicating that the cavity is everted when the organ is), and distally the transverse fold marks the base of a deep, lateral naked pocket. (Thus, the longitudinal lateral pocket does not continue to the base of the hemipenis as it does in most snakes having such a structure, but it almost certainly retains its identity after eversion of the hemipenis.)

REMARKS

Dunn and Bailey (1939) named this species after Herbert C. Clark, first director of the Gorgas Memorial Laboratory and instigator of the Panamanian snake census. Santa Cruz de Cana, the type locality of *Atractus clarki*, is situated at 500 m elevation (my altimeter reading) on the eastern flank of the Serranía de Pirre—roughly at 7°46'N, 77°41'W (map 1). It is the site of gold mining that has been carried on periodically since the end of the 16th century, being usually deserted and reverting to jungle in the intervening periods (Myers, 1969: 22).

The second specimen and first male of *Atractus clarki*, from somewhere in the Colombian Chocó, corroborates the diagnostic features of the species but might be perceived to call into question its generic status. Savage (1960: 29) stated that the hemipenes of *Atrac-*

tus are “bilobed at tips” and “never calyculate.” However, the organ of *A. clarki* is bilobed for a third its length and the lobes are markedly calyculate. Hoogmoed (1980) explicitly mentioned the existence of calyces in several species of *Atractus* in Surinam, although in one instance (p. 23) he described them as “scalloped calyces (Savage, 1960, fig. 4A)” —this reference being to structures described by Savage (1960: 24) not as calyces but as “scalloped transverse flounces” (which conceivably might be derived from calyces by loss of the vertically aligned tissue ridges). Fernandes (“1995” [1996]: 43, 50, fig. 1) added the trait of hemipenial capitulation with calyulation for the Brazilian *A. reticulatus* and some other southern *Atractus*, and Fernandes et al. (2000: 3, 5) described the Brazilian *A. maculatus* and *A. zebrinus* as having hemipenes “capitate, bilobate . . . the distal portion covered by spinulate calyces”.

The taxonomic distribution and nature of both capitulation and calyces/flounces within *Atractus* need to be revisited (male genitalia have been comparatively examined for less than half of the currently recognized species [mainly by Savage, 1960, and Hoogmoed, 1980] and illustrations are regrettably rare). Calyces are probably symplesiomorphic for both xenodontine and dipsadine colubrids, with absence being a presumed secondary loss, as in the tribe Xenodontini (Myers, 1986: 6) and in many or most *Atractus*. When Savage’s seminal study is extended to cover the entire genus, it may be found that *Atractus clarki* is simply primitive in the retention of relatively long, hemipenial lobes bearing typical calyces. See page 9 for a comment on the bifurcation of the sulcus spermaticus.

Atractus clarki also seems primitive in its relatively large eye, which is sufficiently protuberant so as to be visible (holotype) or almost visible (MCZ 13301) in ventral view, more like a generalized terrestrial colubrid than the majority of *Atractus*, most of which seem to be semifossorial on morphological grounds.

Atractus darienensis, new species

Figures 1B, 2B, 3B, 6, 9A; Map 1

HOLOTYPE: KU 110274 (field no. CWM 6095), an adult female caught by C.W. Myers



Fig. 6. *Atractus darienensis*, new species. The holotype in life (KU 110274). The reflective scale surfaces cause the color pattern to be less evident in life than in preservative (compare with fig. 1B).

on January 25, 1966, at 500 m above sea level on the north end of the Serranía de Pirre, Province of Darién, eastern Panama. The type locality, a temporary forest camp, is situated roughly at 8°00'N, 77°43'W (map 1; figs. 7, 8).

ETYMOLOGY: The specific name is an adjective derived from the eastern Panamanian Province of Darién + the adjectival suffix *-ensis* (indicating place of origin).

DIAGNOSIS: *Atractus darienensis* can be distinguished from other Panamanian and most South American species by the pattern of black markings on a medium brown (reddish brown in life) ground color. There are a few black saddles on the neck which are several times wider than the alternating or medially connected black bars that occupy the rest of the body; the shiny scales make this pattern less obvious in life (fig. 6) than when the snake is immersed in liquid (fig. 1B). *Atractus hostilitractus* also has black markings that are anteriorly wider, but these are partially separated by pale rings, and the posterior bars are less numerous than in *darienensis* and set on a much lighter ground color (fig. 1D); *A. hostilitractus* also has black supralabials, and the snout in profile is reminiscent of a coral snake (fig. 9B).

Atractus darienensis resembles *A. imper-*

fectus in having white labials, a similarly vague nuchal collar, and a similar snout shape in profile (compare fig. 9A and 9C). *Atractus imperfectus*, however, has pale bars or broken rings on a black neck (fig. 10 [posterior pattern unknown]), dark serration across upper edges of the supralabials, a relatively larger eye, broader snout, and a dorsally more extensive rostral plate (fig. 3). These differences are elaborated under *Atractus imperfectus*.

DESCRIPTION OF HOLOTYPE

The holotype is a sexually mature female as shown by enlarged, flabby (nonconvoluted) oviducts that appear recently spent.

PROPORTIONS AND SCUTELLATION: Total length 346 mm, tail length 33 mm (9.5% of total). Moderately proportioned, with body noticeably wider than head, wider than high and rounded ventrolaterally; greatest head width 78.9% of head length from snout to end of parietals, about 1.8% of SVL; greatest body width about 2.8% of SVL. Dorsal scales smooth, lacking apical pits, in 17–17–17 rows. Ventrals 159, anal plate undivided, subcaudals in 25 pairs.

Head barely wider than neck; snout bluntly rounded in dorsal view, bluntly pointed in



Fig. 7. Northern end of the Serranía de Pirre, as seen looking SSE from a distance of 15–20 km at El Real, 20 m elevation (December 1965). The twin breastlike peaks were determined by altimeter to be 960 m and 1000 m (from left to right); the still higher prominence (1110 m) farther south is Cerro Cituro (wrongly identified on some maps as “Cerro Pirre”, which lies still farther south at about 1550 m). Arrow indicates general region of the type locality of *Atractus darienensis*—a temporary base camp at 500 m elevation, established prior to exploring higher reaches of the *serranía*. See figure 8.

profile; rostral wider than high, scarcely visible from above; internasals small, as wide as long, less than half (43%) of length of prefrontal suture; prefrontals large, wider than long (greatest prefrontal width 130% of greatest length); prefrontal suture 74% length of frontal plate; supraoculars large, nearly as broad as long; frontal as long as broad, roughly pentagonal in shape; estimated interparietal suture equal to prefrontal suture, 74% of frontal length. The parietals are aberrantly fused with each other and with the right posterior half of the frontal plate (fig. 3B).

Eye small, contained 2.2 times in loreal length, 3.3 times in snout length; eye length smaller (86%) than distance to lip; eyes set close to head, not protruding to edge of lips, thus concealed from ventral view. Nasal weakly divided above middle of naris and

below at its posterior edge, its greatest length 54% of loreal length; loreal long, 3.3 times longer than greatest height, well separated from internasal, entering eye; no preoculars; supralabials 7, third and fourth in eye, fourth somewhat wider than high; two subequal postoculars; temporals 1 + 2, the upper one in row 2 elongated, extending past end of interparietal suture.

Infralabials 7, first pair in contact behind mental, first four on each side in contact with genials; single pair of large genials, 2.4 times longer than wide; four large medial gulars and preventrals between genials and first ventral. Head plate tubercles tiny, sparse, and inconspicuous.

COLOR PATTERN: In life the holotype of *Atractus darienensis* was dark reddish brown above with black dorsal saddles and bars, which, as indicated in my fieldnotes, were



Fig. 8. Type locality of *Atractus darienensis*, at 500-m base camp in forest on northern end of the Serranía de Pirre (see fig. 7). Early dry season (January 14, 1966); within two weeks after this photograph, the saturated ground surface dried and there was abundant leaf fall, with the forest seeming to be nearly 50% deciduous. The crest of the *serranía* supports dense cloud forest (illustrated in Myers, 1982).

not very evident because the smooth shiny scales readily reflected light, so as to reduce contrast in the dorsal pattern (compare life view in fig. 6 with figs. 1B, 2B). Labials and anterior venter pale yellow, turning still paler yellow on posterior half of venter, with ill-defined black ventral markings and with anal plate and underside of tail black. Tiny iris red.

In preservative (figs. 1B, 2B) medium brown with about 33 black dorsal markings: The first six are complete saddles (touching scale row 1 on each side), whereas the posterior markings are shorter (to rows 3 or 4) and several are asymmetrical, forming alternating dorsolateral bars on each side of the vertebral line. The first three black saddles are 6–8 scales wide, the next three are 3–4 scales wide, and posteriorly the dorsal cross-bars are about 2 scales wide; the brown in-

terspaces are only 1–2 scales wide between the first few saddles, but posteriorly the interspaces become somewhat wider than the cross-bars. Very irregularly shaped grayish black lateral blotches on rows 1–3, alternating with the dorsal cross-bars, appear posterior to the neck saddles, with each lateral blotch occupying an area equal to several scales. The last several lateral blotches are longitudinally fused, forming a poorly defined black stripe anterior to the tail. The short tail has half a dozen irregular black bars.

The head is black above, with this color being medially continuous with the first neck saddle and irregularly edging the upper edges of the supralabials, which are mostly white. An oblique extension of the black head cap extends posteroventrally across the rear of supralabial 6 and most of 7 and barely onto

the ultimate infralabial. Posterior to this an irregular anterodorsal extension of the pale throat color forms an incomplete nuchal collar—white ventrally, pale brown dorsally—ending on the posterolateral edge of each parietal.

The underside of the head and throat are white with sparse brown markings; the venter (fig. 2B) is heavily clouded with black and brown pigmentation; the anal plate and underside of the tail are black.

MAXILLO-PALATO-PTERYGOID ARCH: Examined in situ on right side. Maxilla arched, extending anteriorly to middle of first supralabial, with 7 well-spaced recurved teeth, decreasing in size posteriorly (a large replacement tooth close behind and slightly medial to the fourth tooth is not included in this count). First tooth springs from anterior tip of maxilla; first five teeth large, with noticeable gaps (not sockets) between 2 and 5, followed by a larger gap and two very small teeth (ultimate smallest); teeth distally angular in cross section, with an anterolateral edge. Maxilla extending posteriorly past small teeth as an elongate toothless process. An expanded flange on maxilla extending mediad and ventrad adjacent to the two small posterior teeth. Ectopterygoid forked, with one branch forming an apparently expanded flange that is tightly bound against the expanded maxillary flange. Maxillary process of palatine absent.

REMARKS

I found the holotype of *Atractus darienensis* at night in dense forest (fig. 8), as it was crawling across a small bare spot on the forest floor. The species is quite distinct from its geographically nearest neighbor, *A. clarki*, whose type locality is only about 25 km to the south. Both type localities lie at 500 m elevation on the lower slopes of the Serranía de Pirre (map 1), in an evergreen seasonal forest (monsoon rain forest) having a January–March dry season during which many trees are deciduous (Myers, 1969, 1982).

Atractus depressiocellus, new species

Figures 1C, 2C, 3E; map 1

HOLOTYPE: AMNH 119876, an adult female collected by George Barratt, Jr., on Oc-

tober 31, 1974, Cerro Azul [Cerro Jefe] region, Province of Panamá, Panama. The type locality is in the general region of Cerro Jefe on the Piedras-Pacora Ridge, at about 9°14'N, 79°23'W (see Remarks).

ETYMOLOGY: This snake has conspicuously depressed, very small eyes, and hence the specific name, a noun in apposition, is derived from the Latin adjective *depressus* (low or depressed) + the noun *ocellus* (a little eye).

DIAGNOSIS: *Atractus depressiocellus* is immediately distinguished from other Panamanian *Atractus* by its large size, relatively uniform dorsal pattern of irregularly paired black cross-lines on a brown ground, and very small eyes that are notably depressed on a broad, relatively short head. It is the only Panamanian *Atractus* in which head length (tip of snout to end of parietals) is equalled by head width (fig. 1C).

In total length, *Atractus depressiocellus* approaches *A. obesus* from Andean Colombia and the Amazonian *A. major* and *A. torquatus*. These differ from *depressiocellus* in color pattern (photographs in Marx, 1960; Martins and Oliveira, 1993) and in various features of scutellation. *Atractus depressiocellus* also differs noticeably from these in its very small depressed eye and in the associated feature of exceptionally tall supralabials 3–5 (fig. 3E). It may be unique in either lacking or in having exceptionally tiny internasals (see below).

DESCRIPTION OF HOLOTYPE

As suggested by its large size and proved by large ovaries and large convoluted oviducts, the specimen is a sexually mature female. It is rather soft, with internal organs poorly preserved; color pattern and other external features are clearly evident except that the rostral region was rubbed raw or injured in life. The rostral plate and anterior parts of the nasal plates consequently are lacking, and presence of internasals cannot be determined, although the internasals would be exceptionally small if present (fig. 3E).

PROPORTIONS AND SCUTELLATION: Total length 750 mm, tail length 77 mm (10.3% of total). A relatively long and heavy-bodied snake, but body not any wider than the broad

head; body wider than high and rounded ventrolaterally; greatest head width slightly larger (104%) than head length from snout to end of parietals, about 2.9% of SVL; greatest body width about 2.8% of SVL. Dorsal scales smooth, lacking apical pits, in 17–17–17 rows. Ventrals 167, anal plate undivided, subcaudals in 30 pairs.

Head broad, wider than neck; snout broad and bluntly rounded in dorsal view, rounded in profile; missing (damaged) rostral probably was somewhat wider than high; missing internasals either were very small if originally present (see above), or possibly fused completely with large prefrontal plates; prefrontals very large, longer than wide (greatest prefrontal width 67% of greatest length); prefrontal suture longer (118%) than length of frontal plate; supraocular large, a little wider than long; frontal short, noticeably wider than long (length 76% of width), roughly pentagonal in shape; interparietal suture much longer (122%) than length of frontal plate but only slightly longer than prefrontal suture.

Eye very small, contained 3.3 times in loreal length, 4.4 times into snout length; eye length less than half (46%) its distance to lip; eye set in a pronounced depression, with supraocular dropping almost vertically to eye and with all other circumocular plates slanting inward to eye. Nasal weakly divided above and below posterior part of nasal, anteriorly damaged but with a greatest length roughly 28% of loreal length; loreal long, 2.7 times longer than greatest height, entering eye; no preoculars; supralabials 7, third and fourth in eye; correlated apparently with reduced eye size, supralabials 3–5 are very tall (basal widths of labials 4 and 5 are about 72% and 60% of greatest height); two subequal postoculars; temporals 1 + 2, the upper one in row two elongated, extending slightly past ends of parietals, and (on each side of head) with a concavity in posterior edge suggesting fusion with one or more dorsal scales.

Infralabials 7, first pair in contact behind mental, first three on each side in contact with genial; single pair of large genials, 2.2 times longer than wide; four large prementals (gulars wider than long) between geni-

als and first ventral. Head plate tubercles tiny, sparse, and inconspicuous.

COLOR PATTERN: Head and body light yellowish brown, turning slightly grayish brown on rear of body and tail, with many irregular black dorsal cross-bars (fig. 1C). Despite some irregular interconnections, the black bars tend to be paired, with the lateral ends of each pair converging and often connecting on about the third and fourth scale rows. There are about 38 “pairs” of such markings on the body, with the last three individually fused to form single black markings anterior to the tail, which has small irregular black markings. The dorsal areas contained within a pair of markings are somewhat shorter than the interspaces between pairs but are undifferentiated from the overall yellowish brown ground color. There are small ventrolateral black spots between and below some of the paired dorsal bars but they are irregular and show no definite pattern.

The dorsal black bar on the nape is chevron-shaped and anteriorly connected with a vague and irregular black blotch between the eyes. A black spot on top the left side of the head lies on the anterior half of the elongated secondary temporal and adjacent part of the parietal, but there is only a faint outline of this spot on the right side. Lower postocular on left side and both postoculars on right are black, and just in front of the eye there is a suffusion of black on the posterior ends of the loreal and third supralabial. Otherwise the upper parts of the head are colored like the body; supralabials are pale brownish.

Underside of head and throat pale brownish, sparsely and irregularly marked with black. Ends of the ventral plates are light brown like the dorsum, but the venter (fig. 2C) is mostly dark owing to a wide black marking that occupies the major part of every ventral (including anal plate) except in the neck region, where these markings are smaller and less regular. The subcaudals are black except for lateral encroachments of light brown.

MAXILLO-PALATO-PTERYGOID ARCH: Examined in situ on right side. Maxilla robust, not very arched, extending anteriorly past suture between first two supralabials, with 7 recurved teeth. First tooth springs from anterior tip of maxilla; first five teeth subequal,

relatively large, with small gaps between 2 and 5, followed by a larger gap and two sockets for two small teeth (size confirmed on left side); teeth distally angular in cross section, with a lateral edge. No posterior toothless process of maxilla. An expanded flange on maxilla extending mediad and ventrad adjacent to the two small posterior teeth. Ectopterygoid probably forked, with one branch forming an expanded flange tightly bound against the expanded maxillary flange. Maxilla tightly bound to palatine by ligamentous connections, but maxillary process of palatine seemingly absent.

REMARKS

The collector was a former field assistant of the Gorgas Memorial Laboratory, which is relevant to placing the type locality of *Atractus depressiocellus*. “Cerro Azul” of GML field parties was essentially equivalent to Cerro Jefe, the 980-m high point on the Piedras-Pacora Ridge about 37 km NE of downtown Panama City (Myers, 1969: 27). I have added the word “region” to the type locality because of a belief that specimens labeled “Cerro Azul” might have been taken anywhere from about 5 km southwestward of Cerro Jefe to about 5 km to the north. The likely elevational range for most reptiles collected is about 200–800 m in my estimation.

Atractus depressiocellus is morphologically quite divergent from the other Panamanian species, particularly in the depressed and very small eye and in the internasals, which are either lacking or much reduced in size. The dentition is also different from the other four Panamanian species, which have the maxilla strongly arched and bearing well-spaced, *firmly set* teeth that decrease in size posteriorly. In contrast, the maxilla of *A. depressiocellus* is not strongly arched and the anterior teeth are not as widely spaced and are subequal in size; also, the maxillary teeth of *depressiocellus* are not as firmly ankylosed as in the other species and are easily dislodged from their sockets (due partly to the soft state of preservation of the holotype?).

With a total length of 750 mm (673 mm SVL), *Atractus depressiocellus* ranks among the largest of *Atractus*, and it seems extraor-

dinary that it has escaped detection for so long.

Atractus hostilitractus, new species

Figures 1D, 2D, 3C, 9B; map 1

HOLOTYPE: AMNH 130330, an adult female collected by Tomás Quintero on October 29, 1967, at “Morti Hydro” [about 100–200 m elev., at 8°52'28"N, 77°54'19"W], Río Mortí, Province of Darién, Panama.

The type locality was a temporary camp and helicopter pad operated by the Inter-oceanic Canal Survey from October 1966 to about 1969. Coordinates and elevation were determined from Duke and Porter (1970: 10) in conjunction with a 1964 topographic map (1:50,000 *Mulatupo*, sheet 1388-IV). The locality is 2.7 km NNE of the Cuna village of Mortí Arriba, and 7.8 km SW of Camp Summit (Demartagañala), another former helipad and collecting site on the low continental divide (Myers, 1969: fig. 13).

ETYMOLOGY: The specific name, a noun in apposition, is compounded from the Latin *hostilis* (hostile) + the noun *tractus* (region or territory). The associative implication is to the 19th- and early 20th-century history of a part of the Panamanian interior that includes the Río Mortí.⁸

DIAGNOSIS: *Atractus hostilitractus* is characterized by a distinctive, complex color pattern (figs. 1D, 2D), the irregularity of which gives the appearance of possibly being highly variable in life. The holotype of *A. darienensis* has similar numbers of ventrals and subcaudals and seems arguably closest to

⁸ The type specimen of *Atractus hostilitractus* was collected by my former assistant Tomás Quintero in the “forbidden land”, where, as mentioned by Terry (1956: 19, 66), fieldwork had been long discouraged. Through much of the first half of the 20th century, the inland Cuna Indians rather successfully excluded most outsiders from travelling past the mouth of Río Mortí on the upper Río Chucunaque. Caution and diplomacy were needed even as recently as late 1965, when Quintero and I worked along the upper Chucunaque above the village of Mortí Abajo. This atmosphere changed considerably starting in 1966, when the politically independent but numerically small group of inland Cuna (Torres de Araújo, 1970: 46–63, 169) had to acquiesce to an influx of outsiders during survey of “Route 17” of the sea-level canal feasibility studies. This route, explored for possible excavation by nuclear explosives, included the Río Mortí (Commission, 1971).

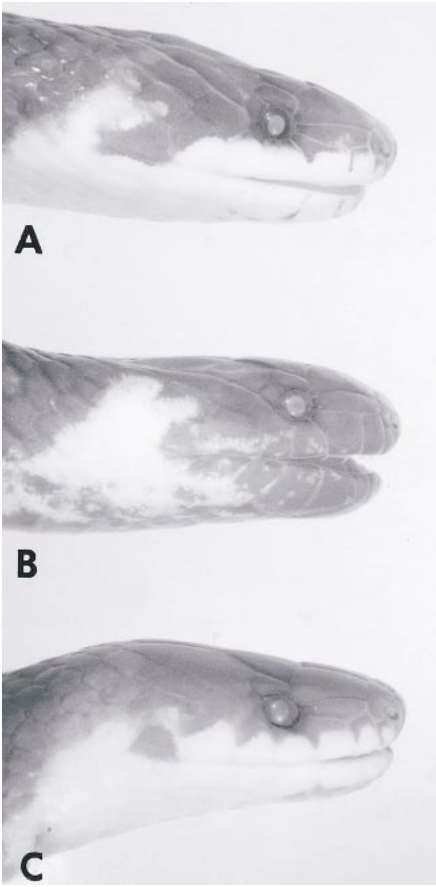


Fig. 9. Heads of three new species of Panamanian *Atractus*, all holotypes $\times 3.8$. A. *A. dariensis*. B. *A. hostilitractus*. C. *A. imperfectus*.

hostilitractus in general color pattern (fig. 1B), but pronounced differences in snout shape (compare fig. 9A and 9B) are strong evidence that these snakes are not color morphs of a single species. The close proximity of the loreal and internasal (in narrow contact in the holotype) may also be a distinctive feature of *A. hostilitractus* (fig. 3C).

The wide-spaced bars in the posterior dorsal pattern of *A. hostilitractus*, and the presence of a black vertebral streak, are suggestive of the red and black *A. schach* of Surinam and Brazil, but that is a smaller snake (<300 mm total length) which does not have the neck conspicuously different from the body (save for one wider saddle) and which has less black pigmentation ventrally (Hoogmoed, 1980: 31, color pl. 1d).

The color pattern of *A. hostilitractus* also is suggestive of the Andean *A. sanguineus* and *A. wagleri* (and perhaps *A. andinus* as well), as based on poorly reproduced photographs and brief type descriptions (Prado, 1944, 1945, also 1946).⁹ But compared with *hostilitractus*, those species have relatively longer tails (12.9–13.7% of total length), many more black bars, and little differentiation between neck and body patterns.

DESCRIPTION OF HOLOTYPE

It is a sexually mature female, with ova >4 mm and enlarged convoluted oviducts. Part of the posterior body was damaged during capture, but the specimen is well preserved.

PROPORTIONS AND SCUTELLATION: Total length 374 mm, tail length 40 mm (10.7% of total). Moderately proportioned, with body rounded ventrolaterally and somewhat wider than head; body wider than high anteriorly but laterally compressed and higher than wide posteriorly (probably not an artifact of preservation); greatest head width 77.7% of head length from snout to end of parietals, 2.3% of SVL; greatest body width about 2.5% of SVL. Dorsal scales smooth, lacking apical pits, in 17–17–17 rows. Ventrals about 160 (including 10 estimated missing in 17 mm of damaged body), followed by a half-ventral in front of undivided anal plate; subcaudals in 27 pairs.

Head slightly wider than neck; snout short and broad, bluntly rounded in dorsal view, rounded in profile (fig. 9B); rostral wider than high, well visible in dorsal view; inter-

⁹ Based on the descriptions and illustrations, one suspects that *A. sanguineus* and *A. wagleri*, and perhaps *A. andinus* (see especially Prado, 1946), might be closely related geographic replacements, if not actually conspecific. The last possibility seems less likely, since they come from different cordilleras. The first is from Yarumal (2300 m) in the northern end of the Cordillera Central; the second is from Humbo (<1000 m), nearly 200 km to the southeast, on the western side of the Cordillera Oriental; the third is from Andes (1500 m), some 150 km SSW of Yarumal in the Cordillera Occidental.

Dunn (1944: 398), incidentally, seems to have considered without explanation that the locality Humbo ($5^{\circ}36'N$, $74^{\circ}17'W$) is synonymous with Muzo ($5^{\circ}32'N$, $74^{\circ}06'W$), a bit of misinformation perpetuated in Medem's (1965: 341) gazetteer and in Pérez-Santos and Moreno (1988: 106).

nasals small, as wide as long, nearly half (48%) length of prefrontal suture; prefrontals large, longer than wide (greatest prefrontal width 86% of greatest length); prefrontal suture 70% length of frontal plate; supraoculars large, slightly longer than broad; frontal slightly wider than long, roughly triangular in shape; interparietal suture slightly longer than prefrontal suture, 76% of frontal length.

Eye small, contained 2.25 times in loreal length, 3 times in snout length; eye length smaller (86%) than distance to lip; eyes set close to head, not protruding to level of edge of lips, hence not visible in ventral view. Nasal divided behind rear edge of naris, its greatest length 56% of loreal length; loreal long, 3.0 times longer than greatest height, in narrow contact with posterolateral corner of internasal, entering eye; no preoculars; supralabials 7, third and fourth in eye, fourth slightly wider than high; two postoculars, upper the largest; temporals 1 + 2, the upper one in row 2 elongated, extending past ends of parietals.

Infralabials 7, first pair in contact behind mental, first three (right) or four (left) in contact with genials; single pair of large genials, 2.2 times longer than wide; four large median gulars and preventrals between genials and first ventral. Head plate tubercles minute but well distributed and easily seen under magnification.

COLOR PATTERN: The dorsal pattern of *Atractus hostilitractus* is complex (fig. 1D). The holotype at a glance has a black neck with pale rings, followed by irregular black bars widely spaced on a light reddish brown body.¹⁰ I interpret the anterior black color to represent several partially connected wide cross-bands as follows: (1) The first band, anteriorly fused with the dorsal head color, is

¹⁰ The appearance of the reddish brown color leads me to suspect that it was red in life, and that the whitish ringlike dorsal markings on the neck may have been yellow, possibly also with weak yellow edging on the posterior black bars. The ground color resembles the faded red of many preserved coral snakes, in which yellow rings fade to white. If in life it is red and black, or red, yellow, and black, *A. hostilitractus* might arguably be called a “false coral”, although the pattern match with broadly sympatric models (e.g., *Micrurus clarki*) would be very crude compared with many coral snake mimics (e.g., see color figures in Greene and McDiarmid, 1981).

13 scales long on the vertebral line and posteriorly bordered by a 1–2-scale-wide whitish (yellow in life?) ringlike interspace that is medially broken by two black scales; at its midpoint the first black band contains a pair of vague reddish spots, each occupying parts of several scales on rows 4–7. (2) The second band is 12 scales long and posteriorly bordered by a medially broken, whitish ringlike interspace whose halves are offset and separated by the black vertebral scales; the middle of this band contains a weak reddish suffusion several scales wide between rows 2 and 3 on each side. (3) The third band is 8–10 scales long and posteriorly bordered by an unbroken 1–2-scale-wide whitish ringlike interspace; there is a weak reddish suffusion, especially on the right side, in the middle of the band. (4) The fourth band is 7 scales long with some reddish spotted scales in the middle.

Posterior to the pale “rings” and four broad black bands, the dorsum is light reddish brown with about 20 black bars on each side—the bars on opposite sides mostly alternate and frequently interconnect at their corners, but in a few places they are aligned and medially connected to form narrow cross-bands. The first few bars are wider than the others and the first six extend from the midline to scale row 1, whereas those posterior end at about row 2. Most bars are about 2 scales wide and separated by wider interspaces up to 6 scales wide. The scales in the reddish brown ground color are moderately peppered with melanophores, a heavier concentration of which form a dark streak on the vertebral row. However, individual scales adjacent to the black bars are whitish and have fewer melanophores—suggestive of the pale yellow edging on the black rings of some coral snakes.

The head is overall black, with vague whitish spots on the supralabials and infralabials and with a wide, incomplete nuchal collar that extends up behind the mouth to end on the temporal plates (fig. 9B). The chin, venter, and underside of the tail are black (fig. 2D), except for a ventrolateral white streak that extends posteriorly from the nuchal collar to the middle of the second black neck band, thence discontinuously to the region of light reddish brown body color,

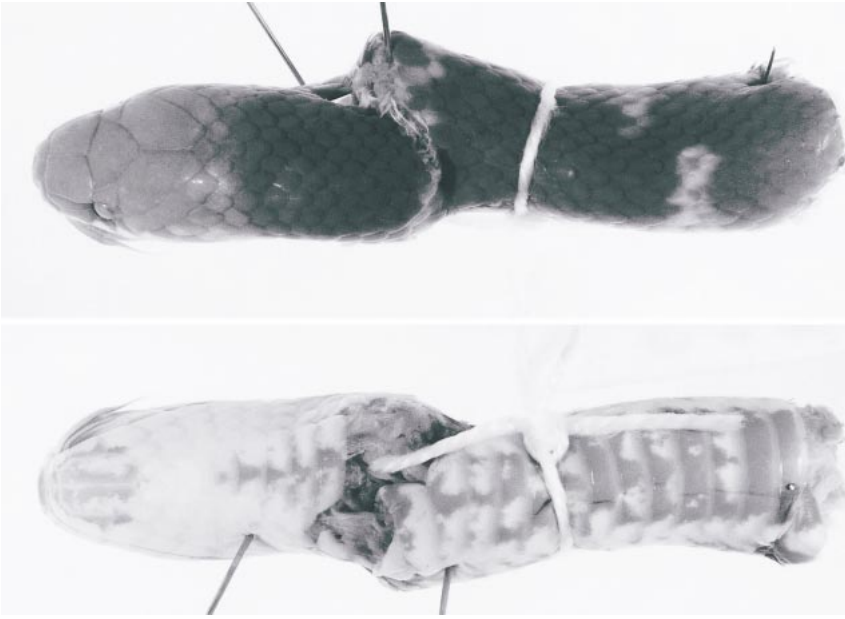


Fig. 10. *Atractus imperfectus*, new species. Dorsal and ventral view of the only known specimen (MCZ 50213, holotype), $\times 2.8$. Collected for the old Panamanian snake census in 1936, this imperfect specimen was the first *Atractus* from Panama.

which edges the ventrals on most of the body.

MAXILLO-PALATO-PTERYGOID ARCH: Examined in situ on right side. Maxilla strongly arched, extending anteriorly to suture between rostral and first supralabial, with 7 well-spaced recurved teeth, decreasing in size posteriorly (first several teeth subequal). First tooth springs from anterior tip of maxilla; first five teeth large, with noticeable gaps (not sockets) between 2 and 5, followed by another gap and two small teeth (the ultimate one smallest); teeth distally angular in cross section, with a lateral edge. Maxilla extending posteriorly past small teeth as an elongate toothless process. An expanded flange on maxilla extending mediad and ventrad adjacent to the two small posterior teeth. Ectopterygoid forked, with one branch an evidently expanded flange that is tightly bound against the expanded maxillary flange. Maxillary process of palatine absent.

Atractus imperfectus, new species

Figures 3D, 9C, 10; map 1

Atractus cf. *crassicaudatus* Duméril and Bibron:
Dunn and Bailey, 1939: 8 (comments on a head

and neck [now MCZ 50213, the holotype] from the Piedras-Pacora Ridge, central Panama).

Atractus crassicaudatus: Smith, 1958: 223 (country checklist—this usage followed by subsequent authors of regional lists).

Atractus sp.: Savage, 1960: 32 (“undescribed population allied to *Atractus crassicaudatus*”).

HOLOTYPE: MCZ 50213, head and neck only (sex ?), killed by a surveying party in 1936 for the Panama snake census, from the Piedras-Pacora Ridge, [Province of Panamá], Panama. (Precise locality unknown, but a more-or-less central point on this divide is $9^{\circ}16'N$, $79^{\circ}20'W$.)

ETYMOLOGY: The specific name *imperfectus* is a Latin adjective used in allusion to the condition of the holotype.

DIAGNOSIS: Although known only from a partial specimen (fig. 10), this species is distinguished from other Panamanian *Atractus* as follows: Resembles *clarki* in having pale bars on black neck but differs in larger size, relatively smaller eye, extensive black pigmentation on anterior ventrals, and in having only the hint of a pale collar. Resembles *depressiocellus* in having anterior black ventral pigmentation but differs in much smaller

size, larger eye, low (vs. tall) supralabials below eye, and narrow pale bars on a black neck. Resembles *darienensis* in white supralabials and a similarly positioned vague nuchal collar, but differs in having pale bars on a black neck, a relatively larger eye, and a shorter but broader snout, with the rostral plate more extensive dorsally. Resembles *hostilitractus* in having pale bars or broken "rings" on a black neck, but differs in having a longer, less rounded snout, loreal not approaching internasal, white labials, and less extensive black pigmentation on underside of head and throat.

See Remarks below for further discussion of differences from *Atractus darienensis*, which seems to be the species most similar to *A. imperfectus*, at least based on accessible characters.

Dunn and Bailey (1939) likened this specimen to the Andean *A. crassicaudatus*, but it is easily differentiated from that species and I see no reason to suspect a close relationship (see Remarks).

PARTIAL DESCRIPTION

Dunn and Bailey (1939) gave some scale counts for this specimen but curiously provided nothing about the color pattern save mention of a "black postocular streak across the last upper labial" (but see below and figs. 9C, 10). Although the posterior color pattern, number of ventrals etc. are unknown, the following description should allow it to be matched whenever a second Panamanian specimen is obtained.

PROPORTIONS AND SCUTELLATION: The specimen fragment comprises 38 mm of head and neck (fig. 10). An original total length of about 350–400 mm seems likely, based on comparisons with *A. darienensis* and *A. hostilitractus*, whose heads are roughly similar in size to that of *A. imperfectus* (table 1). Neck scales smooth, without apical pits, in 17 rows. Head slightly wider than neck, which is a little wider than high, with rounded ventrolateral edges; greatest head width 73.7% of head length from tip of snout to end of parietals. Snout bluntly rounded in dorsal view, bluntly pointed in profile; rostral wider than high, well visible in dorsal view; internasals small, as wide as long, slightly more than half (52%)

length of prefrontal suture; prefrontals large, longer than wide (greatest prefrontal width 82% of greatest length); prefrontal suture 70% length of frontal plate; supraoculars large, longer than wide; frontal slightly wider than long, roughly triangular in shape; interparietal suture longer than prefrontal suture, 83% of frontal length.

Eye small, contained 1.77 times in loreal length, 2.8 times in snout length; eye length about equal or marginally greater than distance to lip; eyes set close to head, not protruding out to level of edge of lips, hence not visible in ventral view. Nasal divided above and below just anterior to rear edge of naris, its greatest length 70% of loreal length; loreal long, 2.6 times longer than greatest height, not approaching internasal, entering eye; no preoculars; supralabials 7, third and fourth in eye, fourth wider than high; two normal postoculars on left side, upper one slightly larger, but three postoculars on right, lowermost a tiny scale; temporals 1 + 2, the upper one in second row elongated, extending past ends of parietals.

Infralabials 7, first pair in contact behind mental, first four on each side in contact with a genial; a single pair of large genials, 2.5 times longer than wide; four large median gulars and prementals between genials and first ventral. Head plate tubercles tiny, sparsely distributed, and inconspicuous.

COLOR PATTERN OF HEAD AND NECK: The short section of neck is black, with two brownish white ringlike markings (1–2 scales wide) that are broken at the vertebral scale row (fig. 10). The first pale ring (damaged by a machete cut) is about 9 scales behind the parietals and about 7 scales anterior to the second; the two halves of the second "ring" are offset by a distance of two scales in the vertebral row. The top and upper sides of the head are dark but, in bright light, are seen to be of a slightly paler hue¹¹ than the dark neck; the slightly lighter aspect of the head is emphasized by a still paler, albeit vague, orangish brown nuchal collar, which extends narrowly and indistinctly across the first nuchal

¹¹ It is not certain that the head would be paler than the neck in life, since I have noticed differential fading of black heads and bodies in some preserved snakes (e.g., *Geophis*).

scales and tips of the parietals, ending abruptly at a lateral white area behind the mouth (fig. 9C). The supralabials are mostly white, with excursions of dark head color forming a serrated pattern above. An isolated blackish mark occupies much of the last supralabial (fig. 9C), but does not convey the impression of a “black postocular streak” as described by Dunn and Bailey (1939).

The underside of the head is mostly white, with a noticeable suffusion of black on the genials, mental, and adjacent edges of the infralabials (fig. 10). A median line of black markings commences on the preventrals, posteriorly widening under the neck to cover most of each ventral. An irregular ventrolateral white line, on the ends of the ventrals and lower part of the first scale row, extends posteriorly from behind the head and connects the pale dorsal rings.

MAXILLO-PALATO-PTERYGOID ARCH: Examined in situ on right side. Maxilla arched, extending anteriorly past suture between first two supralabials, with 7 well-spaced recurved teeth, decreasing in size posteriorly. First tooth springs from anterior tip of maxilla; first five teeth large, with noticeable gaps (not sockets) between 2 and 5, followed by a larger gap and two very small teeth; teeth distally angular in cross section, with an anterolateral edge. Maxilla extending posteriorly past small teeth as an elongate toothless process. An expanded flange on maxilla extending mediad and ventrad adjacent to the two small posterior teeth. Ectopterygoid forked, with one branch being an expanded flange tightly bound against the expanded maxillary flange. Maxillary process of palatine absent or weak.

REMARKS

Obtained in 1936, this partial specimen was the first *Atractus* collected in Panama. Dunn and Bailey (1939) compared it with topotypes of *Atractus crassicaudatus* from Bogotá, Colombia. They (1939: 8) stated that, except for a few minor differences (i.e., number of labials in contact with genials, rarity in *crassicaudatus* of an elongated upper secondary temporal, and position of a postocular marking), the “characters of scalation and markings are within the range of varia-

tion of Colombian *crassicaudatus*.” Comparison of a large series of Bogotá *crassicaudatus* in the American Museum fails to substantiate a close resemblance: For example, the Colombian species differs in having a larger eye relative to a shorter loreal and in having noticeably shorter genials (the main reason why the Panamanian specimen has 4 infralabials in contact with the genials, whereas Dunn and Bailey (loc. cit.) were “unable to find a Colombian specimen with more than three in contact”).

I had originally hoped that this specimen could be assigned to one of two other new *Atractus* described herein, namely *dariensis*, which has a similarly shaped head, vague nuchal collar, and white labials, or *hostilitractus*, which is superficially similar in having a ringed neck and extensive black pigmentation under the throat. But I decided otherwise after direct comparison of snout shapes (see fig. 9), details of anterior color patterns, eye size relative to loreal and distance to lip, and consideration of details of head plate sizes and proportions. I concluded that the species represented by only a head and neck is distinct—as also suspected by Savage (1960: 32), who mentioned “an undescribed population [in Panama] allied to *Atractus crassicaudatus*”.

The closest resemblance seems to be with *Atractus dariensis*, which differs from *A. imperfectus* in a few details of coloration and, more convincingly, in proportions. The first two light brown interspaces (between black blotches) on the neck of *dariensis* (fig. 1B) seem somewhat comparable to the pale broken ringlike markings (on black) in *imperfectus* (fig. 10). The anterior interspaces in *dariensis* are brown to the top of the first scale row, which is white like the anterior ventrals; the paler broken “rings” in *imperfectus* have some slight suffusions of pale brown, but are mainly yellowish white like the adjacent edges of the ventrals. The supralabials in *dariensis* have little encroachment of dark pigment from above, whereas those of *imperfectus* are boldly serrated (compare fig. 9A and 9C).

The holotypes of *A. imperfectus* and *A. dariensis* seem roughly comparable in size, with the latter having a slightly shorter head that is, however, slightly wider across the tem-

poral region than the head of *imperfectus* (table 1). But direct comparison of the specimens shows *imperfectus* to have a relatively broader snout in dorsal view, with this being reflected in proportions of the paired prefrontal plates, which are anteriorly tapered to a greater extent in *darienensis* (fig. 3B) than in *imperfectus* (fig. 3D). The width across the posterior margin of the paired prefrontals is the same (4.3 mm) in both specimens, but the anterior margin narrows to 2.0 mm in *darienensis* vs. 2.9 mm in *imperfectus*. Closer to the snout tip, the width across the internasals is 1.9 mm in *darienensis* vs. 2.1 mm in *imperfectus*. The rostral plate extends more dorsad in *imperfectus* than in *darienensis*. The somewhat smaller head of *darienensis* is slightly longer in snout length (table 1), which is reflected in length of the loreal plate (2.6 mm in *darienensis*, 2.3 mm in *imperfectus*) and also in relative eye size. The eye is relatively larger in *imperfectus* (36% of snout length, 56.5% of loreal length) than in *darienensis* (30% of snout, 46% of loreal). The eye of *imperfectus* also is relatively larger compared with its distance to the edge of the lip (eye length/eye-to-lip distance = 1.08 in *imperfectus*, 0.857 in *darienensis*).

All the differences elaborated above convince me that *Atractus imperfectus* is a species different from *A. darienensis*. Nonetheless, one can scarcely predict the extent of variation in diagnostic characters derived from two specimens from widely separated populations, particularly when one specimen is only a fragment! If a whole specimen of "*imperfectus*" ever turns up and disproves this hypothesis, I would urge that the species name *darienensis* be given priority simply because that name is based on a complete holotype from a more precise type locality.

In a first draft of this description written a decade ago, I treated *Atractus imperfectus* as a "species inquirenda", even stating in manuscript that it "would seem poor judgement to add a name to the literature without being able to describe the posterior color pattern and other missing details." But, considering the real rarity of this apparently diagnosable species, I now join my paleontological brethren in recognizing that specimens oftentimes are not perfect. *Atractus imperfectus* therefore joins several other snakes named from

incomplete specimens gathered by Clark's Panama snake census: *Sibynomorphus nicholsi* Dunn, 1933 (= *Dipsas nicholsi*); *Hydromorphus clarki* Dunn, 1942; and *Micrurus nigrocinctus yatesi* Dunn, 1942 (= *M. alleni yatesi*).

GENUS *GEOPHIS*

This genus was admirably revised by Downs (1967), who recognized four species in Panama—*brachycephalus*, *championi*, *godmani*, and *hoffmanni*. Among subsequently described species were two from neighboring Costa Rica (*G. downsi* Savage, 1981; *G. talamancae* Lips and Savage, 1994) and one from Colombia (*G. betantiensis* Restrepo and Wright, 1987).¹²

There has been confusion concerning the distribution of this genus in Panama, where there have been no good published records east of El Valle de Antón in Coclé Province (*G. hoffmanni*). Reports of *G. godmani* and *G. brachycephalus* in central or even eastern Panama are based on apparently mislabeled specimens from the GML snake census and extrapolations therefrom. Nonetheless, as evidenced by a specimen reported herein, a widely disjunct population of *G. brachycephalus* does occur in the uplands east of the Panama Canal, and *G. hoffmanni* also occurs there, as well in the central Panamanian lowlands and probably in northern Colombia. As also to be discussed, *Geophis brachycephalus* s.l. seems to include an unrecognized sibling species in western Panama.

One new species seemingly endemic to central Panama is described herein. The following key includes the species now known to occur in Panama.

KEY TO PANAMANIAN *GEOPHIS*

1. Supraocular present, parietal plate not in contact with eye; tip of snout not noticeably paler than rest of head 2
- Supraocular absent, parietal bordering posterodorsal part of eye; tip of snout whitish, contrasting with adjacent head scales *G. godmani*

¹² Another South American species (*G. alasukai*) was described by Gasc and Rodrigues ("1979" [1980]) from French Guiana, but according to Hoogmoed ("1982" [1983]: 230) the name is a junior synonym of *Atractus flammigerus*.

- 2. Six supralabials, posterior temporal plate present; body either uniformly dark or conspicuously patterned above 3
- Five supralabials (a large postlabial does not border free edge of lip), temporals absent (i.e., no scales positioned *between* ultimate supralabial and parietal); uniformly dark above except for light collar in juveniles *G. hoffmanni*
- 3. At least posterior dorsal scales keeled; rostral plate not posteriorly extended between internasals; color variable 4
- Dorsal scales smooth throughout; rostral posteriorly extended between internasals; dorsum uniformly dark, venter weakly to strongly banded *G. championi*
- 4. Venter uniformly dark (glossy black in life) like dorsum; conspicuous white nape collar; size small and slender (holotype, an adult male, 201 mm total length) *G. bellus*
- Venter pale, never uniformly dark; dorsum uniformly dark or with light blotches or lateral stripe; juveniles with or without a light collar; size larger (adults attaining maximum total lengths greater than 400 mm) *G. brachycephalus* and *G. species inquirenda*

RECORDS EXCLUDED FROM CENTRAL PANAMA

Geophis brachycephalus (Cope): This is the most common Panamanian *Geophis* in collections, but Downs' (1967: 146) statement that it ranges from "Costa Rica southward through Panama to Colombia" needs correcting. South America was included in the range because of Downs' synonymizing of the Colombian *Geophis nigroalbus*, which is shown herein to be distinct based on proportional and hemipenial characters (see Comparisons under *Geophis bellus*, new species).¹³

¹³ Some confusion concerning the range of *Geophis brachycephalus* may stem from my long delay in publishing the present paper. I showed Downs the holotype of *Geophis bellus* sometime in the mid-1960s, which led him (Downs, 1967: 146, footnote) to publish a statement doubting that his inclusion of *G. nigroalbus* in the synonymy of *G. brachycephalus* was justified. Possibly encouraged by this, Restrepo and Wright (1987) resurrected the Colombian *G. nigroalbus* without comment. In turn, Wilson et al. (1988: 416), followed by Lips and Savage (1994: 413–414), retained *G. brachycephalus* for Colombia and added *G. nigroalbus* for "eastern Panama and Colombia". The few Colombian specimens assigned by Downs (1967: 153) to *G. brachycephalus* are tentatively reassigned to *G. nigroalbus* (see footnote 16), a species not known from Panama.

The only Panamanian specimens of *G. brachycephalus* with definite locality seen by Downs (1967: 153) are from far western Panama. Central Panama was included on the basis of a series of specimens (ANSP 24723–24734) from "Panama Sabanas". These specimens, consecutively numbered with a partial specimen (ANSP 24723) of *G. godmani* (see below) having the same locality data, are from the GML snake census (see Introduction).

As summarized by Dunn (1949a: 47), the GML "sabanas collection" was accumulated from various localities in the central Pacific lowlands, "from Capira to the west to Canita [Cañita] in the mid-basin of the Bayano to the east"—a straight-line distance of 120 km—although "the majority of the specimens come from the true 'Panama sabanas' which lie between Panama City and Chepo." Dunn (1949a: 47, table 7) reported on over 3900 snakes from this collection, with no mention of *Geophis* in this or in any other part of the GML lowland collection, even though Dunn presented the "sabanas" *Geophis* to the Academy of Natural Sciences in 1942, seven years before publication of his summary analysis.

The "sabanas" locality seems wrong on the face of it. Neither *G. brachycephalus* nor the rare *G. godmani* are lowland savanna snakes, and the thought that both might have been found in sympatry in such an unlikely habitat is hard to swallow and harder to digest. Furthermore, several specimens of the little montane snake *Trimetopon slevini* (ANSP 24717–24719) also were presented by Dunn in 1942 and were cataloged as "Panama Sabanas"; neither were these mentioned in Dunn's 1949a paper. I surmise that Dunn either knew that the locality had to be wrong for these specimens and ignored them, or there was a cataloging error that he either was unaware of or never got around to correcting.

Although the "sabanas" record for *Geophis brachycephalus* must be discarded as erroneous, this species does occur in upland wet forest in east-central Panama, as demonstrated later in this paper.

Geophis godmani Boulenger: This is a rare snake in Panama, and it evidently is a montane species throughout its range. Downs



Fig. 11. *Geophis bellus*, new species. The holotype (KU 110703) shown approximately two times life size.

(1967: 72), followed by Peters and Orejas-Miranda (1970: 119), gave its distribution as “Caribbean and Pacific slopes of central Costa Rica southward to the Canal Zone of Panama [at known localities] between 1300–2100 meters above sea level.”

The three Panamanian specimens of *G. godmani* seen by Downs (1967: 75) are all from the GML snake census—two from Finca Lérica in extreme western Panama, the third (ANSP 24722) purportedly from the “Panama Sabanas” in central Panama. This last specimen is cataloged consecutively with the series of *G. brachycephalus* and in proximity with the series of *Trimetopon slevini* discussed above, and the *godmani* record must be discarded for the same reasons. The most likely correct locality for the “sabanas” *Geophis brachycephalus*, *G. godmani*, and *Trimetopon slevini* is Finca Lérica in Chiriquí Province, which provided some census material and where all three species occur.¹⁴

Geophis bellus, new species

Figures 11–14, 15C; map 2

HOLOTYPE: KU 110703 (field no. CWM 3223), an adult male caught by C.W. Myers on December 13, 1964, at 700 m above sea

¹⁴ After reading the above discussion in manuscript, J. M. Savage kindly consulted Dunn’s notes in his possession and concurs that the “sabanas” records of *Geophis* and *Trimetopon* must be a cataloging error. Dunn’s notes contain no reference to specimens of either genus as having been part of the composite “sabanas” collection.

level near community of Altos de Pacora (east of Cerro Jefe), Province of Panamá, central Panama. The type locality is a few km northeastward of the summit of Cerro Jefe, upper Río Pacora drainage, at roughly 9°15'N, 79°22'W.

ETYMOLOGY: The specific name *bellus* is a Latin adjective meaning “pretty” and “charming”, referring to the appearance of this elegant little snake in life.

DIAGNOSIS: A small, slender member of the *sieboldi* group of *Geophis* distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth anteriorly but moderately keeled and striated on posterior part of body; (2) anterior temporal present or absent; (3) six supralabials; (4) eye small, going about 3.5–4 times into snout length; (5) dorsal and ventral surfaces uniformly dark (black in life) except for vivid white band across rear of head; and (6) hemipenis unicapitate, about one-fourth bilobed, nearly acalyculate, with calyces confined distally to lobes of the large capitulum.

The overall color pattern (fig. 11) alone distinguishes *Geophis bellus* from any other small colubrid in Panama. Other small Panamanian snakes having blackish or dark brown bodies, and heads partially or mostly white, are *Enuliophis sclateri*, *Ninia atrata*, and *Tantilla albiceps*—all of which have pale venters. See Comparisons for discussion and contrast with relevant congeners (including *G. betaniensis*, *G. brachycephalus*, *G. nigroalbus*, and *G. talamancae*).

DESCRIPTION OF HOLOTYPE

Despite its small size and slender habitus, the male holotype is unambiguously sexually mature because (1) the hemipenial spines had hardened, (2) the relatively large testes (about as long as the snake’s head) are strongly tubular, (3) the slender vasa deferentia are convoluted, and (4) sperm were present in a small fragment of testis examined under a compound microscope. The anterior (right) testis is 6.8 mm long and the posterior is 6.5 mm long, both being about 2.1 mm wide as measured in situ.

PROPORTIONS AND SCUTELLATION: It is a very small, short-tailed snake, 201 mm total length, 32 mm tail length (tail 15.9% of to-

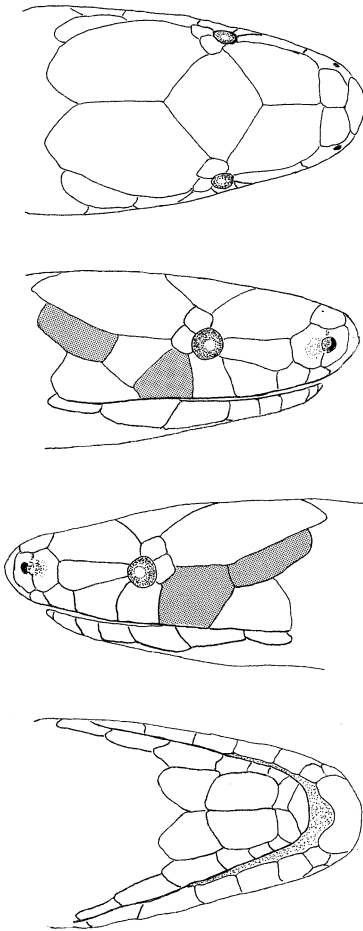


Fig. 12. Head scutellation of *Geophis bellus*, new species (holotype), $\times 6$. Fifth supralabial and posterior temporal shown in gray in lateral views.

tal). Body quite slender, barely wider than high (at maximum of about 4.8×4.6 mm), rounded ventrolaterally. Dorsal scales in 15 rows throughout, smooth on anterior half of body, with rows 4–12 becoming moderately keeled and striated on posterior half; inconspicuous anal knobs present on lower lateral scales above cloaca; apical pits not detected at $40\times$ magnification under reflected light. One preventral (undivided gular), 131 ventrals, undivided anal plate, 33 pairs of subcaudals.

Following description of head (fig. 12) after Downs' format (1967, for *G. brachycephalus*); see also table 2 for measurements: Head barely distinct from neck; snout long,

bluntly pointed, projecting well beyond lower jaw; rostral well visible from above, where its length is about 23% of its distance to frontal, not projecting between internasals; internasals small, slightly wider than long, less than half as long as prefrontal suture; prefrontal suture 64% length of frontal plate; frontal broader than long, roughly rhomboidal in shape (strongly angular anteriorly); parietals the largest head plates, their median suture shorter than frontal plate; supraocular forming posterior two-thirds of upper eye margin.

Nasal deeply grooved above naris, divided below, anterior and posterior parts subequal, their combined lengths four-fifths that of loreal; long loreal entering eye; no preocular; eye very small, contained about 4 times in snout (left eye $3.6\times$, right eye $4.1\times$), its length (and height) smaller than its distance from lip; supralabials 6, third and fourth in eye on left side, fourth only on right side; fifth supralabial largest and in contact with parietal on left side only; one postocular, higher than long, subequal in size to supraocular; temporals $0 + 1$ on left side, $1 + 1$ on right (first temporal the apparent result of a division of supralabial 5).

Chin tapered, anteriorly rounded; mental rounded, wider than long, separated from genials by first pair of infralabials, which are in medial contact; infralabials 7, pairs 1–4 in contact with anterior genials, 4–5 with posterior genials; posterior genials small and posteriorly rounded, in contact with each other; short posterior intergenial suture 33% the length of anterior intergenial suture; two median gulars and one preventral (gular wider than long) between posterior genials and first ventral. Tubercles sparsely present on some dorsal and ventral head plates, but these presumed sensory organs are minute and inconspicuous.

COLOR PATTERN: Color in life uniform glossy black above and below, with a conspicuous white band across rear of head (fig. 11). The white band anteriorly includes the posterior halves of supralabials 4 and the rear edges of the frontal plate, encroaching slightly on supraocular and postocular scales; the band extends posteriorly onto the nape for a distance of two scales behind the parietal plates; the rear lateral edges of the band an-

TABLE 2
 Measurements (in mm) of an Adult Male *Geophis bellus*, New Species, and Juvenile Males of
Geophis brachycephalus and *Geophis nigroalbus*

| | <i>G. bellus</i> adult ♂ ^a | <i>G. brachycephalus</i> juvenile ♂ ^b | <i>G. nigroalbus</i> juvenile ♂ ^c |
|--------------------------------|--|---|---|
| Total length | 201 | 202 | 134 |
| Tail length | 32 | 40 | 24 |
| Tail/total length × 100 | 15.9% | 19.8% | 17.9% |
| Head length ^d | 7.0 | 7.5 | 6.9 |
| Greatest head width | 4.5 | 5.6 | 4.6 |
| Greatest body width | 4.8 | 5.3 | 4.0 |
| Eye to tip of snout | 2.9 | 3.1 | 2.7 |
| Eye length | 0.8/0.7 ^e | 1.1 | 0.8 |
| Lower edge eye to lip | 0.9 | 0.9 | 0.9 |
| Nasal length | 1.2 | 1.4 | 1.3 |
| Loreal length | 1.5 | 1.6 | 1.5 |
| Greatest length of internasal | 0.8 | 0.7 | 0.8 |
| Greatest width of internasal | 0.8 | 1.0 | 1.0 |
| Length of internasal suture | 0.6 | 0.4 | 0.5 |
| Greatest length of prefrontal | 2.0 | 2.3 | 2.0 |
| Greatest width of prefrontal | 1.4 | 1.6 | 1.5 |
| Length of prefrontal suture | 1.4 | 1.5 | 1.4 |
| Length of frontal | 2.2 | 2.5 | 2.4 |
| Greatest length of parietal | 3.6 | 3.5 | 3.5 |
| Length of interparietal suture | 1.9 | 2.1 | 1.9 |

^a Holotype (KU 110703).

^b GML specimen (fig. 18). The locality for this specimen, from central Panama, is close to the type locality of *Geophis bellus* (map 2).

^c Holotype (BMNH 1946.1.6.50), from Pavas, [03°41'N, 76°35'W, Valle del Cauca], Colombia.

^d Head length from tip of snout to ends of parietals.

^e Asymmetrical variation on left/right sides.

gle anteroventrally under the head and extend to the posterior genials as a pair of whitish streaks. After some 20 years in alcohol the black parts of the dorsum and venter have faded to dark brown, and the front part of the head has differentially faded to a lighter brown than the body.

MAXILLO-PALATO-PTERYGOID ARCH: Right maxilla (fig. 13) extending slightly anterior to the suture between second and third supralabials (equal to anterior extension of palatine), bearing 10 rather stout, subequal teeth; anterior tip of maxilla pointed, toothless; posterior end of maxilla with slight ventral curve, tapering to blunt point; maxilla somewhat dorsoventrally compressed, bearing large palatine process. No maxillary process on palatine. Anterior end of ectopterygoid single, not expanded.

HEMIPENIS: Fully everted right hemipenis about 6.5 mm long, reaching to subcaudal 6.

Following account based mainly on left everted organ, except for description of the lobes which is based on right organ¹⁵: Moderately bifurcate (fig. 14), with lobes comprising about one-fourth of total length. Distinctly capitate, but on asulcate side the nude collar is almost interrupted medially by spines; capitulum comprising half the length of organ on asulcate side but nearly 70% on

¹⁵ The hemipenes were only half everted at time of preservation. Both were subsequently dissected out, soaked in glycerin, then in a saturated solution of trisodium phosphate, and inflated with carmine-dyed petroleum jelly. The right organ everted fully but is somewhat twisted, and many of the spines are evidently bent out of normal alignment. The left organ is straight and the spines are aligned more symmetrically, but owing to small tears the lobes could only be partially everted.

The above description therefore is based mainly on the left hemipenis, with recourse to the right organ for the distal parts of the lobes. The figure likewise is a composite.

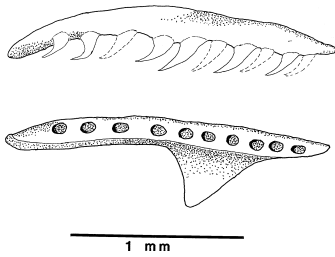


Fig. 13. Right maxilla of *Geophis bellus*, new species (holotype), shown in lateral and ventral views.

sulcate side. Sulcus spermaticus divides below midpoint of hemipenis but well onto capitulum, where the branches diverge and distally curve slightly around to other side (a modified centrifugal configuration if the lobes are not abnormally twisted), terminating close to the apices of lobes.

Organ entirely spinose (but spines distad from base of capitulum rather flexible, seeming less or not calcified): Proximal part of hemipenis with spinules and small spines, then two fairly large spines that are widely separated, one on each side of sulcus spermaticus. Midsection with a few dozen moderate-sized hooked spines that are most concentrated on asulcate side. Capitulum rather sparsely covered with small spines (or spine-like papillae, see above); in lateral view, the spines proximal and lateral to the sulcus branches are seen to be aligned in oblique rows, but between the branches of the sulcus spermaticus and on the lobes the arrangement is one of vague horizontal rows; tips of lobes spinose. Capitulum acalyculate, except for indication of weak calyces on lobes, these calyces being formed by elongated low tissue ridges connecting bases of some spines. An elongated lateral naked pocket on basal fourth of organ; from the perspective of the asulcate side, the nude pocket is on the left-hand side of the left organ and the right-hand side of the right organ.

COMPARISONS

Geophis bellus is a member of Downs' (1967: 137) *sieboldi* species group, with which it generally agrees in features of scutellation, small eye, long projecting snout, and, especially, in the simple (unforked,

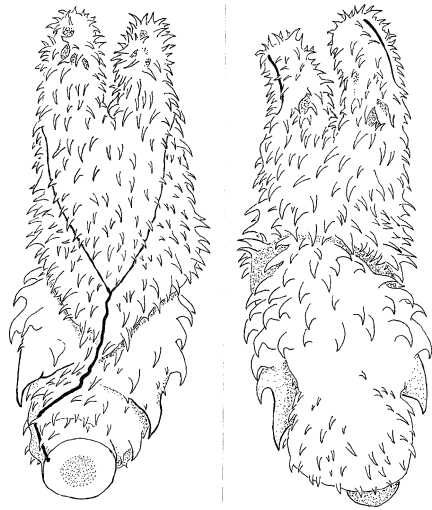


Fig. 14. Hemipenis of *Geophis bellus*, new species. Everted organ of holotype shown in sulcate and asulcate views, $\times 10$. The drawing is a composite, based on left hemipenis except that the lobes are added from right organ (see footnote 15). The relatively large capitulum is nearly acalyculate, with weak calyces being confined to the small lobes.

unexpanded) distal end of the ectopterygoid process and in maxillary features. Pertinent maxillary characters include a small number of subequal teeth, dorsal and ventral flattening of the maxilla, a toothless anterior projection, and a ventrally curved, bluntly pointed posterior end (compare fig. 13 with that of *G. brachycephalus* [Downs, 1967: 26]). The presence of an anterior temporal plate—on the right side of the holotype of *G. bellus*—is a rare condition in the *sieboldi* group. It seems quite clearly to have arisen by division of the fifth supralabial (compare lateral views of head in fig. 12), thus providing a clue to the method of original loss of the primary temporal in the *sieboldi* group (see Downs, 1967: 14).

The single specimen of *Geophis bellus* was shown to F. L. Downs shortly after he had completed his monograph of the genus. It is the specimen mentioned in a footnote (Downs, 1967: 146) as leading him “to doubt that my inclusion of *G. nigroalbus* Boulenger in the synonymy of *G. brachycephalus* is justified.” Downs (1967: 152) had not seen the Colombian type of Boulenger.

ger's *nigroalbus*, but direct comparison of the holotypes of *bellus* and *nigroalbus* convinces me that they are different species (see below). I also closely compared the type of *bellus* with the only central Panamanian specimen of *brachycephalus*, which probably was collected within a few kilometers of the former. Measurements of these specimens are given in table 2, with further comparisons following.

Geophis bellus is a much smaller snake than the Colombian *G. nigroalbus*, in which males attain a total length of at least 370 mm, and the slender *bellus* is relatively less robust. The juvenile holotype of *G. nigroalbus*, although 67 mm shorter than the adult holotype of *G. bellus*, nonetheless has a slightly larger head (figs. 15A, 16, and table 2). The holotype of *nigroalbus* resembles *bellus* in having a dark body and a similarly positioned and vivid pale band across the head and nape (absent or vestigial in other specimens of *nigroalbus* seen), but differs in the uniformly pale venter (adult *nigroalbus* may acquire dark transverse banding ventrally).¹⁶

Although the adult male holotype of *G. bellus* is essentially identical in total length to the nearly sympatric juvenile male of *G. brachycephalus*, the latter specimen (figs. 15B, 18) is a more robust snake with a longer and wider head and noticeably larger eye;

¹⁶ Unfortunately, I have seen too few Colombian specimens to be able to fully characterize *Geophis nigroalbus*, or even to conclude that but a single species is represented. The juvenile holotype (134 mm total length) from Pavas in Valle de Cauca is the most distinctive of five specimens because of its broad, well-demarcated nape band. A smaller juvenile (116 mm total), from Santa Rita in Antioquia, has a less extensive, poorly defined nape band that is dorsally incomplete, and this specimen has a relatively larger eye (but ontogenetic change in relative eye size is not uncommon). Three adults, one with a faint trace of a nape band, differ from the two juveniles in having dark bands across the ventrals.

The holotype of *G. nigroalbus* and three other Colombian specimens (BMNH 98.10.27.3, FMNH 43727, 54882) examined by me are listed in Downs (1967: 153) under the name *brachycephalus*. The fifth specimen examined is LACM 136675, one of a series reported by Restrepo and Wright (1987) from Betania in Valle de Cauca. The specimens with data are from roughly 1500–1700 m in the Cordillera Occidental, but Downs also listed one (not seen by me) from the Cordillera Oriental (Landázuri [900 m fide Medem, 1965: 342], Depto. Santander).

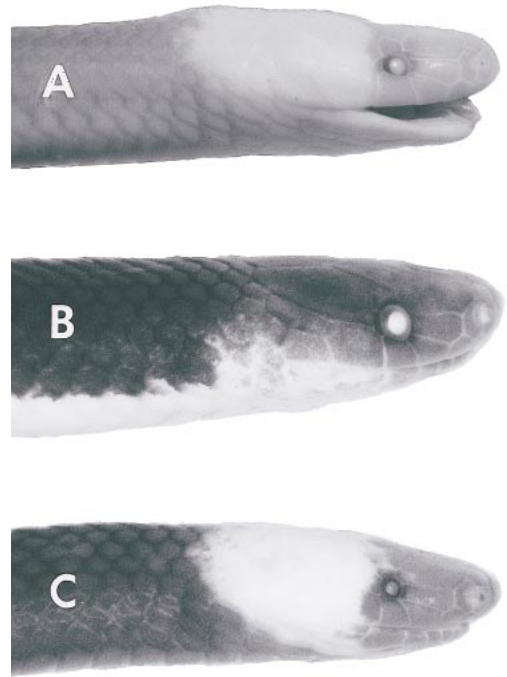


Fig. 15. Heads of *Geophis*, all $\times 4.5$. **A.** Colombian holotype of *G. nigroalbus*, juvenile male 134 mm total length (see fig. 16 for whole body). **B.** Central Panamanian specimen of *G. brachycephalus* (GML), juvenile male 202 mm total length (see fig. 18 for whole body). **C.** Central Panamanian holotype of *G. bellus*, new species, an adult male 201 mm total length (pale lateral streak behind head band is reflected light; body uniform black above and below, as seen in fig. 11).

most of the various head plate and suture measurements are smaller in *bellus*, except for slightly longer internasals and parietals. The central Panamanian specimen of *brachycephalus* also differs from the probably sympatric *bellus* in having a pale-spotted dorsum and a pale venter (fig. 18).

Comparisons of the holotype of *G. bellus* with specimens of *G. brachycephalus* from western Panama lead to similar conclusions: *Geophis bellus* is a much smaller, more slender species. The striking nape band of *bellus* seems to be a retention of a variably present-or-absent juvenile feature in *brachycephalus* and *nigroalbus*. Downs (1967: 150) noted that a pale collar, if present, is usually lost in *brachycephalus* by 150 mm SVL (adult ho-

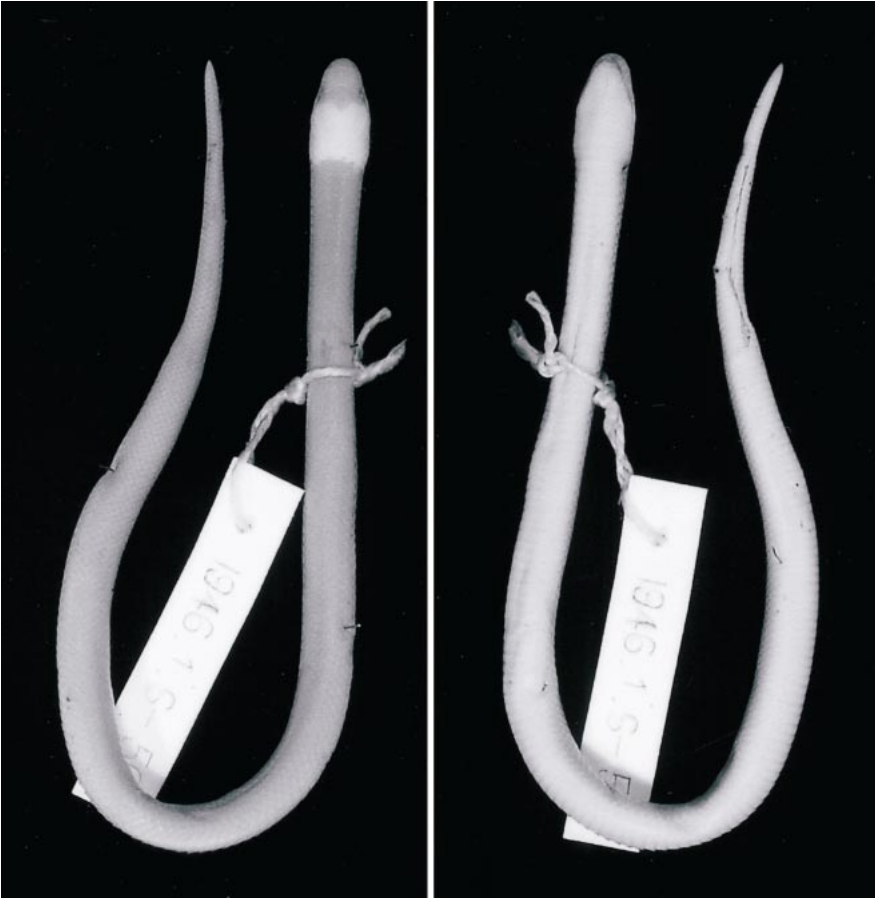


Fig. 16. Colombian holotype of *Geophis nigroalbus* Boulenger. BMNH 1946.1.6.50 (formerly 1906.4.30.71), a juvenile male 134 mm total length, shown $\times 1.7$.

lotype of *bellus* = 169 mm SVL), with traces of the collar only occasionally persisting to a larger size. According to Downs, *brachycephalus* attains a maximum total length of 418 mm in males and 460 mm in females.

I also compared the holotype of *Geophis bellus* directly with the Costa Rican holotype of *G. talamancae* Lips and Savage (1994), which is similar in size, relative tail length, and in numbers of ventrals and subcaudals.¹⁷ The juvenile female holotype (the only re-

¹⁷ The holotype of *Geophis talamancae* is now cataloged as LACM 147196. My own scale counts and measurements for this specimen include 133½ ventrals, 32 pairs of subcaudals, 212 mm total length, 33 mm tail length (15.6% of total). It is a juvenile female (said to be an adult in the original description), with inactive ovaries containing a few tiny ova and with flat, nonconvoluted oviducts.

ported specimen) of *G. talamancae*, is 11 mm longer than the adult male specimen of *bellus*, but it obviously is a more robust snake, with a much stockier body and a relatively larger head (greatest body width in *talamancae* = 7.2 mm vs. 4.8 mm in *bellus*; greatest head width \times head length to end of parietals in *talamancae* = 6.0 \times 8.5 mm vs. 4.5 \times 7.0 mm in *bellus*). *Geophis talamancae* appears to be close to *G. brachycephalus* and perhaps *G. nigroalbus*. Extent of keeling probably does not distinguish it from *brachycephalus* as thought by Lips and Savage (1994: 411), but the ventral color pattern (dark pigmentation across bases of ventrals causing a fuzzy pattern of alternating dark and white cross-bands) distinguishes *talamancae* at least from Panamanian *G. brachy-*

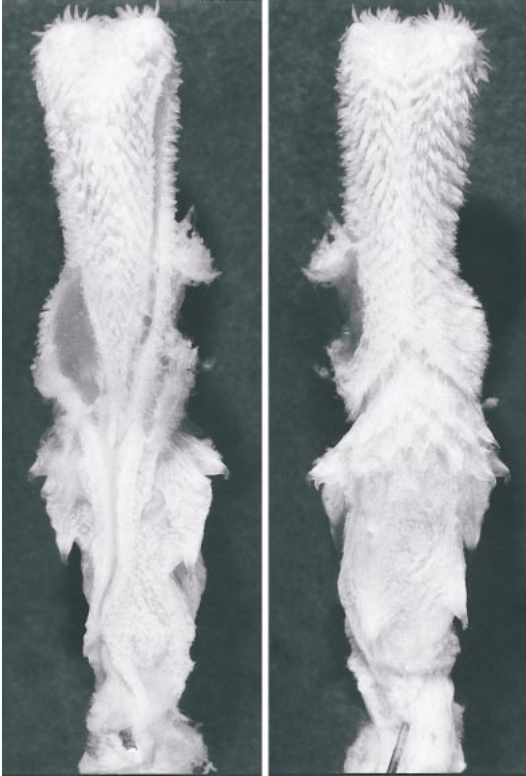


Fig. 17. Hemipenis of *Geophis nigroalbus* Boulenger. Left organ of FMNH 43727 from Colombia (no other data) shown left to right in sulcate and asulcate view, $\times 5.9$.

cephalus and *Geophis*, *species inquirenda*. This type of ventral pattern (suggested in one case to mimic noxious millipedes [Leonard and Stebbins, 1999]) is approached in some specimens of the Colombian *G. nigroalbus* (FMNH 54882, LACM 136675). Although I do not suggest conspecificity, it needs noting that *G. nigroalbus* is not distinguished from *talamancae* by separation of postocular and supraocular by an anterior projection of the parietal (Lips and Savage, 1994: 411).¹⁸

Finally, a word on the Colombian *Geophis betaniensis* Restrepo and Wright (1987), which is known from two specimens col-

¹⁸ This character comes from Restrepo and Wright (1987: 195), who evidently observed the condition in one population of *Geophis nigroalbus* (I have seen LACM 136675 from their sample; the parietal extends to the eye above exceedingly small postoculars), but the condition does not pertain to the holotype nor to the few other *nigroalbus* that I have seen (footnote 16).

lected in sympatry with the similar-sized *G. nigroalbus*. It is a distinctive species, separated from *nigroalbus* at a glance by dark ventrolateral stripes that sharply confine and set off the pale midventral area. *Geophis betaniensis* may be more closely related to *G. nigroalbus* than initially thought. Restrepo and Wright (1987: 191) provisionally assigned *G. betaniensis* to the *championi* species group, but Lips and Savage (1994: 414) later moved it to the *sieboldi* group based on “a complete concordance” in head shape and scutellation. cursory examination of the paratype of *G. betaniensis* shows that it lacks certain derived maxillary characteristics shared by most members of the *sieboldi* group; the maxilla is not ventrolaterally compressed and lacks a toothless anterior projection (the first tooth springs from the anterior tip of the bone). Nonetheless, a Costa Rican member of the *sieboldi* group—*Geophis zeledoni*—also lacks a “distinct toothless tip” on the maxilla, which is dorsoventrally flattened only along its posterior half (fide Downs, 1967: 145, 175). But the maxilla of *Geophis betaniensis* is relatively high and I see no sign of dorsoventral compression even posteriorly (right maxilla examined in situ). Tentatively accepting Lips and Savage’s (1994: 414) reassignment of *betaniensis* (as a species with presumably plesiomorphic maxillary features) makes the *sieboldi* group of *Geophis* the only one known from South America.

Geophis betaniensis was described as having “a small tentacle-like projection from the posterior margin of the nostrils” (Restrepo and Wright, 1987: 191–192, fig. 3). A photograph shows the “hair-like ‘tentacle’” on the right side of the holotype. A tentacle was said to be present only in the left nostril of the paratype (LACM 136189), but I could see no sign of it when I examined the specimen in early 2002. My own guess is that these structures, initially present in three of four nostrils, were foreign to the two snakes—perhaps defensive arthropod urticating hairs that might glance off the snakes’ head scales but temporarily lodge in their nostrils.

It is of course impossible to determine at this time whether there is significant color and size variation in *Geophis bellus*, but its

specific status, as first suggested by the striking coloration and small adult size, is strongly corroborated by hemipenial differences: In *G. bellus* the hemipenis (fig. 14) is bilobed for about a fourth of its length, with weak calyces only on the distal lobes; the large capitulum otherwise is sparsely covered with small spines (or large papillae). In *G. nigroalbus* (fig. 17) and *G. brachycephalus* (fig. 20) the organ is barely or not bilobate and the entire capitulum is covered with well-developed calyces.

REMARKS

I found the unique specimen of *Geophis bellus* at night, while walking on a muddy road through cut-over evergreen seasonal forest, at 700 m above sea level. The type locality is on the “Piedras-Pacora Ridge”, the low continental divide that separates the watershed of the Río Pacora (Pacific versant) from that of the upper Río Chagres (Atlantic). *Geophis bellus* shares the Piedras-Pacora Ridge with *G. brachycephalus* and *G. hoffmanni* (see below), and also with the new species *Atractus depressiocellus* and *A. imperfectus* of this paper. The one new species of *Geophis* and two new *Atractus* are known only from single specimens collected over a period of 29 years. The two previously named species of *Geophis* seem to be just as rare on the Piedras-Pacora Ridge (although common in other parts of their ranges), since each is known there from a single specimen, as follows.

Geophis brachycephalus (Cope)

Figures 15B, 18, 20A; map 2

A RANGE EXTENSION: I assign to *Geophis brachycephalus* a GML specimen from “Cerro Azul” on the Piedras-Pacora Ridge in central Panama; it was collected for the Gorgas Memorial laboratory by A. Herrera in October 1965. It is a juvenile male with uncalcified hemipenial spines, 202 mm in total length. It has 15–15–15 rows of dorsal scales that are smooth on the neck, becoming striated and weakly keeled by ventral 13 and then progressively more strongly keeled posteriorly; the posterior half of the body and proximal half of the tail are quite strongly keeled, with the keels becoming



Fig. 18. *Geophis brachycephalus* (Cope), a juvenile male from the Piedras-Pacora Ridge in central Panama (GML specimen, 202 mm total length; see fig. 15B for lateral view of head).

weak and disappearing toward the end of the tail; however, the fine striations of the dorsal caudal scales continue up to the terminal spine. Supraocular present; no preocular; one postocular; 0 + 1 temporals; six supralabials (3–4 in eye); seven infralabials (1–4 touching anterior genials, 4–5 touching posterior genials); 138 ventrals, undivided anal, 50 pairs of subcaudals; see table 2 for measurements. The dorsal color is blue in alcohol, with 11 pale dorsal rings or paired spots on the posterior body and several on the tail (fig. 18).

As remarked under *Atractus depressiocellus*, the “Cerro Azul” of GML field parties is equivalent to Cerro Jefe, the 980 m high point on the Piedras-Pacora Ridge about 37 km NE of downtown Panama City. Specimens so labeled might have been taken anywhere from about 5 km southwestward of

Cerro Jefe to about 5 km to the north, most likely in an elevational range of about 200–800 m.

The distribution of *Geophis brachycephalus* is partly clarified earlier in this paper (under Records Excluded from Central Panama). The present specimen is the only one known to me from central Panama. It appears to mark the eastern and southern limit of the range, where *brachycephalus* seems very rare compared with its abundance in the highlands of Costa Rica and western Panama. As already mentioned, South American records of this species are tentatively assigned to the Andean *Geophis nigroalbus*.

TAXONOMIC COMMENT

Downs (1967: 149) commented that “The color pattern is the most perplexing variable in *G. brachycephalus*, and is at least partly responsible for the lengthy synonymy”. Some populations appear to be highly polymorphic in color pattern, as exemplified in Panama by Slevin’s (1942: 474–476) description of a large population sample from the vicinity of Boquete in the Chiriquí highlands:

- 26 specimens show reddish spots, blotches or short stripes,
- 23 specimens are uniform in color,
- 2 specimens show a white collar and no lateral spots,
- 2 specimens show a white collar and red lateral spots.

Such populations, as well as the single specimen (fig. 18) from central Panama, seem to fit in with the original descriptions of *Colobognathus* [= *Geophis*] *brachycephalus* and its simultaneously described synonym *C. dolichocephalus* (Cope, 1871: 211–212).

However, I strongly suspect that some snakes with uniformly dark dorsa from along the Atlantic versant of western Panama (and Costa Rica?) are currently masquerading in collections under the name *Geophis brachycephalus*. Although I am not prepared to give adequate attention to this problem, it may be helpful to call attention to it by segregating the possible sibling species as follows.

Geophis, species inquirenda [*G. brachycephalus, auctorum*]

Figures 19, 20B

MATERIAL: *Bocas del Toro*: About 3 km W Almirante, 40 m (KU 110701); La Loma (MCZ 19325–19326); Río Changena, 830 m (KU 110702); Río Changena (FMNH 130969). *Chiriquí*: Upper Río Chiriquí, Fortuna Dam Site, 1000 m (AMNH 114317–114319); south slope Quebrada de Arena, 1120 m (AMNH 124015).

COMMENTARY

The earliest specimens, from La Loma in Bocas del Toro, were collected and identified as *Geophis brachycephalus* by Dunn (1942: 4). Downs (1967: 154) had no additional specimens from Bocas del Toro, but he did mention a few small Costa Rican samples lacking blotches. I have not seen these, but I have collected and examined additional Panamanian specimens that may be conspecific with the La Loma specimens and distinct from *brachycephalus*.

These specimens are uniformly black or brown in preservative (not bluish as in some albeit not all preserved *G. brachycephalus*) and all lack pale spots or partial ringlike markings (a vague pale nape band present or absent). The hemipenis of an Atlantic-versant specimen differs from that of a highland specimen of *G. brachycephalus* in having a relatively long, slender capitulum with no trace of bilobation (fig. 20). However, part of the difference (especially relative slenderness—but not relative length—of the capitulum) conceivably might be an artifact of eversion technique (see comment under Methods of Study).

Several of the newer specimens are from low and intermediate elevations (40–830 m) in Bocas del Toro, but four are from a collection that I made in the highland valley of the Río Chiriquí in Chiriquí Province (1000–1120 m). This valley may be considered as delimiting the eastern end of the Cordillera de Talamanca and the western end of the Serranía de Tabasará. This high Pacific-side valley is influenced by moisture-laden air spilling southward over the low continental divide, providing access to animals and plants from the Caribbean versant (the herpetofauna

TABLE 3
 Comparison of Segmental Counts between the Boquete Population of *Geophis brachycephalus* and Combined Samples of *Geophis, species inquirenda* in Western Panama^a

| | Ventrals | | Subcaudals | |
|------------------------------------|----------------------------------|----------------------------------|-------------------------------|-------------------------------|
| | Males | Females | Males | Females |
| <i>brachycephalus</i> ^b | 126.2 ± 4.00 121–142 (N = 18) | 127.4 ± 3.09 118–132 (N = 24) | 39.4 ± 2.03 37–46 (N = 16) | 33.6 ± 2.37 26–38 (N = 24) |
| <i>sp. inquirenda</i> ^c | 136.0 ± 2.83 134–138 (N = 2) | 139.0 ± 2.00 137–142 (N = 7) | 46.0 ± 1.41 45–47 (N = 2) | 39.6 ± 4.93 34–44 (N = 7) |
| Comparison of means | t = 3.03128, P = 0.0072 | t = 9.33695, P = < 0.0001 | t = 4.37714, P = 0.0005 | t = 4.49257, P = 0.0001 |

^a Data shown as mean ± 1 SD above, range and number below.

^b Boquete population. Data calculated from counts given by Slevin (1942: 475–476), excluding unsexed specimens and subcaudal counts on incomplete tails.

^c Data from specimens listed under “Material” in species account.

also has a strong Talamancan component, but only two of 50 species collected have primarily Pacific-drainage distributions [Myers and Duellman, 1982: 14]). Unfortunately, the *Geophis* collected in the valley of the upper Chiriquí are all females, and their assignment to the Atlantic-versant population is based on segmental counts and absence of pale spots or partial rings in all four specimens.

There is a pronounced difference in numbers of ventrals and subcaudals between Panamanian populations with color polymorphism (*brachycephalus*) and those apparently without (*species inquirenda*). For purposes of comparison, I calculated population statistics from the counts given by Slevin (1942: 474–476) for his large collection of *Geophis brachycephalus* from the vicinity of Boquete, where it was the most abundant snake in the cafetals. As shown in table 3, Boquete specimens of *brachycephalus* have significantly higher numbers of ventrals and subcaudals in both sexes. There is no overlap in female ventral counts. Overlap in male ventrals and subcaudals is caused by one *brachycephalus* (CAS 78983) with exceptionally high counts of 142 + 46, without which the Boquete ranges would be 121–129 ventrals and 37–41 subcaudals. The high ventral count, however, was confirmed by Downs (1967: 148), who gave 140 ventrals for this specimen. The differences are maintained when adjustments

are made for somewhat dissimilar methods of counting ventrals.¹⁹

Downs (1967: 148) remarked that ventral counts are somewhat lower in Panamanian *G. brachycephalus* from Finca Lériða to the west of Boquete, and that both these Panamanian populations have considerably lower counts than in Costa Rican populations. The ranges and means for all his Costa Rican specimens combined were given as 131–148 (138.5) in 54 males and 135–145 (140.7) for 70 females. These ranges encompass those for *species inquirenda* in Panama, but little more can be said without detailed examination of the situation in Costa Rica, from where considerably more material is now available. See Remarks below.

COLOR IN LIFE

In life, the dorsa are uniformly black; preserved specimens (MCZ 19325–19326, KU

¹⁹ There is, as noted under Methods of Study, a difference in methods of counting ventrals, with Slevin's counts expected to average probably one or a few ventrals more. Downs (1967: 148) recounted Slevin's material and determined sex of some specimens (e.g., juveniles) left unsexed by Slevin. Downs, whose counting method was closer to the one I used, gave the following ranges and means for the Boquete sample of *Geophis brachycephalus*: 34 males, 119–140 (mean, 124.9), 28 females, 123–132 (mean, 127.1). Adding the “pre-ventrals” to my counts for *Geophis, species inquirenda* yields 2 males, 134–140 (mean, 137.0 ± 4.24), 7 females, 138–144 (mean, 140.4 ± 2.07).



Fig. 19. *Geophis, species inquirenda?* A specimen (AMNH 114317♀) collected in 1976 near the Fortuna Dam Site (prior to construction), 1000 m, upper valley of the Río Chiriquí (Chiriquí Province, western Panama). Although it is Pacific drainage, the highland valley has a climate comparable to that of the Atlantic versant. Pending further investigation, four female *Geophis* from the area are tentatively associated with unicolorated specimens from the Atlantic versant of western Panama.

110701 [see below]) may fade to brown with the head becoming lighter than the body. Two specimens from the Río Changuena (FMNH 130609, KU 110702) in preservative have pale but vague nape bands, which may have been more pronounced in life (grayish white in KU 110702). My field descriptions for several specimens follow:

KU 110701: Shining black above and on tip of chin and infralabials. Venter immaculate white except subcaudals heavily marked with black. [Specimen has faded to brown in preservative, with the head becoming paler than the body.]

AMNH 114317–114319 [see fig. 19]: Uniform shining black above [one bluish, see below]; lower, posterior edge each scale white in scale row 1. Venter greenish white, turning black on chin and under tail. Iris dark, appears black. Tongue pale gray to base of fork, tips of fork unpigmented.

AMNH 124015: Black above (with slight grayish white tinge on lower side of neck behind jaw), white below, turning grayish black under tail. Iris dark. Tongue pale gray becoming white (unpigmented) on tips of fork.

W.E. Duellman noted one to be gray dorsally and subcaudally—but this specimen (KU 110702) is black in preservative and probably was preparing to shed—with a creamy white belly and a grayish white nuchal collar. Similarly, I noted that a specimen in the series AMNH 114317–114319 above was

somewhat bluish because it was about to shed.

NATURAL HISTORY

The habitat is lowland and lower montane rain forest and cloud forest in an elevational range of 40–1120 m. One (KU 110702) was under a log by day. I found a lowland specimen (KU 110701) as it was crawling on a log across a rocky forest stream, at night in the rain. The highest elevation specimen (AMNH 124015) was active at night, on the ground in cloud forest, at the edge of a small seepage pool in which *Hyla gracieae* was calling. Three specimens (AMNH 114317–114319) from the area of the Fortuna Dam site were found on a second-growth hillside; a workman found one, I caught another at night on a trail near the river, and I found the third by day—on the ground near a rocky stream, at about 10 a.m. on a sunny morning.

REMARKS

A satisfactory resolution of the taxonomic problem presented by this *species inquirenda* is outside the scope of the present paper, which I had intended to confine to problems in eastern Panama. Costa Rican specimens and names currently in the synonymy of *Geophis brachycephalus* will need to be considered. There especially needs to be examination of more hemipenes to determine if the differences seen in figure 20 are correlated with presence or absence of color-pattern polymorphism.

Geophis hoffmanni (W. Peters)

Map 2

Downs (1967: 155) gave the range of this species as “low and moderate elevations in Honduras . . . and Nicaragua, southward along both Caribbean and Pacific versants of Costa Rica into Panama”. This little snake evidently is common in parts of Costa Rica and has long been known to occur in extreme western Panama; Downs’ easternmost station in Panama was El Valle de Antón in Coclé Province, based on AMNH 76016; a second specimen (KU 116902) has subsequently been collected there. El Valle de Antón, an

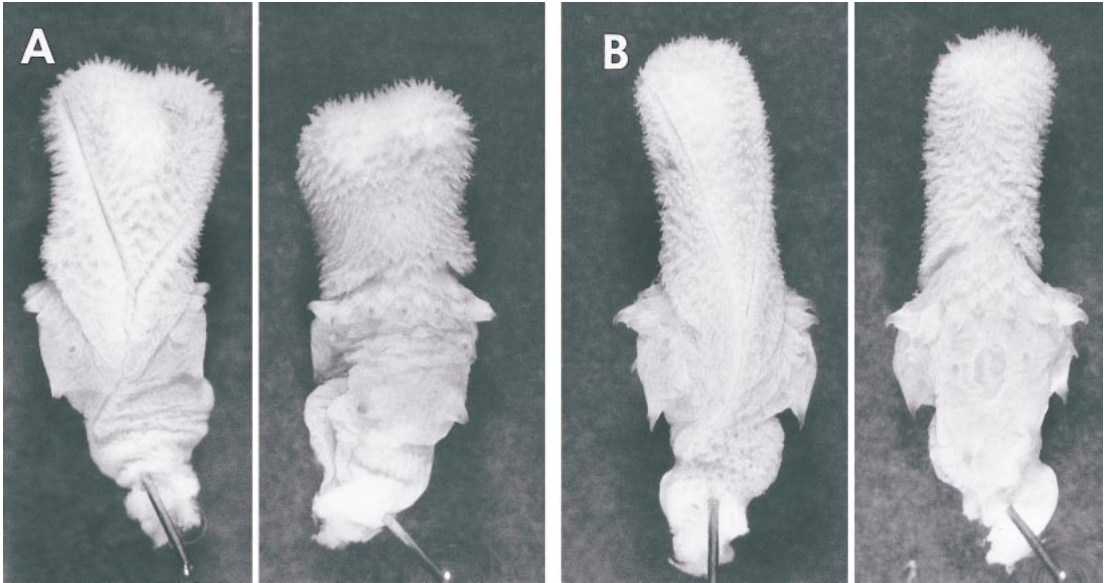


Fig. 20. Hemipenes of *Geophis*. Right-side organs shown at same scale ($\times 6.7$) in sulcate and asulcate view. **A.** *Geophis brachycephalus*, from a highland population with pattern polymorphism (UMMZ 57958; Boquete, western Panama). **B.** *Geophis, species inquirenda*, from Atlantic-versant population apparently lacking pattern polymorphism (La Loma, western Panama; MCZ 19326).

old volcanic crater, is shown as the western-most station in map 2.

As listed below, two additional specimens extend the range eastward in Panama from El Valle to the central lowlands and thence to the Piedras-Pacora Ridge (map 2), and a third specimen indicates the occurrence of *G. hoffmanni* in Colombia. All three specimens are dark brown above, whitish below, with dorsal scales smooth or mostly smooth, in 15–15–15 rows, supralabials 5 (3–4 in eye); temporals absent (see Remarks); infralabials 6 (1–3 in contact with first genials).

MADDEN FOREST: The late Howard W. Campbell collected a specimen (AMNH 113561) of *Geophis hoffmanni* in the former Canal Zone in July 1968. It was found on “Madden Forest Rd. 20 yds. N George Green Pk.” It is a male 200 mm in total length, including 29 mm (14.5%) tail length, with 125 ventrals and 29 pairs of subcaudals. In addition to the presence of anal ridges, the dorsal scales are weakly keeled at the end of the body and are striated on the rear of the body and tail.

As discussed elsewhere (Cadle and Myers, 2003),

The Madden Forest Preserve (formerly in the Canal Zone, now in Prov. Panamá) straddles Madden Road, a paved highway between Summit and Madden Dam. The roughly rectangular Preserve, about 3×5 km, lies across the very low continental divide, which swings close to the Pacific coast and seldom exceeds 200 m above sea level on this part of the isthmus. The northerly (Atlantic) drainage via the upper Río Chilibre system flows into the Chagres below Madden Dam; the southerly (Pacific) drainage adds to the Canal waters via the Río Pedro Miguel. The vegetation is lowland monsoon rain forest.

The surprising thing about this specimen is that it is the *only* verifiable specimen of *Geophis* from the central lowlands, which, however, are not as well known as might be expected, nor is the lowland fauna as uniformly distributed as might be expected (for a recent contribution, see Ibáñez et al., “1995” [1997]). The poorly collected Madden Forest has several snakes that are not found on the well-known Barro Colorado Island only about 24 km to the northwestward, including *Dipsas nicholsi* and *Dipsas viguieri* (Cadle

and Myers, 2003), as well as *Geophis hoffmanni*.

PIEDRAS-PACORA RIDGE: A specimen (FMNH 152049) of *Geophis hoffmanni* was collected by Harold Trapido and Emmett Reid Dunn on May 3, 1952, at 2200 ft [670 m] on “Cerro La Victoria”. Trapido²⁰ was at that time a staff scientist at the Gorgas Memorial Laboratory and Dunn was a visiting scientist. As expounded below under Remarks, Cerro La Victoria was an important GML field station that I place in the Piedras-Pacora ridge system a few km south of Cerro Jefe (map 2).

The specimen is a female 125 mm in total length, including 15 mm (12%) tail length; the smooth dorsal scales become striated (but not keeled) at the posterior end of the body; ventrals 125; subcaudals in 23 pairs.

COLOMBIA: A single specimen (AMNH 108373) is available from Colombia. It was one of a several specimens with disassociated data sent as a gift by J.R. Tamsitt from the Universidad de Los Andes in Bogotá, being the “smaller, pointed-head snake” that has only “Colombia” for locality data (Tamsitt, in letter to R.G. Zweifel, June 8, 1965). It is cataloged as having been collected by James R. Tamsitt and Dario Valdivieso in 1960–1963. These workers collected too widely in Colombia for an itinerary to be informative (e.g., see locality list in Valdivieso and Tamsitt, 1963), although the snake presumably came from northern Colombia.

²⁰ Harold Trapido (1916–1991) started his professional life as a herpetologist but ended it as an Emeritus Professor of Medical Entomology. His name appeared on about 20 herpetological publications, but army service in the Sanitary Corps starting in 1942 led to his assignment in 1944 to the Gorgas Memorial Laboratory, where he was involved in the early testing of DDT for malarial control. About 360 herpetological specimens collected during his military service in Panama (1944–1945) were given to the American Museum.

“Trap” afterwards served as Biologist on the GML staff from 1946 to 1956, and made significant contributions to the epidemiology of yellow fever in Central America. But he continued to collect amphibians and reptiles on the side, ostensibly “to get good pictures in color of important species” (Clark, 1952: 20), and he sent valuable Central American material to the Field Museum (Resetar and Voris, 1997: 503), including about 1200 specimens from Panama. He also helped arrange for the Field Museum to receive selected material from the Panamanian snake census conducted by Clark at GML (footnote 4).

The specimen is a female 189 mm in total length, including 23 mm (12.2%) tail length; the dorsal scales are weakly keeled above the tail and the dorsal caudal scales are striated; ventrals 132; subcaudals in 28 pairs. The snout seems unusually acuminate compared with eight Panamanian specimens, and the parietal plate is in contact with the eye between a reduced supraocular and postocular. But the supraocular and postocular also are separated by the parietal in occasional Central American specimens (Downs, 1967: 157). Therefore, the Colombian snake is tentatively assigned to *Geophis hoffmanni*, with which it agrees in most particulars.

REMARKS

As discussed by Downs (1967: 159), the reduction to five supralabials in *Geophis hoffmanni* appears to be the result not of scale fusion but of a shortening of the jaw. A postlabial (i.e., the first scale not bordering the free edge of the lip) appears to be a homologue of the sixth supralabial in related species. And a scale dorsal to the postlabial and ventral to the posterior part of the parietal appears to represent the original posterior temporal—temporals being pragmatically defined simply as scales positioned mainly or completely *between* the parietals and posterior supralabial(s).

The easternmost record of *Geophis hoffmanni* in Panama is in the Piedras-Pacora ridge system (map 2) and is of particular interest in the context of the present paper. Of the snakes from the eastern half of Panama that are treated herein, five of the eight species occur in that relatively small area. The following remarks document the locality for *Geophis hoffmanni*, the most widely occurring of the five species.

After the event of several fatal human cases of sylvan yellow fever in 1948–1949, the Gorgas Memorial Laboratory established temporary field stations in the forest at *Cerro La Victoria* in Panamá Province east of Panama City. Primary objectives were to collect mosquitoes simultaneously from the forest floor and from platforms up into the upper canopy, and to survey arboreal forest mammals in order to discover natural reservoirs of the yellow fever virus.

Cerro La Victoria is not shown on standard maps nor is it listed in Fairchild and Handley's (1966) gazetteer of GML collection sites, but it was an important GML collecting area during the early 1950s. I know Cerro La Victoria only through the publications of Galindo et al. (1950, 1951, 1956), the first two of which contain outline maps showing a series of collecting stations aligned northwest of the Pacific lowland town of Pacora, about midway between Pacora and the mouth of the upper Río Chagres at Madden Lake.

The series of stations lettered from "B" to "D" was located along a woods road, recently built, which gives access to a ridge now called Cerro La Victoria, between the Río Juan Díaz to the west and the Río Cabra to the east, while to the north it is limited by the drainage of the Río Cascades, a tributary of the upper Río Chagres. These three stations are all on the side of the ridge draining to the Río Cabra . . . Before the advent of the road . . . this region was loosely spoken of as "Cerro Azul" and appears with that designation in various botanical and zoological publications. The natives of the region now commonly reserve the term "Cerro Azul" for the ridges to the east of the Río Cabra, while Cerro La Victoria rises to the west of this river . . .

The summit of the ridge at Cerro La Victoria is 2300 feet [700 m] above sea-level and is exposed to far more wind than the slopes of the mountain. The more exposed places along the summit have a cover of low trees not exceeding 30 feet in height. Station D was located at 2100 feet [640 m] and about 200 feet below the summit, in a ravine with taller trees. (Galindo et al., 1950: 536–537)

Photographs included an aerial view "from above the forested slopes of Cerro La Victoria [looking] down the valley of the Río Cabra", and magnificently high forest with "a covering canopy 80 to over 100 feet high" (Galindo et al., 1950: figs. 2, 5). The lower elevation forest at elevations of 400–1200 ft (120–365 m) was "intermediate in appearance between deciduous forest and rain-forest", with a marked dry season (Galindo et al., 1956: 543).

From the above information, it is evident that Cerro La Victoria is a high, forested ridge above the west side of the south-flowing Río Cabra, which drains the southern slopes of the Piedras-Pacora Ridge (i.e., the continental divide) to the west of the headwaters of the Río Pacora. It is an area of premontane rain forest. The La Victoria Ridge connects to the main divide probably

in the general vicinity of Cerro Tobova (9°12'N, 79°23'W).²¹

Therefore, the northern end of Cerro La Victoria on the Pacific versant is only several km south of the better known Cerro Jefe in the Atlantic versant (shown as "El Jefe" in the Madden Lake Watershed inset in the old 1:100,000 map *Canal Zone and Vicinity* published by the U.S. Army Map Service). Cerro Jefe lies just to the north and higher than the continental divide, at 9°14'N, 79°23'W, with an elevation of 3254 ft (982 m) according to the aforesaid map and as confirmed by my altimeter reading of 980 m (Myers, 1969: 27). From the summit of Cerro Jefe, during the occasional clear period, the Cerro La Victoria region (including Cerro Tobova) and the Pacific coastal plain are visible to the south.

Trapido and Dunn's specimen of *Geophis hoffmanni*, from 2200 ft. (670 m), apparently was collected above station D near the crest of Cerro La Victoria (Galindo et al., 1950: fig. 7 [aerial photo showing location of station D]). The specimen was said to have been found "in bromeliads" (presumably ground bromeliads) with a curious assemblage of other small reptiles.²² Half a century ago, the Pacific-versant forest in the immediate region was already being encroached by road building and slash-and-burn agriculture (Galindo et al., 1950: figs. 2–3, 7–8), and the forest by now has either disappeared or reverted to second growth.

MUSEUM ABBREVIATIONS AND ACKNOWLEDGMENTS

ABBREVIATIONS: The following collection abbreviations are used in this paper:

| | |
|------|--|
| AMNH | American Museum of Natural History, reptile collection, New York |
| ANSP | Academy of Natural Sciences of Philadelphia, Philadelphia |

²¹ The map elevation for the neighboring summit of Cerro Tobova is 2430 ft (740 m), only 40 m higher than given for Galindo et al. (1950) for Cerro La Victoria.

²² Alan Resetar (personal commun.) could find no explicit information in Trapido's notes, but observed that the FMNH catalogue has "several other specimens with the same collection event information (same locality, same date, "in bromeliads") . . . *Lepidophyma flavimaculatum*, *Gymnophthalmus speciosus*, and *Ninia maculata*".

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| BMNH | The Natural History Museum, London |
| CAS | California Academy of Sciences, San Francisco |
| FMNH | Field Museum of Natural History, Chicago |
| GML | Gorgas Memorial Laboratory, Panama |
| KU | Museum of Natural History, University of Kansas, Lawrence |
| LACM | Natural History Museum of Los Angeles County, Los Angeles |
| MCZ | Museum of Comparative Zoology, reptile collection, Harvard University, Cambridge |

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