Zootaxa 1400: 1–26 (2007)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Eleven new species of snakes of the genus *Typhlops* (Serpentes: Typhlopidae) from Hispaniola and Cuba

RICHARD THOMAS[1] & S. BLAIR HEDGES[2]

[1] *Department of Biology, PO box 23360, University of Puerto Rico, San Juan, Puerto Rico 00931–3360, USA.*
E-mail: rthomas@uprrp.edu
[2] *Department of Biology, 208 Mueller Laboratory, Pennsylvania State University, University Park, Pennsylvania 16802-5301, USA.*
E-mail: sbh1@psu.edu (Corresponding author)

Abstract

Here we describe 11 new species of blindsnakes of the genus *Typhlops* from the West Indies. Four of the new species are from southern Hispaniola and were previously confused with *T. hectus* Thomas. Seven other species are described from Cuba and are related to *T. biminiensis* Richmond. Diagnostic morphological differences distinguish all of these species, and at least three pairs are known to be sympatric. With these new taxa, 40 species of *Typhlops* are now recognized from the West Indies, all of which are endemic to the region. Nearly all species are found on single islands or island banks. We classify West Indian *Typhlops* into nine species groups, most of which exhibit geographic patterns. The West Indian species form two clades: the *T. biminiensis* Group with its 12 species is centered in the western Caribbean (Bahamas, Cayman Islands, Cuba) and the remaining species, grouped into eight species groups, form a large clade (Major Antillean Radiation) centered in Hispaniola, but with a closely related pair of lineages in the Puerto Rico region (7 sp.) and northern Lesser Antilles (5 sp.).

Key words: Reptilia, Squamata, Serpentes, Speciation, Cryptic species, West Indies, Caribbean, Greater Antilles

Introduction

The blindsnake genus *Typhlops* is cosmopolitan in distribution, and occurs primarily in tropical regions (Pough, et al., 2003; Zug, et al., 2001). Most species are small (10–30 cm), have tubular-shaped bodies, reduced eyes, and are pinkish or brownish in coloration. They burrow in soil and feed primarily on social insects (ants, termites) and their larvae. Twenty-seven species are recognized from the West Indies, and most of those are endemic to single islands (Breuil, 1999;2002; Powell, et al., 1996; Schwartz & Henderson, 1991).

We have collected specimens of most species of West Indian *Typhlops* and have constructed phylogenetic trees from DNA sequences of three mitochondrial genes from all but one of the new species described herein (the one from Rancho Luna, Cuba). These analyses suggested that at least 15 cryptic species, some of which are sympatric, are confused with two species from Hispaniola (*T. hectus* and *T. pusillus* Barbour) and one species from Cuba (*T. biminiensis*). This result prompted us to examine morphological variation to determine if diagnostic characters could be found that were consistent with the sequence-defined clades. This paper reports the results of those morphological analyses for two of the species (*T. hectus* and *T. biminiensis*) and provides formal descriptions of 11 species. Although the molecular results, which are being presented elsewhere (S. B. Hedges, unpublished), helped to focus our attention on these hidden species, the morphological evidence is sufficient on its own merits to diagnose the new taxa. We also elevate two subspecies to the rank of full species, hence increasing the number of West Indian taxa to 40 species.

Accepted by P. David: 9 Dec. 2006; published: 29 Jan. 2007

Materials and methods

Specimens were collected and exported with permission of governmental authorities from the countries of origin. Field and laboratory research was approved by the Institutional Animal Care and Use Committee of Pennsylvania State University (#17632). The location of islands sampled and discussed in the text is indicated in Figure 1.

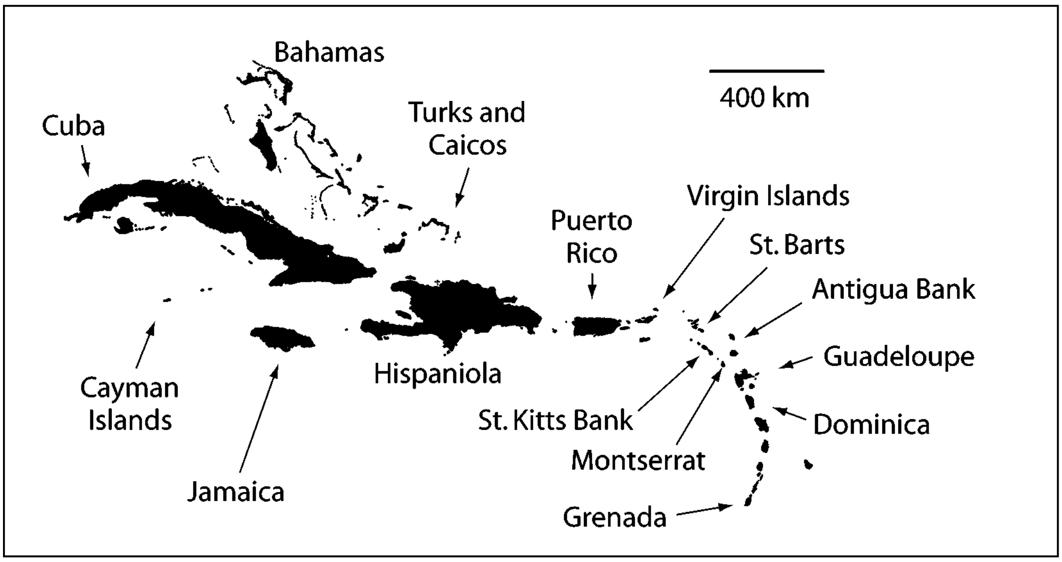

FIGURE 1. Map of the West Indies.

In addition to the standard scale counts on these *Typhlops* and measurements of head scales defined elsewhere (Thomas, 1989; Thomas & Powell, 1994), we have used other measurements to quantify shape differences of the scales (Fig. 2). The following measurements of head structures are used in the description and analysis of variation. **ANTNAS**, width of the upper arm of the anterior nasal, measured between the rostral and the eye. **ED** (eye diameter), diameter of the eye measured dorsoventrally. The importance of eye diameter is in its relation to other size measurements. The maximum eye diameter of the blindsnakes confused with *T. biminiensis* is generally the same across species. In other words, the body continues growing after a maximum eye diameter is reached resulting in a proportional but not an absolute difference in eye diameter. Thus most species appearing to be smaller eyed are really larger bodied. This is not the case in the species associated with *T. hectus*. **HL** (head length snout to occiput), found by moving the side of a pin along the dorsum of the head until the drop-off at the occiput is found. **HR** (head radius), the distance from the tip of the snout to a transverse line through the middle of both eyes. **HWE,** head width at the level of the eyes. **HWM,** maximum head width. **IN** (internarial distance), the distance between the innermost margins of each naris. **IOD** (interocular distance), distance between the median edges of the eyes. **MBD**, midbody diameter (mm). **NE** (naris-eye distance), the distance between the middle of the eye to the nearest (posterodorsal) margin of the naris. **OL** (ocular length), the length from the eye level out to the posterior most point of the scale. **OS** (ocular sinuosity), a ratio of A (the distance from the most posterior part of the preocular-ocular suture to the posteriormost point of the ocular) to B (the distance from the anteriormost point of the preocular-ocular suture to the posteriormost point of the ocular), subtracted from one. **PA** (preocular angle), the angle of the anteriormost extension of the preocular. We measured the preocular angle with a vernier protractor on camera lucida tracings of the anterior extension of the preocular. Because the facial region of typhlopids is curved, it is necessary to view the apex of the preocular as nearly perpendicular to the apical region as possible in order to measure the preocular angle. To do this the specimen is clamped in the visual field of the microscope and rotated to obtain an anterodorsal view, as nearly perpendicular to the apex of the preocular as possible. **PD** (preocular apical diameter), apical diameter of the preocular is a measurement of the sharpness of the preocular apex and is obtained by finding the diameter of a circle that fits as closely as possible into the apex. We placed circles of different diameters drawn on tracing paper over the camera lucida tracings of the preoculars to find the closest fit. **PE** (preocular-eye distance), distance from the anteriormost projection of the preocular to the middle of the eye. **PL** (preocular length), maximum length of the preocular. **PS** (preocular suture length) the length of the suture between the preocular and third upper labial. **RI** (rostral indent), the distance from a line through the middle of both eyes and the posteriormost tip of the rostral. **RL1**, the standard length of the rostral from the internasal sutures to the posterior tip. **RL2**, the length from the anteroventral tip of the snout to the posterior dorsal tip of the rostral. **RL3**, the total rostral length from the labial border following its curvature around the snout to the posterior tip. **RW1**, the standard maximum width of the dorsal portion of the rostral posterior to the internasal sutures. **RW2** (apical width), the width of the rostral on the apex of the snout between the internasal sutures. **RW3**, the width of the rostral at the labial border. **RWP** (rostral wide point), a ratio indicating the relative position of widening of the rostral, measured by dividing the distance between the internasal suture and the widest point (first attained proceeding posteriorly) by the total distance between the internasal sutures and the posterior tip of the rostral (RL1). **SVL**, snout-vent length (mm). **TA**, tail length (mm). **TL**, total length (mm).

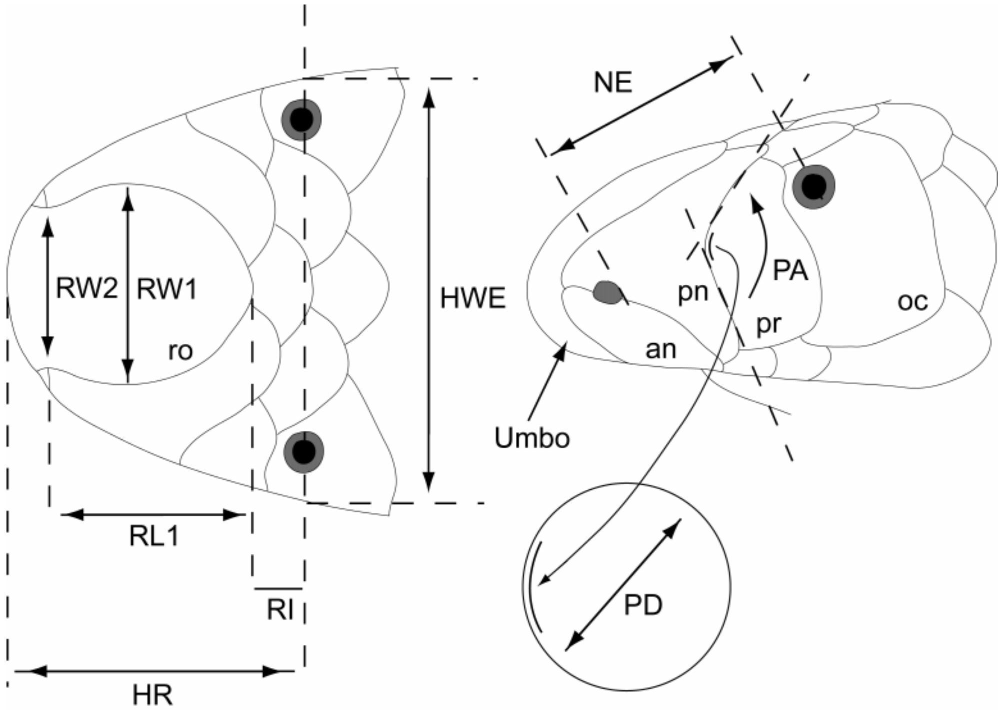

FIGURE 2. Terminology of head scales of *Typhlops* used in this study, and illustrations of how some measurements were taken. Lower case letters indicate names of scales: an, anterior nasal; oc, ocular; pn, posterior nasal; pr, preocular; ro, rostral. Upper case letters indicate measurements as defined in Methods.

We took all measurements of head scales using a Mitotuyo spindle-and-anvil micrometer clamped onto a base in the visual field of a binocular dissecting scope. Sex was scored in many specimens, especially where it was obvious, such as snakes with everted hemipenes or those with developing ova or eggs. However, significant sexual dimorphism in scale counts has not been found in the past, with the exception of tail length in some species, and therefore we have not reported data separately for each sex unless clear differences existed. Museum abbreviations follow standard usage (Leviton, et al., 1985); MNHNCu refers to the Museum of Natural History, Havana, Cuba. RT designates a specimen in the collection of Richard Thomas (University of Puerto Rico).

Taxonomic Accounts

New Species from Hispaniola Associated with Typhlops hectus

The Antillean *Typhlops* with 20 (unreduced) or 20–18 scale rows with low to moderate longitudinal scale counts (ca. 250–300), inhabiting Cuba and Hispaniola, have been shown since the 1970s to be taxonomically diverse. Long lumped into *Typhlops lumbricalis* Linnaeus, this group was first shown to be a composite by Thomas (1974) who described the higher-count populations as *Typhlops hectus* from southern Hispaniola, leaving the lower-count *Typhlops* "*lumbricalis*" inhabiting Cuba and widely scattered localities in Hispaniola. In 1989, Thomas described the Hispaniolan populations of *Typhlops* "*lumbricalis*" as *T. schwartzi* Thomas, *T. tetrathyreus* Thomas, and *T. titanops* Thomas, based principally on differences in head scale shape (Thomas, 1989). In the original description of *T. hectus*, Thomas (1974) noted that some of the eastern and northern populations differed from the near topotypical populations in having more individuals with reduction to 18 scale rows and reduction occurring farther anteriorly. The largest series of *T. hectus* were known from the western Tiburon Peninsula of Haiti. Some of the eastern samples differed in scale row reduction level and in having higher middorsal scale counts. As more material was acquired, at least one sample showed notable differences in head scale shape. In the intervening years, more material attributable to *T. hectus* has been collected.

In this study we do not assess the status of the populations of *Typhlops hectus* occurring to the north of the Cul-de-Sac-Valle de Neiba trough. There are a number of specimens from this area, the southern part of the North Island of Hispaniola, both from Haiti and the Dominican Republic. In some ways they are united in having relatively high middorsal scale counts and scale row reduction far anterior on the body, although they also form four isolated and differentiated populations (Thomas, 1974). Whether or not those specimens represent additional undescribed species must await collection of tissue samples and analysis of DNA sequences. At this time, we leave them as associated specimens of *T. hectus sensu stricto* and refer the reader to that earlier treatment of those North Island populations.

We redescribe *Typhlops hectus,* and later *T. biminiensis,* since the new species include specimens that were formerly included within those species.

Typhlops hectus Thomas, 1974 (Figs. 3A, 4A)

Holotype: MCZ 81149, collected at Martineau, ca. 9 km (airline) W Jérémie, Dépt. de La Grande Anse, Haiti.

Diagnosis: A moderate sized, 20-scale-row species of *Typhlops*, having moderate middorsal scale counts (284–328) and a low frequency of posterior reduction. *Typhlops hectus* differs from the other 20-row species with ~300 middorsal scales in its clavate rostral shape in which the rostral broadens posteriorly, becoming broadly rounded at the tip (Fig. 3A). The anterior projection of the preocular has a relatively small angle and sharp apex. The posterior nasal-preocular suture curves gradually ventrad. The suture between the preocular and the 3rd infralabial is relatively short. The edges of the posterior nasals flanking the rostral tend to bowed out. The pigmentation is variable but most populations are relatively lightly pigmented, ranging from medium to pale brown or tan, often with irregularities or mottling and a pale snout. The hemipenes are trumpet-shaped.

Description: Rostral in dorsal aspect narrow anteriorly, widening toward the tip (RW1/RL1 0.45–0.64), preocular angle 42–72º, with an apex that is typically relatively sharp (low apical diameter) to more broadly rounded but without breaks interrupting its curvature (apical diameter 0.14–0.57 mm); lower portion of preocular contacting only the 3rd of the upper labials. The angled anteriormost point is so pronounced that in a few animals a suture actually extends partly or all the way to the naris, resulting, in the latter case, in a divided anterior nasal. Ocular length is approximately 1/2 height; sinuosity 0.23–0.1. The rostronasal pattern is parenthesis-like to parallel or slightly divergent with the dorsal limb of the posterior nasal typically having a slight bend rather than being smoothly curved, the bend being often most visible in the glandular edges of the scale papilla. There are two postoculars (cycloid). The first parietal is standard, spanning two scale rows, occasionally narrower, spanning slightly more than one scale row. The second parietal is present and equal in size to first or absent. TL 135–218 ($\bar{x}$ = 174, N = 75) mm, excluding two 116 mm juveniles. (10) TL/TA: males 20–24, females 28–44. TL/MBD 31–46. Middorsal scales 284–328 ($\bar{x}$ = 306, N = 75).

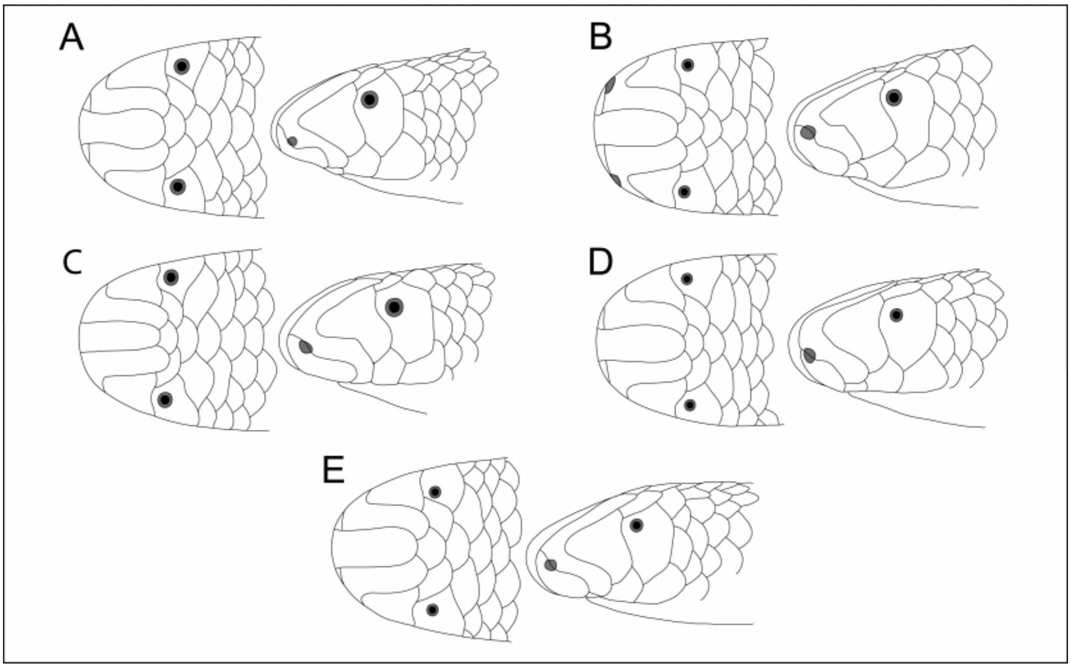

FIGURE 3. Head scalation in the blindsnake *Typhlops hectus* and four new species from Hispaniola. (A) *T. hectus* (MCZ 81149), holotype, from Martineau, ca.9 km (airline) W Jérémie, Dépt. de La Grande Anse, Haiti. (B) *T. proancylops* (KU 272267), holotype, from Soliette, 5 km airline NW Fond Verettes, 363 m, Dépt. du Sud-Est, Haiti. (C) *T. agoralionis* (USNM 564777), holotype, from 8.0 km S Marché Léon, Dépt. de la Grande Anse, Haiti. (D) *T. sylleptor* (USNM 564804), holotype, from 5.0 mi. WSW Baradères, Dépt. De la Grande Anse, Haiti. (E) *T. eperopeus* (USNM 564785), holotype, from 3.9 km airline SSW Barahona, Barahona Prov., Dominican Republic.

In Tiburon Peninsula specimens of *T. hectus* the modal number of initial scale rows is 20 with 9% having 22 or 21 and reducing to 20 before midbody; reduction below 20 scale rows occurs on the posterior body (73–94% of TL) in 42% of the specimens with about half of these (19%) reducing only to 19 rows. The North Island *T. hectus* are similar in having an initial scale row number of 20 (30% have 22 or 21 rows for a short distance anteriorly), but all reduce to 18 scale rows farther anteriorly than Tiburon Peninsula *T. hectus,* at 46–86% of TL, or somewhat beyond midbody on the average. Pigmentation is generally light (brown or tan) and fades ventrally with some dropping out of pigmented scales. The rostral and adjacent upper wings of the posterior nasals are largely unpigmented, making the snout distinctively pale. The population of *T. hectus* around Morne Salagnac, west of Miragoane, Haiti (the easternmost samples on the Tiburon Peninsula; Fig. 5), contrasts with other populations in being very heavily and extensively pigmented. The pigmentation fades ventrally but pigmented scales extend irregularly onto the venter, often completely across it. The North Island populations are somewhat more heavily pigmented than those of the distal Tiburon Peninsula. Hemipenes are trumpet-shaped and flat apically. The sulcus spermaticus enters the organ medially, spirals posteriorly and laterally for 1/4 turn, proceeding to the distal region.

Distribution: The distribution of *T. hectus sensu stricto* extends from the distal Tiburon Peninsula east to the vicinity of Miragoane and Île la Gonâve. The associated specimens of *T. hectus* occur on the North Island of Hispaniola from the vicinity of Lascahobas, Haiti, in the west to the southern slopes of the Cordillera Central, north of San Juan de la Maguana, Dominican Republic, in the east (Fig. 5).

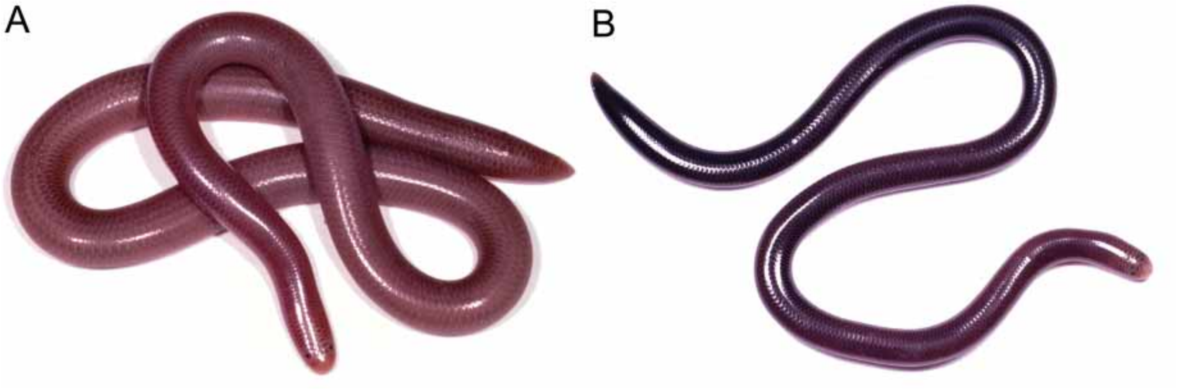

FIGURE 4. Two species of blindsnakes (*Typhlops*) from Hispaniola. (A) *T. hectus* (USNM 564794), from 2.4 km N Ducis, Département du Sud, Haiti. (B) *T. eperopeus* (USNM 564788), from 13.5 km SW Barahona, Barahona Province, Dominican Republic. Photographs by S. Blair Hedges.

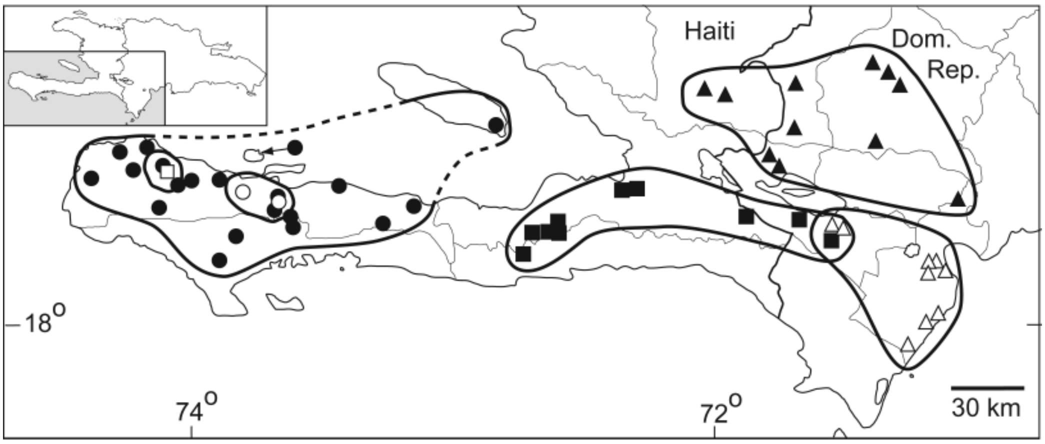

FIGURE 5. Geographic distribution of the blindsnake *Typhlops hectus* and five cryptic species from Hispaniola. Closed circle = *T. hectus*, open circle = *T. sylleptor*, open square = *T. agoralionis*, closed square = *T. proancylops*, open triangle = *T. eperopeus*, and closed triangle = *T.* sp. (undescribed populations tentatively assigned to *T. hectus*).

Specimens examined: Specimens of *Typhlops hectus* in the Albert Schwartz Field Series (ASFS) listed by Thomas (1974) are presently deposited in the University of Kansas Museum of Natural History (KU) and were re-examined for this paper; the specimens of geographic sample "a" (Thomas, 1974) are herein designated as paratypes of two species described below. ASFS V9821 (KU 269825), examined by Thomas (1974) is one of the associated specimens of a new species described below. Additional specimens of *Typhlops hectus* are all from Haiti. Dépt. du Sud: USNM 564793–795, 1.5 km N Ducis; KU 288519, 5.1 km W Anse a Veau; Dépt. de la Grande-Anse: USNM 564792, ca. 3 km N Bois Sec, 360 m; USNM 564796, 3.6 km S Baradères; ASFS V44239, V44427, 18.8 km N Cavaillon; ASFS V44499–515, 20.6 km N Cavaillon; KU 288520–525, 288542–562, Caye Morbette, 5.1 km SW Paillant, 727 m; KU 288523, Paillant, 575 m; KU 288534–541, 1.1 km SW Paillant, 606 m; KU 288526–532, Dimisaine, 1.6 km SW St. Michel du Sud; KU 288563, Ile de la Gonâve, Haiti. As noted above, this list does not include "associated specimens" of *T. hectus*, *sensu stricto*, from the North Island of Hispaniola.

Comments: An unusual excess of females is present in several large samples of this species. For example, all 32 specimens examined from the North Island are females, with the possible exception of a very small individual. All 23 snakes that were sexed from the region of the type locality in the western part of the Tiburon peninsula were also females. Nearly all (102 out of 107) snakes from Fond de Nègres (Dépt. de la Grande-Anse) were females, although that percentage was lower (73%) in a nearby sample of 37 snakes from the Paillant region. In other areas, such as near Camp Perrin, the sex ratio was more even. Whether this indicates parthenogenesis, facultative parthenogenesis, or sexual dimorphism in habits remains to be determined.

The first of the new species occurs on the northern slopes of the Massif de la Selle and Sierra de Baoruco. It may be known as

Typhlops proancylops **new species (Fig. 3B)**

Holotype: KU 272267, an adult male, collected at Soliette, 5 km airline NW Fond Verettes, 363 m, Dépt. du Sud-Est, Haiti, on 13 July 1979 by Haitian collectors.

Paratypes: Haiti. Dépt. du Sud-Est: KU 272262–268, 272269–278, same data as the holotype; RT 5609–13, same locality as holotype, 12 July 1978, Haitian collectors; 5664–671, same locality as the holotype, 23 July 1978, Haitian collectors; USNM 564801–802, 24 October 1984, Haitian collectors. Dépt. de l'Ouest: KU 269813, ca. 10 km by road W Pétionville, N versant, Morne l'Hôpital, 818 m, 1 March 1966, R. Thomas; KU 269814, KU 269899, ca. 7 km airline W Pétionville, N versant of Morne l'Hôpital, 606 m, 1 March 1966, R. Thomas. Dominican Republic. Independencia Prov.: KU 272525, 5 km W Puerto Escondido, 30 June 1969, R. K. Bobilin; USNM 564803, Rabo de Gato (ca. 3 km S Puerto Escondido), 383 m, 23 March 2004, S. B. Hedges.

Associated specimens (all from Haiti)*:* Dépt. de l'Ouest: KU269825, 2.4 km S Trouin; RT 5301, 2.9 km S Découzé, 424 m; RT 7476, Vendal, 1.4 km N Découzé, 363 m (Coq Chanté); ASFS V45526–527, V45546, 5.0 km. S Béloc; ASFS V46092, 1.2 km N Découzé. Dépt. du Sud-Est: RT 7575, ca. 5 km airline SW Blockhaus, 393 m.

Diagnosis: A large, 20-scale-row species of *Typhlops,* having no posterior reduction. This species was previously included within *T. hectus* (Thomas, 1974) and the major comparison is with that species (Table 1). *Typhlops proancylops* is allopatric with *T. hectus* and differs from that species in having a narrower rostral that is widest more anteriorly than in *T. hectus* and which tapers towards the tip, in contrast to the clavate rostral of *T. hectus* that widens towards the tip (Figs. 3, 6A). It has a larger, broader anterior projection of the preocular that is not smoothly rounded but has two angles near the apex, in contrast to *T. hectus*, which has, on the average, a more acuminate apex (Fig.3). The posterior nasal-preocular suture has an angled deflection, rather than a continuously curved suture as in *T. hectus*. The suture between the preocular and the 3rd infralabial is relatively long in comparison to *T. hectus* (Fig. 6B). The edges of the posterior nasals flanking the rostral tend to be straight or very slightly divergent, whereas those of *T. hectus* are more bowed out. Also, *T. proancylops* is more heavily pigmented, with pigment in the facial region on the preoculars, posterior nasals, and rostral, in contrast to the pale-snouted *T. hectus* (excepting the Morne Salagnac snakes referred to above). The hemipenes of *T. proancylops* are distinctive in being trumpet-shaped and capitate with a fleshy rim around the apex; no other West Indian species is known to have this morphology (Thomas, 1976). Other species of West Indian *Typhops* have trumpet-shaped organs that are flat apically (Thomas, 1976); in one species, *T. rostellatus* Stejneger, the organ is domed or rounded apically, but none have a comparable rim.

Description: Rostral narrow in dorsal aspect (RW1/RL1 0.37–0.50), varying from somewhat hastate (with widest part anterior to the middle) to a narrow oval (widest point about the middle), always tapering to a relatively narrow tip; labial flare 0.64–0.80. Preocular angle 42–61°, with a non-acuminate apex with breaks interrupting its curvature (apical diameter 0.4–0.71 mm; lower portion of preocular contacting only the 3rd of the upper labials. The angled anteriormost point is so pronounced that in a few animals a suture extends partly or all the way to the naris, partly or fully dividing the anterior nasal. Ocular length is approximately 1/2 height, sinuosity 0.23–0.10. The rostronasal pattern is parallel to slightly divergent with the dorsal limb of the posterior nasal typically having a slight bend rather than being smoothly curved, the bend being often most visible in the glandular edges of the scale papilla; postoculars, two (cycloid). The first parietal is standard, spanning two scale rows, occasionally narrower, spanning slightly more than one scale row. The second parietal is equal in size to first or absent. TL 127–243 mm ($\bar{x}$ = 197, N = 28). (10) TL/TA: males 20–24, females 25–31. TL/MBD 31–46. Middorsal scales 283–312 ($\bar{x}$ = 299, N = 28). Scale rows 20–20. Pigmentation is extensive, including the facial region and the venter; pigmentation on the venter is lighter but pigmented scales extend completely across the venter in the middle part of most specimens with dropping out of pigmented scales occurring on the anterior and posterior venter. Hemipenes are trumpet-shaped with a domed apex having a fleshy rim. The sulcus spermaticus enters the organ medially, spirals posteriorly and laterally for 1/4 turn, proceeding to the distal region.

TABLE 1. A summary of variation in selected characters of *Typhlops hectus* and associated species of Hispaniolan blindsnakes.

	Species[1]				
Character	A	B	C	D	E
Rostral club-shaped, widening towards tip	Yes	No	No	No	No
Rostral oval, tapering toward tip	No	Yes	No	Yes	No
Rostral with parallel sides, narrow	No	No	Yes	No	No
Rostral with parallel sides, broad	No	No	No	No	Yes
Preocular V-shaped, pointed	Yes	No	No	No	No
Preocular V-shaped, rounded	No	No	No	Yes	Yes
Preocular with rounded anterior projection	No	No	Yes	No	No
Preocular with bent anterior projection	No	Yes	No	No	No
SVL (mm)	132–212	122–235	134–186	114–206	135–272
TL (mm)	135–218	127–243	139–193	118–214	140–281
Middorsal scales	284–328	283–312	291–310	305–324	305–329
Scale rows anterior	22–20	20	20	20	20
Scale rows posterior	20–18	20	20	20	20–18
Scale reduction (% TL)	73–94	0	0	0	57–66
RWP	0.41–0.70	0.16–0.56	0.14–0.32	0.39–0.47	0.43–0.58
TL/TA, males	20–24	20–24	27–31	27–43	N/A
TL/TA, females	28–44	25–31	30	30	27–31
RW1/RL1	0.45–0.64	0.37–0.50	0.41–0.45	0.44–0.50	0.51–0.58
Sample size	69	46	6	4	11

1-A, *Typhlops hectus*; B, *T. proancylops*; C, *T. agoralionis*; D, *T. sylleptor*; E, *T. eperopeus*.

Distribution: This species occurs from the proximal Tiburon Peninsula, west to the uplands south of Port au Prince, to the type locality on the Dominican-Haitian border and east into the Dominican Republic, to the region of Puerto Escondido. All are upland localities from around 300 to 600 m. The type locality is where the Rivière Soliette (on one map given as Soleilet) crosses the road from Fond Parisien to Fond Verrettes. It is also the type locality for *Leptotyphlops leptepileptus*. In the description of that species (Thomas, et al., 1985), it was noted that the site was "tree-lined" and shady compared to the more open cultivation-scrub mosaic of the surrounding limestone hills. However, most of those specimens and all of the topotypes of *T. proancylops* were collected by Haitian collectors; and we have no way of knowing the exact sites where they were found. In general, this area is more mesic than the scrubbier area a couple of kilometers below Soliette at Plain Thoman. Likewise, the Morne l'Hôpital locality, along Route Boutilliers, is mesic, compared to the lowlands of Port-au-Prince and the Cul-de-Sac Plain, immediately to the north. At the time of collection, in 1966, there was a certain amount of habitation and cultivation above Route Boutilliers and steep slopes below it. The unpaved roadbed itself provided some less exposed, moist sites where the three specimens of *Typhlops proancylops* were collected by turning rocks. However, Haitian cultivators obtained specimens of *Typhlops capitulatus* Richmond and *Amphisbaena innocens* from their fields above the road. The localities to the west near Découzé and Béloc lie in mesic upland areas of coffee cultivation along the road that crosses the Tiburon Peninsula from Carrefour Dufort to Jacmel. The most xeric habitat in which *Typhlops proancylops* has been found are the localities near Puerto Escondido in the Dominican Republic. These sites lie in the northern foothills of the Sierra de Baoruco, and the habitat was dry gallery forest and xeric woods (*Acacia* and *Bucida*).

Etymology: Proancylops is from the Greek *pro*, before, *ancistros*, bent, and *ops*, eye, in reference to the bent or broken outline of the preocular.

The second of the new species occurs on the northern slopes of the Massif de la Hotte in the distal part of the Tiburon peninsula of Haiti. It may be known as

Typhlops agoralionis **new species (Fig. 3C)**

Holotype: USNM 564777 (field tag number 191925), collected 8.0 km S Marché Léon, 435 m, Dépt. de la Grande Anse, Haiti, on 28 May 1991, by S. B. Hedges, M. Leal, N. Plummer, R. Thomas.

Paratypes: USNM 564778–564782, same data as holotype.

Diagnosis: This is a moderate sized 20-scale-row species of *Typhlops* having no posterior reduction. *Typhlops agoralionis* is sympatric with *T. hectus* and differs from that species in having a narrow, nearly parallel-sided rostral, in contrast to the clavate rostral of *T. hectus* that widens towards the tip (Fig. 6). The rostral difference also is reflected in lower, essentially non-overlapping, RW1/RL1 values (0.41–0.45 versus 0.45–0.64). It also has a large, broadly rounded anterior projection of the preocular and a shorter, more steeply angled suture between the preocular and the second supralabial; this is in contrast to the preocular of *T. hectus* which is V-shaped and pointed (Fig. 6). The rostral wide point of *T. agoralionis* is smaller and does not overlap with that of *T. hectus* (0.14–0.32 versus 0.41–0.70). The edges of the posterior nasals flanking the rostral are parallel-side or slightly divergent. *Typhlops agoralionis* is also a shorter-tailed species (TL/TA 27–31, males) than either *T. hectus* or *T. proancylops* (TL/TA 20–24, males). Heavy pigmentation with pigment on the facial region and on the body extends irregularly across the venter, although the ventral pigmentation is lighter by virtue of both lessened intensity and dropping out of scales. *Typhlops agoralionis* is generally more similar to *T. proancylops* than to *T. hectus* but differs from *T. proancylops* in having a more straight-sided, somewhat narrower rostral and in the anterior extension of the preocular being rounded rather than with breaks (Fig. 3); the apical diameter averages larger (Fig. 6D) and the suture length between the preocular and third labial scale is shorter (Fig. 6E) in *T. agoralionis* versus *T. proancylops*.

Description: Rostral narrow in dorsal aspect (RW1/RL1 0.40–0.45), parallel to slightly hastate, with widest point anterior to the middle and tapering to the tip; labial flare 0.65–0.75. The preocular angle is 45–53º, with a broadly rounded apex (apical diameter 10–25 mm); lower portion contacting only the 3rd of the upper labials in a relatively short, steeply angled suture. The ocular length is approximately 1/2 height; sinuosity 0.19–0.09. The rostronasal pattern is parallel. There are two postoculars (cycloid). The first parietal is standard, spanning two scale rows; the second is present and equal in size to first or slightly narrower. TL 139–

193 ($\bar{x}$ = 168) mm, excluding a 107 mm juvenile. TL/TA: males 27–31, female 30. TL/MBD 31–39. Middorsal scales 291–310 ($\bar{x}$ = 300). Scale rows 20–20. Coloration very pale brown above, fading gradually onto venter by lightening and dropping out of scales, pigmented scales irregularly continuing across the venter, more so anteriorly; the rostral is largely unpigmented, but the flanking upper wing of the posterior nasal and the preocular are both pigmented. Hemipenes are trumpet-shaped with a flat apex and no rim; the sulcus spermaticus enters the organ medially, spirals posteriorly then laterally for 1/4 turn and proceeds to the apex of the organ.

Distribution: Known only from the type locality (435 m) on the north slope of the Massif de la Hotte in the distal part of the Tiburon Peninsula.

Etymology: From the Greek, *agora*, market place, and Latin, *lionis* (genitive), lion, in reference to the town of Marché Léon, whence the type locality is reckoned, and may be more or less rendered “of the lion of the marketplace.”

Another new species from the distal Tiburon Peninsula of Haiti may be known as

Typhlops sylleptor **new species (Fig. 3D)**

Holotype: USNM 564804 (field tag number 192317), collected 8.0 km WSW Baradères, Dépt. de la Grande Anse, Haiti, 420 m, 7 June 1991, by M. Leal and R. Thomas.

Paratypes: USNM 564807, same data as holotype; USNM 564805–806, 5.0 km S Pestel, Dépt. de la Grande Anse, Haiti, 375 m, 24 May 1991, by S. B. Hedges, M. Leal, N. Plummer, and R. Thomas.

Diagnosis: This is a moderate sized 20 scale-row species of *Typhlops* having no posterior reduction. *Typhlops sylleptor* is sympatric with *T. hectus*. It differs from *T. hectus* in being more blunt-snouted, having smaller eyes, and having a narrowly oval rostral (Fig. 3D), in contrast to the clavate rostral of *T. hectus* (Fig. 3A) that widens towards the tip. A large, broadly rounded anterior projection of the preocular also differentiates it from *T. hectus*, which has preocular with sharply pointed apex (Fig. 3A). These differences can be seen also in graphs of RW1/RL1 versus HR (Fig. 6F), RWP versus RW1/RL1 (Fig. 6G), and PD versus HR (Fig. 6H). *Typhlops sylleptor* is also a shorter tailed species (TL/TA 27–43, males) than either *T. hectus* or *T. proancylops* (TL/TA 20–24, males). From *T. proancylops* (Fig. 3B), *T. sylleptor* also differs in having a preocular scale without a bent edge, and a relatively larger preocular angle and smaller preocular diameter (Fig. 6I). The edges of the posterior nasals flanking the rostral are parallel-sided or slightly divergent in *T. sylleptor* compared with *T. proancylops*. From *T. agoralionis* (Fig. 3C), *T. sylleptor* differs in having differently-shaped rostral and preocular scales, a larger, non-overlapping, rostral wide point (0.39–0.47 versus 0.14–0.32), and a wider rostral in relation to rostral length, reflected in graphs of RWP versus RW1/RL1 (Fig. 6G) and RL1 versus RW1 (Fig. 6J). Also, pigmentation in *T. sylleptor* is heavy, with pigment on the facial region extending irregularly across the venter.

Description: Snout relatively short. The rostral is oval, wide at midpoint and tapering to the tip; labial flare 1.0–1.3. PA 51–68°, with a rounded apex (PD 0.29–0.54 mm; lower portion contacting only the 3rd of the upper labials in a relatively short, steeply angled suture. Ocular length approximately 1/2 height, sinuosity 0.16–0.14. Rostronasal pattern parallel. Postoculars two (cycloid). First parietal standard, spanning two scale rows. Second parietal present (absent unilaterally in one) and equal in size to first or slightly narrower. TL 118–214 ($\bar{x}$ = 166) mm, excluding 105 and 107 mm juveniles. TL/TA: males 27–43, female 30. TL/MBD 33–34. Middorsal scales 305–324 ($\bar{x}$ = 313). Scale rows 20–20, no posterior reduction. Coloration medium brown above fading onto venter by lightening and dropping out of scales; all specimens pigmented across the throat, pigment continuing across venter irregularly, becoming less continuous posteriorly; in one specimen the venter is almost completely pigmented on the anterior half of the body. The rostral is largely unpigmented, but the flanking upper wing of the posterior nasal and the preocular are both pigmented.

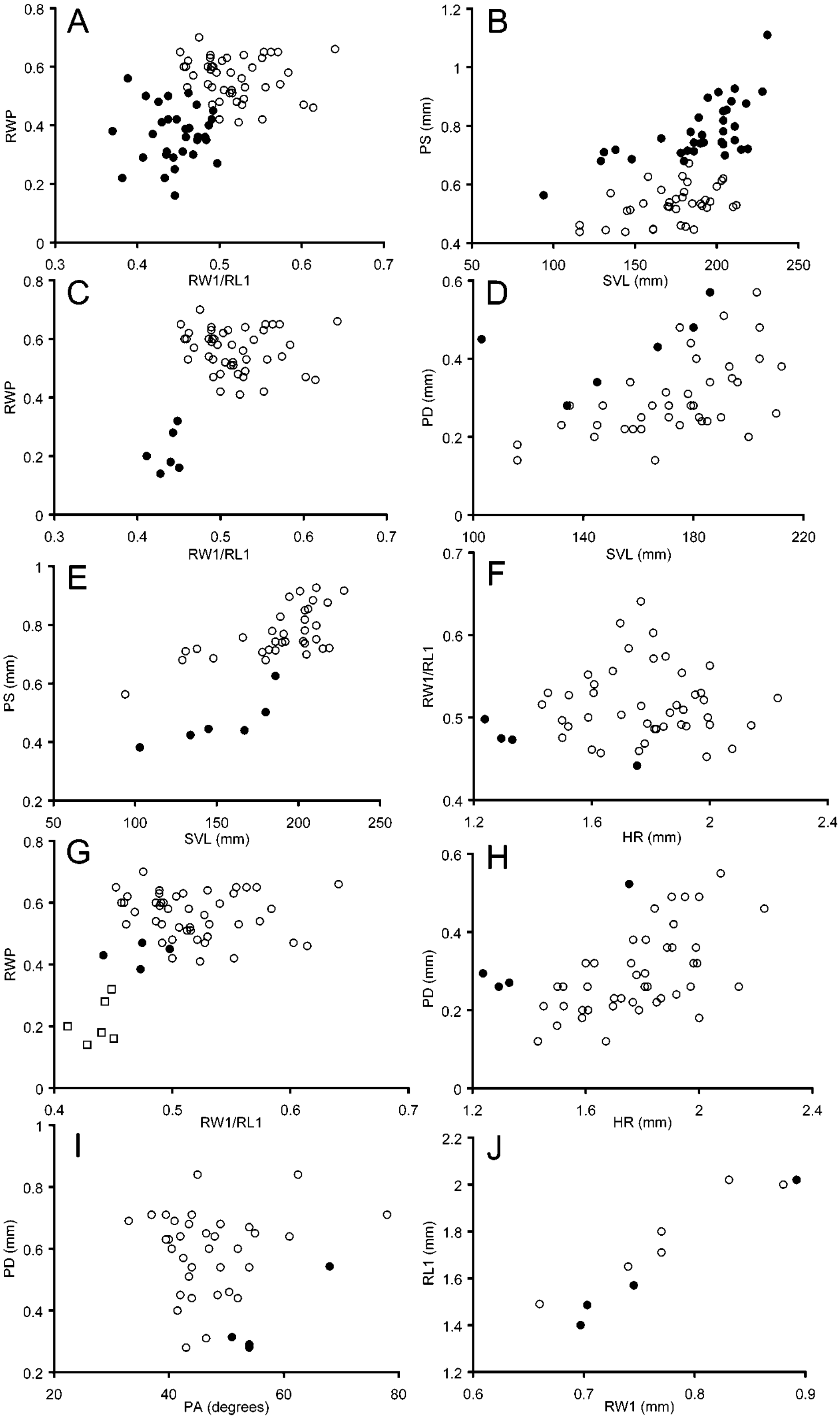

FIGURE 6. Variation in measurements of Hispaniolan *Typhlops*. (A) *Typhlops proancylops* (closed circle) versus *T. hectus* (open circle). (B) *Typhlops proancylops* (closed circle) versus *T. hectus* (open circle). (C) *Typhlops agoralionis* (closed circle) versus *T. hectus* (open circle). (D) *Typhlops agoralionis* (closed circle) versus *T. hectus* (open circle). (E) *Typhlops agoralionis* (closed circle) versus *T. proancylops* (open circle). (F) *Typhlops sylleptor* (closed circle) versus *T. hectus* (open circle). (G) *Typhlops sylleptor* (closed circle) versus *T. hectus* (open circle) and *T. agoralionis* (open square). (H) *Typhlops sylleptor* (closed circle) versus *T. hectus* (open circle). (I) *Typhlops sylleptor* (closed circle) versus *T. proancylops* (open circle). (J) *Typhlops sylleptor* (closed circle) versus *T. agoralionis* (open circle). See text for definition of abbreviations.

Distribution: Known only from the karst region between Baradères and Pestel in low but hilly, mesic habitat (375–420 m elevation). It occurs sympatrically with *Typhlops hectus*. In this karst region we also discovered an undescribed species of *Amphisbaena* (Thomas and Hedges, *in press*).

Etymology: From the Greek, *sylleptor*, meaning a companion, in reference to the other 20-row *Typhlops* of similar morphology found on the distal part of the Tiburon Peninsula.

The species from the eastern extreme of the La Selle-Baoruco massif, in the Dominican Republic, may be known as

Typhlops eperopeus **new species (Figs. 3E, 4B)**

Holotype: USNM 564785 (field tag number 266250), an adult female, collected 3.9 km airline SSW Barahona (4.5 km S Barahona along coast road and 2.8 km inland), 18° 9.854' N, 71° 5.497' W, 305 m, on 30 July 1999 by R. Thomas.

Paratypes: All from the Dominican Republic. Barahona Prov.: AMNH 51496, above Del Monte's Finca (mountains southwest of Barahona), 697 m, 1 August 1932, W. G. Hassler; USNM 564788, 13.5 km by road SW Barahona, 580 m, 18 August 1984, S. B. Hedges; USNM 564787, 4.5 km S Barahona, thence 4.0 km W, 460 m, 8 August 1975, R. Thomas; USNM 564786, 2.4 km WNW Paraiso, 200 m, 12 August 1983, S. B. Hedges, R. Thomas; KU 272423, 6 km NE Paraiso; RT 3516, 4 km NW Enriquillo, 212 m, 8 August 1975, R. Thomas. Independencia Prov.: AMNH 41265–266, Duvergé; USNM 564789–791, 6 km W Duvergé at La Zurza (N 18°23.978' W 71° 34.358', minus 7 m, 22 March 2004, S. B. Hedges.

Diagnosis: This is a large, 20-scale-row species of *Typhlops*, not reducing to 18 scale rows posteriorly or reducing about 2/3 the way along the body. Despite the fact that specimens of this species were previously included within *T. hectus* (Thomas, 1974), *T. eperopeus* agrees with *T. titanops* in the presence of reduction from 20 to 18 scale rows fairly far anteriorly (60–65% of the TL) in some individuals (all *T. titanops* reduce at around midbody; *T. hectus* reduce at 73–94% TL). It differs from *T. titanops* in having a greater number of middorsal scales (307–329 versus 231–264). In body size (TL), *T. eperopeus* averages larger: 140–281 ($\bar{x}$ = 234) mm versus 145–216 ($\bar{x}$ = 185) mm in *T. titanops*.

From the standpoint of size, middorsal counts and head scale shapes, however, the major comparisons are with *T. hectus* and the other species described herein. *Typhlops eperopeus* is sympatric with *T. proancylops* and differs from that species in having a nearly parallel-sided rostral (oval in *T. proancylops*), having a rostral wide point relatively far posterior (anterior in *T. proancylops*; Fig. 7A) and having a preocular with rounded apex (two angles near the apex in *T. proancylops*; Fig. 3B). *Typhlops eperopeus* differs from *T. hectus* in having a nearly parallel-sided rostral (distinctly clavate in *T. hectus*), and having a preocular with rounded apex (pointed in *T. hectus*; Figs. 3, 7B). *Typhlops eperopeus* differs from *T. agoralionis* in having a broader rostral (RW1/RL1 0.51–0.58 versus 0.41–0.45 in *T. agoralionis*), having a straight-edged (V-shaped) preocular extension (lower edge with angled bend in *T. agoralionis*; Fig. 3C). *Typhlops eperopeus* differs from *T. sylleptor* in having a broader rostral (RW1/RL1 0.51–0.58 versus 0.44–0.50 in *T. sylleptor*), a nearly parallel-sided rostral (oval in *T. sylleptor*), and in having a rostral wide point relatively far posterior (Fig. 7A).

Description: Rostral nearly parallel-sided or only slightly clavate with widest point beyond the midpoint; labial flare 1.3. Preocular angle 46–58°, with a broad but angled apex; lower portion contacting only the 3rd of the upper labials. Ocular length approximately 1/2 height, sinuosity 0.25–0.19. Rostronasal pattern parallel to slightly divergent. Postoculars 2 (cycloid). First parietal standard, spanning 2 scale rows, occasionally narrower, spanning slightly more than 1 scale row. Second parietal present and equal in size to first. TL 140–281 mm ($\bar{x}$ = 234, excluding 140 mm juvenile). TL/TA: 22–31. TL/MBD 29–39. Middorsal scales 305–329 ($\bar{x}$ = 314). Scale rows 20–18, reduction occurring at 57–66% TL. Coloration bicolor with dorsal pigmentation (pale tan to dark brown) fading ventrally; facial area generally pigmented, although the rostral may lack pigment, as in the holotype. AMNH 51496 and KU 272423 are very heavily pigmented individuals. No males of this species have been identified; see comments above for *T. hectus*.

Distribution: Known from below sea level in the Valle de Neiba up to relatively high elevations in the eastern Sierra de Baoruco. The elevational range is 7 meters below sea level to 697 m. In the lower elevations of its range, this species occurs sympatrically with *T. pusillus* and *T. sulcatus* (Schwartz & Henderson, 1991), and with *T. proancylops* in the vicinity of Puerto Escondido and Duvergé.

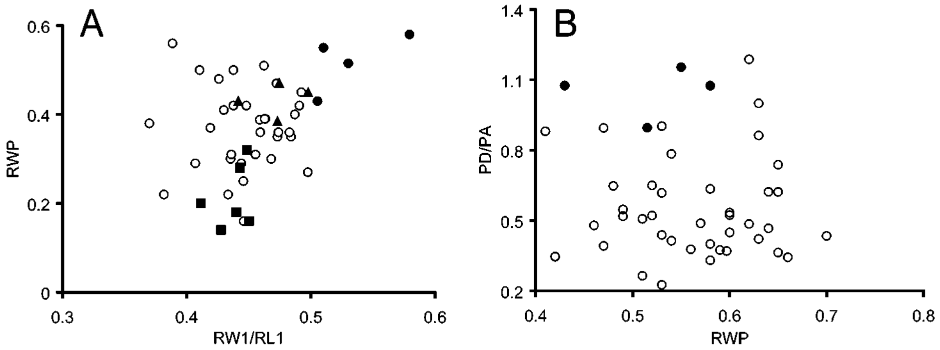

FIGURE 7. Variation in measurements of Hispaniolan *Typhlops*. (A) *Typhlops eperopeus* (closed circle) versus *T. proancylops* (open circle), *T. agoralionis* (closed square), and *T. sylleptor* (closed triangle). (B) *Typhlops eperopeus* (closed circle) versus *T. hectus* (open circle). See text for definition of abbreviations.

Etymology: Eperopeus, which we use appositionally, is Greek for deceiver, in allusion to the deceptive morphological similarity of this species to *Typhlops hectus* and the other species described herein, in contrast to its presumed relationship to *T. titanops* based on molecular and some morphological characters.

New Species from Cuba Associated with *Typhlops biminiensis*

Thomas (1968; 1976) recognized a *Typhlops biminiensis* Group comprising two species occupying Bahaman islands, the Cayman Islands, and Cuba. One of those species, *T. biminiensis*, was proposed to occupy all of this range except for Grand Cayman. Cayman Brac has a species, *T. epactius* Thomas, which was originally described as a subspecies of *T. biminiensis*. Thomas (1968) also described *T. b. paradoxus* from Great Inagua Island. At that time, only four specimens of *T. b. biminiensis* were known from two widely separated localities in Cuba. Most specimens of this species group have been collected on or near the coasts of islands, near sea level. Our field work in Cuba 1987–1994 yielded additional specimens representing seven new species. We now consider *T. biminiensis* (Fig. 8A) to be restricted to the Bahamas (Great Bahama and Cay Sal banks). Further, we recognize *T. paradoxus* (Fig. 8B) from Great Inagua as a full species. Diagnostic differences among *T. epactius* (Fig. 8C), *T. paradoxus*, *T. caymanensis* Sackett (Fig. 8D), and Bahamian *T. biminiensis* are discussed elsewhere (Thomas, 1968;1976). Below we redefine *T. biminiensis* and describe the seven new species from Cuba.

Ideally, we would prefer to have larger sample sizes of some of these new species from Cuba. Although 18 specimens are available from the U. S. Naval Station, only a few specimens of "*T. biminiensis*" were known from elsewhere in Cuba (Thomas, 1968) until now. Nonetheless, our extensive fieldwork in Cuba during 1989–1994, outside of the Naval Station, has yielded only nine additional specimens. Considering only the south coast of eastern Cuba, we estimate that more than 1000 man-hours were spent searching specifically in suitable habitats during our expeditions, resulting in a collection rate of one snake of this complex per >100 hours of search time. This slow rate of accumulation of specimens has provided some impetus for drawing taxonomic conclusions from all available material currently at hand. Fortunately, the relatively large series from the Naval Station, noted above, provided us with an important assessment of population variation in the taxonomic characters and have provided evidence for the recognition of seven new species that we describe below.

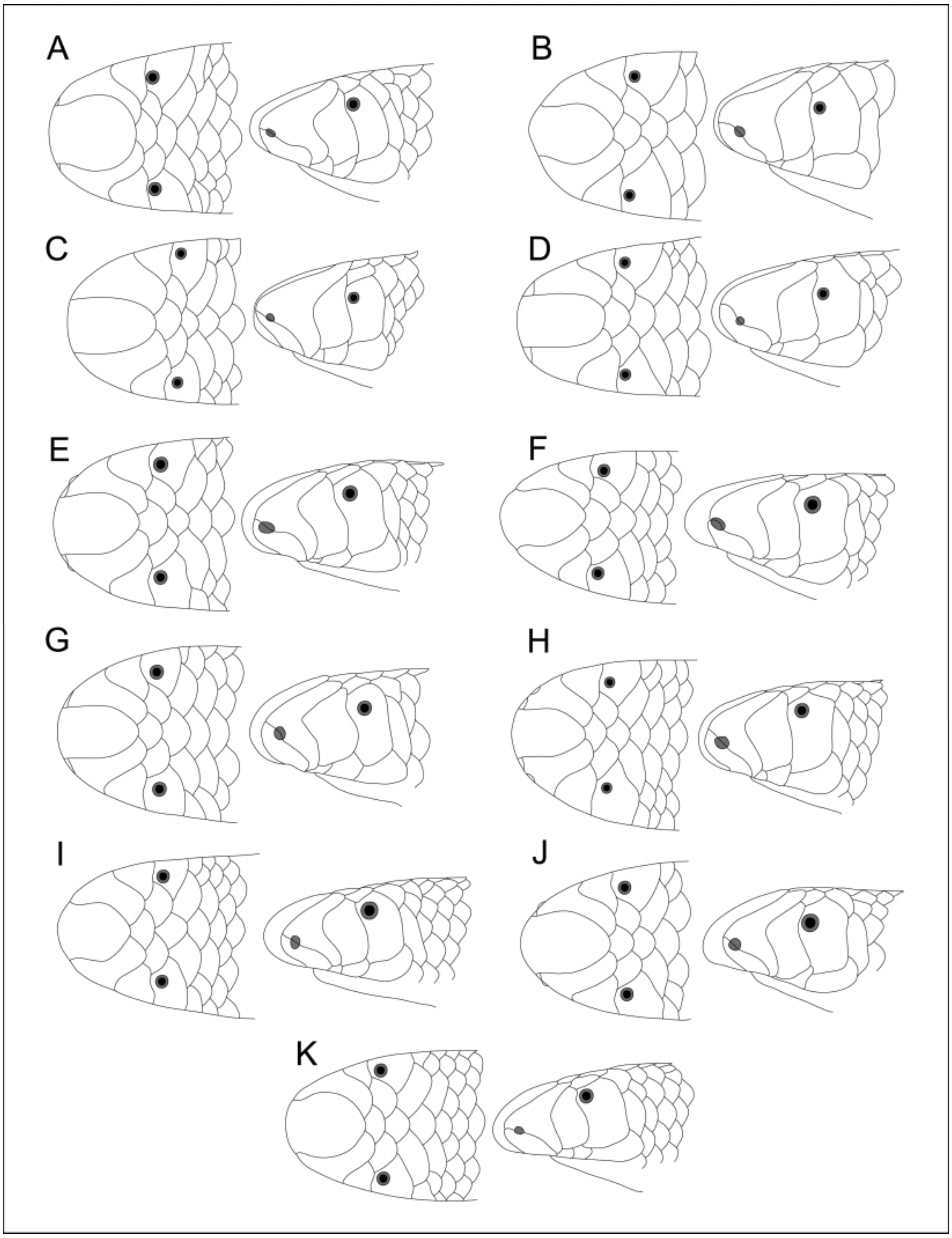

FIGURE 8. Head scalation in the *Typhlops biminiensis* Group, including seven new species from Cuba. (A) *T. biminiensis* (ASFS V11655), from Elbow Cay, Cay Sal Bank, Bahamas. (B) *T. paradoxus* (ASFS V12067), from Great Inagua, Bahamas. (C) *T. epactius* (ASFS V11673), from Cayman Brac, Cayman Islands. (D) *T. caymanensis* (ASFS V17112), from Grand Cayman, Cayman Islands. (E) *T. perimychus* (USNM 564800), holotype, from Guantanamo Bay Naval Station, Cuba. (F) *T. arator* (MNHNCu 191), holotype, from El Narigon, La Habana, Province, Cuba). (G) *T. anousius* (MNHNCu 4550), holotype, from 3.5 km E Tortuguilla, Guantánamo Province, Cuba. (H) *T. notorachius* (MNHNCu 4551), holotype, from 9.4 km W Imias, Guantánamo Province, Cuba. (I) *T. contorhinus* (MNHNCu 4552), holotype, from 4.9 km S La Tinta, Guantánamo Province, Cuba. (J) *T. anchaurus* (MNHNCu 4553), holotype, from within 1 km of Cueva de Agua (2.5 km airline NW Maisí), Guantánamo Province, Cuba. (K) *T. satelles* (SMF 61303), holotype, from Rancho Luna, about 12 km airline S Cienfuegos, Cienfuegos Province, Cuba.

Typhlops biminiensis (Fig. 8A)

Diagnosis: Typhlops biminiensis sensu stricto is one of the largest West Indian species of *Typhlops*, TL (total length) to 370 mm. The preocular contacts supralabials 2 and 3, which is a characteristic of the *T. biminiensis* Group (Richmond, 1955; Thomas, 1968) of West Indian species. This feature also occurs in all mainland Central and South American species (Dixon & Hendricks, 1979) but not most West Indian species, which belong to another West Indian radiation of *Typhlops*, the major Antillean radiation (MAR) (Thomas, 1976). Aside from the preocular-contact character, *T. biminiensis* is distinguished from members of the MAR by its broadly angled preocular (93–125°) and its broad rostral scale (RW1/RL1 0.81–1.08). The only currently recognized member of the Major Antillean Radiation occurring within the range of *T. biminiensis* is *T. lumbricalis* of Cuba and the Great and Little Bahama Bank islands. From described members of the *Typhlops biminiensis* group (*T. caymanensis*, *T. epactius*, and *T. paradoxus*), *T. biminiensis sensu stricto* differs in its larger size and broad, nearly round, rostral scale (Fig. 8A) with RW1/RL1 values of over 0.81. It further differs from *T. caymanensis* by its greater number of scale rows (24 or 22 initially versus 20 rows for *T. caymanensis*) and greater number of middorsal scales (454–537 versus 351–408). From the Cuban species (Fig. 8) it differs in having a larger rostral size (RW1+RL3; Fig. 10A), longer snout (NE; Fig. 10B), and smaller preocular apical diameter (PD; Fig. 10C). Because the new Cuban species can thus be distinguished from *T. biminiensis*, *T. caymanensis*, *T. epactius*, and *T. paradoxus*, our discussion below will focus mostly on diagnostic traits among the Cuban species previously confused with *T. biminiensis*.

Description: Snout rounded, slightly lobed. Rostral broad and rounded in dorsal aspect, nearly as broad as long in most specimens (RW1/RL1 0.81–1.08), broadly oval, almost circular; not flared on apex; minimal umbo; no labial flare. PA 93–125°, apex rounded; lower portion of preocular contacting upper labials two and three. Anterior nasal width as a proportion of RW1 0.30–0.37. OL 1/2 height, OS 0.09–0.28. Rostronasal pattern strongly divergent. Postocular 3–4 times higher than long, rarely two postoculars as a result of a second scale encroaching minimally on the postocular space. First parietal standard, spanning two scale rows or slightly less. Second parietal present and similar in size to the first, or absent. TL to 380 mm. TL/TA 42–60. TL/MBD 39–51. Middorsal scales 454–537. Scale rows 22 with no posterior reduction or 24 reducing to 22 at about midbody or not reducing at all. Coloration bicolor with dorsal pigmentation (pale brown) ending abruptly along a midlateral or dorsolateral line by dropping out of pigmentation on individual scales, resulting in a jagged line of separation between pigmented and non-pigmented scales; or color fading gradually over 2–3 scale rows, without dropping out of pigment; a combination of these effects may occur with a gradual transition anteriorly and dropping out of pigmented scales posteriorly. Hemipenes attenuate.

Distribution: Bahamas: Bimini Islands, Andros Island, New Providence, Elbow Cay (Cay Sal Bank), and Ragged Islands.

The first of the new species having affinities with *T. biminiensis* occurs on the southern coast of eastern Cuba, in the region of Guantánamo Bay. It may be known as

Typhlops perimychus new species (Figs. 8E, 9A)

Holotype: USNM 564800 (field tag number 161982), from Blue Beach, U. S. Naval Base Guantanamo Bay, Cuba, five meters elevation, collected on 22 March 1987 by S. B. Hedges and C. A. Hass.

Paratypes: All from the U. S. Naval Base Guantanamo Bay, Cuba: KU 268435, windward (east) side of Bay, Kittery Beach, 8 Nov. 1968, P. J. Tolson; KU 268655–656, windward side of Bay, 5 April 1969, J. A. Rodgers, A. Schwartz; USNM 192797, nursery, east side of Bay, 9 May 1969, P. J. Tolson; USNM 192802, nursery, east side of Bay, 21 May 1969, P. J. Tolson; USNM 192811, nursery, east side of Bay, 10 July 1969, P. J. Tolson; KU 268657, windward nursery, 1969, P. J. Tolson; KU 269658, windward nursery, 11 Sept. 1969, P. J. Tolson; KU 269659, windward nursery, 6 April 1969, P. J. Tolson; KU 269660, windward nursery, 2 May

1969, P. J. Tolson; KU 269661, windward nursery, 5 May 1969, A. Schwartz; MCZ 68726; MCZ 68944; MCZ 69443; USNM 315999, near grounds of Fil-Am Club, just N Glass Beach; USNM 316000, John Paul Jones Hill on Perimeter Road, 16 August 1988, R. I. Crombie, L. K. Gordon, G. Zustak.

Associated specimen: USNM 317824, Kittery Beach Road, just past Graffiti Hill, R. I Crombie and G. K. Pregill, 9 June 1987.

Diagnosis: A moderately large species of the *Typhlops biminiensis* Group differing from *T. biminiensis* in having a rostral with an acuminate posterior edge, not broadly rounded. Also, the rostral has parallel sides and is not indented at the apex of the snout (Fig. 8). *Typhlops perimychus* additionally differs from *T. biminiensis* in having a more protuberant snout (NE) and a larger preocular apical diameter (PD), as noted above (Figs. 10A–10C). Diagnostic characters distinguishing this species from the other Cuban species will be discussed below as those species are described. Diagnostic characters distinguishing all Cuban species are presented in Table 2.

TABLE 2. A summary of variation in selected characters of *Typhlops biminiensis* and associated species of Cuban blind-snakes.

	Species[1]							
Character	A	B	C	D	E	F	G	H
Rostral acuminate posteriorly	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Rostral umbo	No	No	Yes	No	No	Yes	Yes	No
Rostral flared on apex	No	No	Yes	No	No	No	Yes	No
Pigmentation present	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes
Middorsal scales	454–537	453–496	578–579	465–513	475–529	502	514	514–527
Scale rows anterior	22,24	22,24	26	24	24	24	24	22,24
Scale rows posterior	22,24	22	24	22	22	22	22	22
Scale reduction (% TL)	50	50	34–41	2	15–40	31	31	11
ANTNAS/RW1	0.30–0.37	0.34–0.39	0.35	0.40–0.64	0.42–0.53	0.49	0.36	0.32–0.33
SVL (mm)	221–373	128–273	235-450	107–193	277–297	310	235	302–343
TL (mm)	225–380	130–280	240–460	109–197	282–301	316	240	307–350
TA (mm)	2–6	2–6	5–10	2–4	4–5	6	5	5–7
TL/TA	42–60	46–85	46–48	55–56	48–75	53	48	55–61
TL/MBD	39–51	41–59	51–55	45–55	45–57	63	63	62–75
PD	2–20	13–29	21	13–20	21–30	40	18	24–30
RI/RL1	0.19–0.33	0.19–0.49	0.25	0.40–0.41	0.37–0.43	0.68	0.35	0.23–0.27
RW1/RL1	0.81–1.08	0.79–1.05	0.97	0.74–0.77	0.78–0.87	1.03	0.87	0.99
RW2/RW1	0.75–0.94	0.76–1.05	1.04	0.83–0.94	0.91–0.99	0.96	0.92	0.79–0.83
((RW1+RL3)/TL)*100	1.88–2.50	1.80–2.96	2.46	2.11–2.75	1.60–1.80	1.67	2.10	1.58–1.91
Sample size	17	20	3	2	4	1	1	2

1—A, *Typhlops biminiensis*; B, *T. perimychus*; C, *T. arator*; D, *T. anousius*; E, *T. notorachius*; F, *T. contorhinus*; G, *T. anchaurus*; H, *T. satelles*.

Description: Snout rounded, slightly lobed (truncate-ogival). Rostral varying from broad and rounded, almost circular, to broadly oval in dorsal aspect (RW1/RL1 0.8–1.0); not flared on apex; minimal umbo; no labial flare. Anterior nasal width as a proportion of RW1 0.34–0.39. Preocular angle 104–131°, apex rounded; lower portion contacting labials 2 and 3 of upper labial series. OL 1/2 height, OS 0.14–0.25. Rostronasal pattern strongly divergent. Postocular 4–7 times higher than long. First parietal standard, spanning two scale rows or slightly less. Second parietal present and similar in size to the first or absent (= standard scale). TL to 280 mm (see below). TL/TA 46–85. TL/MBD 41–69. Middorsal scales 453–496. Scale rows 22 with no posterior reduction or 24 reducing to 22 at about midbody. Coloration bicolor (medium to dark brown dorsally) with the transition to an unpigmented venter by both fading and dropping out of pigmented scales anteriorly, with less fading posteriorly, resulting in a jagged transition due to dropping out of pigment posteriorly. Hemipenes attenuate.

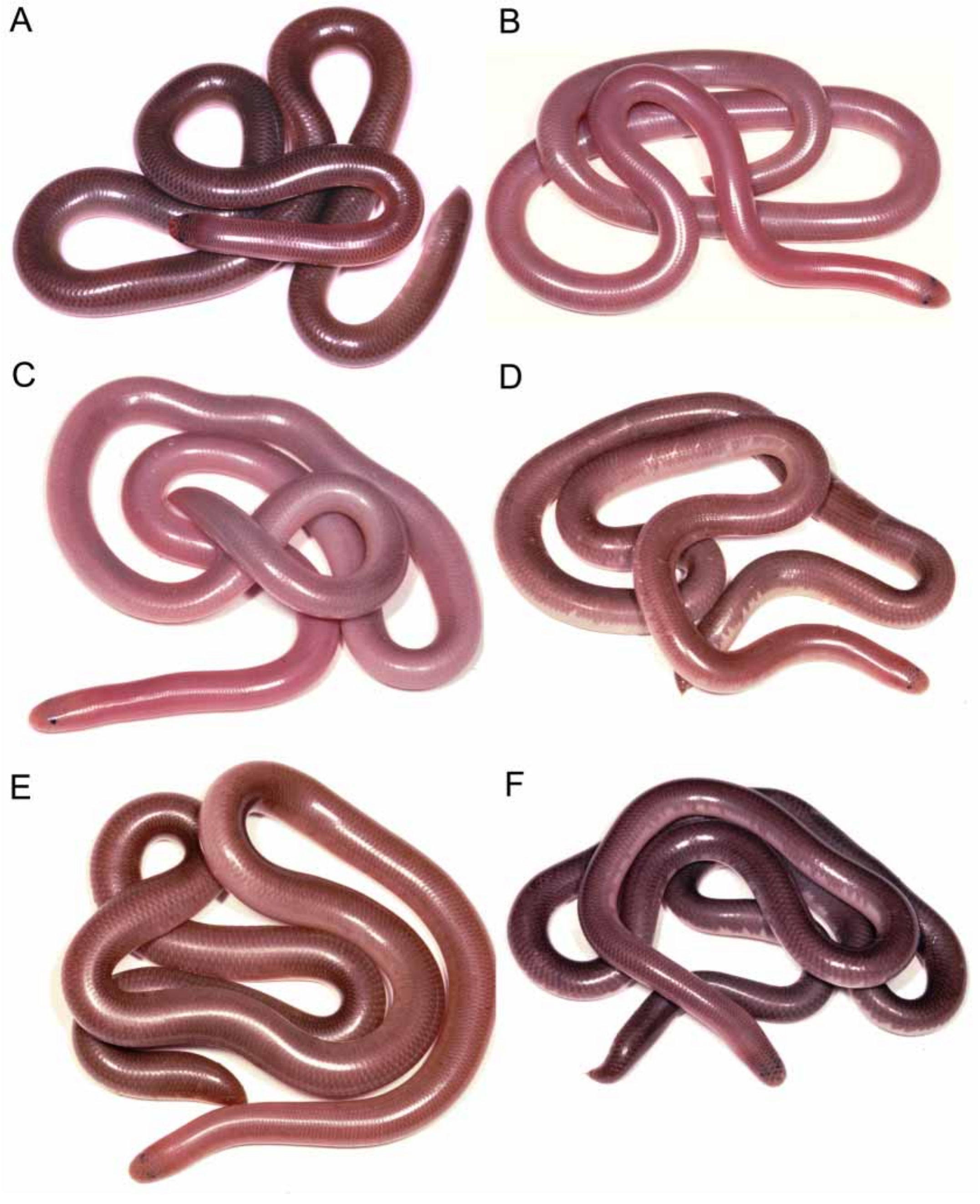

FIGURE 9. Species of blindsnakes (*Typhlops*) from Cuba. (A) *T. perimychus*, from Guantanamo Bay Naval Station. (B) *T. arator* (USNM 564784), from Narigon, La Habana Province. (C) *T. anousius* (USNM 564783), from 3.5 km E Tortuguilla, Guantánamo Province. (D) *T. notorachius* (USNM 564799), from 9.4 km E Imias, Guantánamo Province. (E) *T. notorachius* (USNM 564797) from Playitas de Cajobabo, Guantánamo Province. (F) *T. contorhinus* (MNHNCu 4552) from 4.9 km S La Tinta. Photographs by S. Blair Hedges

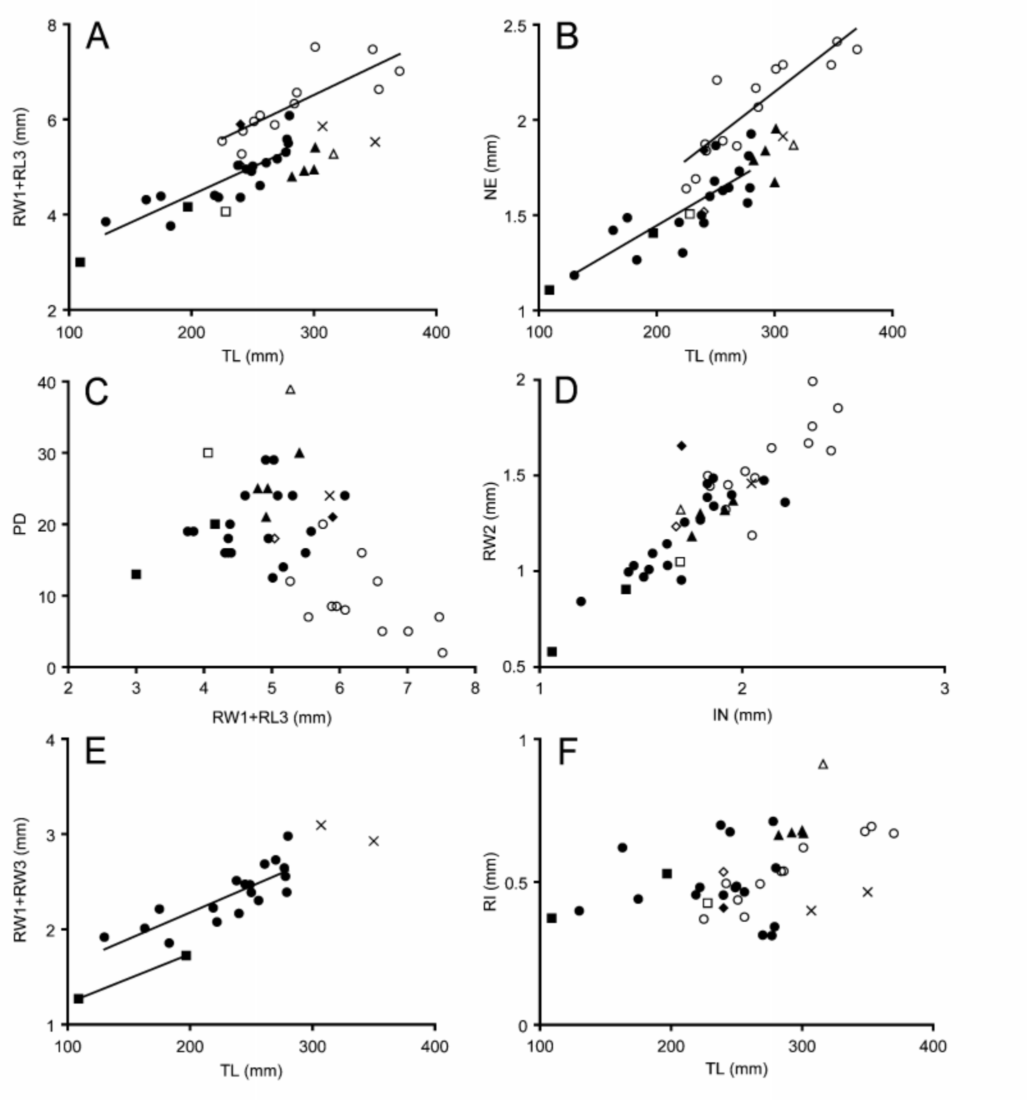

FIGURE 10. Variation in measurements of *Typhlops biminiensis* and Cuban species of the *Typhlops biminiensis* Group. For all graphs (A–F), the following species are indicated by symbols: *T. anchaurus* (open diamond), *T. anousius* (closed square), *T. arator* (closed diamond), *T. biminiensis* (open circle), *T. contorhinus* (open triangle), *T. notorachius* (closed triangle), *T. paradoxus* (open square), *T. perimychus* (closed circle), *T. satelles* ("X"). Trendlines are indicated on some graphs for *T. biminiensis* and *T. perimychus*. See text for definition of abbreviations.

Distribution: Known only from the eastern ("windward") side of the U. S. Naval Station Guantanamo Bay in eastern Cuba (Fig. 11).

Etymology: From the Greek, *peri* (around, near) and *mychos* (bay) in allusion to the distribution of the species, next to Guantánamo Bay.

Comments: This is the best represented species of the *T. biminiensis* Group in Cuba. It is unclear why it appears to be so abundant on the U.S. Naval Station while species in this group have been rarely collected elsewhere in Cuba, despite considerable searching. However, most specimens from the base have been collected at the nursery, next to the golf course, where there is abundant moisture and vegetation. We suspect that this artificial habitat has allowed this species to increase locally in numbers. On the other hand, the series of 18 specimens has accumulated over a period of decades from collections made by many persons, and therefore the combined search effort has been great. A single specimen collected at a different location on the base, USNM 317824 (407 mm TL), is the second largest specimen of the genus in the West Indies (see below). It is 45% larger than the next largest specimen (280 mm) of *T. perimychus*. No tissues are available from this specimen. Although in rostral shape it agrees with other material of *T. perimychus*, the large size difference makes comparisons of measurements difficult and the possibility exists that it is an undescribed species. For these reasons we have treated it here as an associated specimen.

The next new species having affinities with *T. biminiensis* occurs in western Cuba. It may be known as

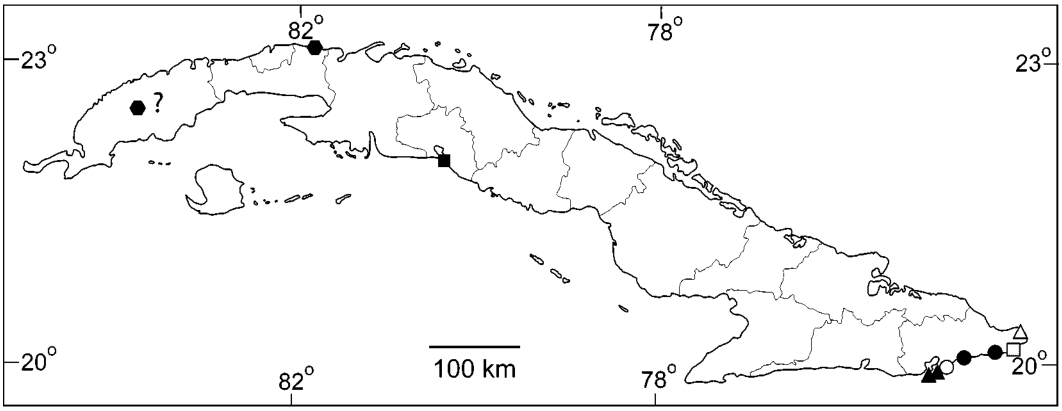

FIGURE 11. Geographic distribution of seven species of blindsnakes (*Typhlops*) in Cuba. Closed triangles = *T. perimychus*, closed hexagons = *T. arator*, open circle = *T. anousius*, closed circle = *T. notorachius*, open square = *T. contorhinus*, open triangle = *T. anchaurus*, closed square = *T. satelles*.

Typhlops arator **new species (Fig. 8F, 9B)**

Holotype: MNHNCu 191, a female, collected at “El Narigon and La India,” near Puerto Escondido, La Habana, Province, Cuba, by Ruben Regalado and Carlos Wotzkow, on 20 April 1988.

Paratype: USNM 564784, same locality as holotype, collected by Richard Thomas and Daniel McCallister on 10 July 1990.

Diagnosis: A large species of the *Typhlops biminiensis* Group that has a greater number of middorsal scales than any other West Indian species (578–579). Also, it has 26 scale rows anteriorly, more than any other West Indian species. It also has a uniquely shaped rostral (Fig. 8), which differs from *T. biminiensis* in having an acuminate posterior edge (as in other Cuban species), not broadly rounded (Fig. 8F). The rostral scale also rounds the tip of the snout without narrowing, which is unique among Cuban species in the group, reflected in a high RW2 (Fig. 10D). *Typhlops arator* additionally has a large protrusion (umbo) of the snout (Fig. 8F).

Description: Snout narrow and ogival in outline, lobed, tapering from maximum width of head. Rostral broad and nearly parallel-sided, curving gently mesiad to apex (RW1/RL1 0.97), distinctly flared on apex and with a prominent apical (not ventral) umbo; no labial flare. Anterior nasal width as a proportion of RW1 0.35. Preocular angle 110°, apex rounded; lower portion contacting labials 2 and 3 of upper labial series. OL 1/2 height, OS 0.19. Rostronasal pattern strongly divergent. Postocular about twice as high as long. First parietal wide and wing-like, spanning two scale rows. Second parietal present on left and equal in size to the first, absent on right. TL 460 mm. TL/TA 46–48. TL/MBD 51–55. Middorsal scales 578–579. Scale rows 26 with posterior reduction to 24 rows occurring at 34–41% of TL. Coloration bicolor with dorsal pigmentation (very pale brown) ending abruptly along a midlateral or dorsolateral line by dropping out of pigmentation on individual scales; the pigmentation is so light that this is difficult to discern; pigmented scale rows at midbody 9–11.

Distribution: Known only from Narigon (Habana Prov.), although possibly more widely distributed in western Cuba (see comments below) (Fig. 11).

Etymology: From the Greek, *arator*, a plow, in allusion to the prominent rostral umbo.

Comments: In addition to the holotype and paratype, both from the same locality in La Habana Province, we are aware of a very large specimen collected by Julio Novo at Cueva de San Miguel near Viñales (Pinar del Rio Prov.) in Western Cuba during the 1980s. It was even larger than the holotype of *T. arator*, and probably one of the largest scolecophidians known from the Western Hemisphere. Although that specimen apparently is lost (L. Diaz, pers. comm.), DNA sequences (S. B. Hedges, unpublished) indicate that it is most closely related to *T. arator*, suggesting that it is either a closely related species or that *T. arator* is more widely distributed in western Cuba. Until that specimen is located, or additional material is collected, we are unable to speculate further.

The next new species having affinities with *T. biminiensis* occurs on the southern coast of eastern Cuba, east of the region of Guantánamo Bay. It may be known as

Typhlops anousius **new species (Fig. 8G, 9C)**

Holotype: MNHNCu 4550 (field tag number 191295), 3.5 km E Tortuguilla, Guantánamo Province, Cuba, 10 meters elevation, on 28 June 1990 by S. Blair Hedges, Richard Thomas, and Daniel McCallister.

Paratype: USNM 564783, same data as holotype.

Diagnosis: An apparently small species of *Typhlops* of the *T. biminiensis* species group distinguished from other members of the group by a lack of pigment (except for the eyes). From *T. arator* it can be distinguished by a relatively smaller and differently shaped rostral (Figs. 8, 10A) and fewer dorsal scales (465–513 versus 578–579). The rostral of *T. anousius* is narrower dorsally (RW1) and at the labial border (RW3) than that of its closest relative, *T. perimychus* (Fig. 10E); RW1/RL1 = 0.74–0.77 versus 0.79–1.05 in *T. perimychus*. *Typhlops anousius* is the most extreme all the species in the width of the upper arm of the anterior nasal: ANTNAS/RW1 = 0.40–0.64 versus 0.34–0.39 in *T. perimychus*. In its narrow rostral *T. anousius* is somewhat similar to *T. epactius*, although its rostral is narrower (RW1/RL1, 0.74–0.77 versus 0.78–0.85) and straighter sided. Additionally, *T. anousius* differs from *T. epactius* in its lack of pigment with the latter having normally pigmented scale rows 9–11 (neck-midbody), its shorter tail (TL/TA 55–56 versus 40–48) and in being somewhat heavier bodied (TL/MBD 45–55 versus 55–58), and in having 24 scale rows (reducing at 2% TL) rather than 22 (no reduction).

Description: Snout rounded, not lobed. Rostral straight-sided in dorsal aspect (RW1/RL1 0.74–0.77), not flared on apex or at labial border; no umbo. Preocular angle 105–126°, apex rounded; lower portion contacting labials 2 and 3 of upper labial series. Anterior nasal width as a proportion of RW1 0.40–0.64. OL 1/2 height, OS 0.22–0.24. The ocular below the eye is very narrow in the holotype, but not so narrow in the paratype, a juvenile, which may not be typical, since head scale shape undergoes some ontogenetic change in *Typhlops*. Rostronasal pattern strongly divergent. Postocular 3–4 times higher than long. First parietal standard, spanning 2 scale rows (short on left side of USNM 564783). Second parietal present and similar in size to the first or absent. TL to 197 mm. TL/TA 55–56. TL/MBD 45–55. Middorsal scales 465–513. Scale rows 24 reducing to 22 very far anteriorly (9–12 ventral scales posterior to mental), roughly 2% TL. Coloration: completely lacking in pigment except for the eye and a few melanophores in the orbit.

Distribution: Known only from the type locality, an extremely xeric ravine along the coast (Fig. 11).

Etymology: From the Greek, *anousios*, meaning without substance, ghostly, in reference to its lack of pigment.

Comments: The unusual lack of pigment in this species apparently is not related to its small size, in that the four specimens of *T. perimychus* that are smaller than the paratype of *T. anousius* are all pigmented. Although this species is most closely related to *T. perimychus* (confirmed by DNA sequence evidence; S. B. Hedges, unpublished) and the two species are separated by only 18 km (Fig. 11), their degree of morphological divergence (see diagnostic traits above) suggests that they are different species, and this is further supported by their sequence divergence.

Typhlops notorachius **new species (Figs. 8H, 9D–E)**

Holotype: MNHNCu 4551 (field tag number 191322), a male from 9.4 km W Imias, Guantánamo Province, Cuba, 5 meters, collected on 1 July 1990 by S. Blair Hedges, Richard Thomas, and Daniel McCallister.

Paratypes: USNM 564799, a male, same collection data as holotype; USNM 564797–798, Playitas de Cajobabo, Guantánamo Province, Cuba, 0 meters, collected on 1 August 1989 by Richard Thomas and S. Blair Hedges.

Diagnosis: A relatively large species of the *Typhlops biminiensis* group differing from *T. biminiensis* in having a rostral with an acuminate posterior edge, not broadly rounded. Also, the rostral has parallel sides and is not indented at apex of the snout (Fig. 8). Additionally, *T. notorachius* has a proportionately smaller rostral than the preceding species (*T. biminiensis*, *T. arator*, *T. perimychus*, and *T. anousius*) (Figs. 8, 10A). The difference in body size between *T. notorachius* and *T. perimychus* is striking; not considering the associated specimen of the latter species (which may be a different species), all four specimens of *T. notorachius* (282–301 mm TL) are larger than all 18 specimens of *T. perimychus* (130–280 mm TL). Because each species was collected at multiple localities and, in the case of *T. perimychus*, over four decades, we surmise that the body size difference is real and not the result of collecting bias. Also, *T. notorachius* differs from *T. perimychus* in having a greater anterior nasal width (ANTNAS/RW1): 0.42–0.53 versus 0.34–0.39 in *T. perimychus*. From *T. anousius*, *T. notorachius* also differs in its point of scale row reduction: 15–40% TL versus 2% TL in *T. anousius*.

Description: Snout smoothly rounded. Rostral broad and rounded in dorsal aspect, nearly as broad as long in most specimens (RW1/RL1 0.78–0.87), nearly straight-sided, parallel or widening somewhat posteriorly; not flared on apex; no labial flare. Anterior nasal width as a proportion of RW1 0.42–0.53. Preocular angle 108–120°, apex rounded; lower portion contacting labials 2 and 3 of upper labial series. OL 1/2 height, OS 0.23–0.34. Rostronasal pattern strongly divergent. Postocular 3–4 times higher than long. First parietal standard, spanning 2 scale rows or slightly less. Second parietal present and similar in width to the first or absent. TL to 301 mm. TL/TA 48–75. TL/MBD 45–57. Middorsal scales 475–529. Scale rows 24 reducing to 22 at 15–40% TL. Coloration bicolor with dorsal pigmentation (pale brown) fading ventrad anteriorly but ending abruptly by dropping out of pigmented scales posteriorly; 9 (mode) to 11 pigmented scale rows at midbody.

Distribution: Known only from the south coast of eastern (Oriente) Cuba, over an extent of about 27 km between the two known localities, east of Guantánamo Bay. The westernmost of the localities, 9.4 km W Imias, is about 30 km east of the type locality for *Typhlops anousius* (Fig. 11).

Etymology: An adjective made from the Greek, *notos*, south, and *rhachia*, shore, meaning “of the southern shore.”

The next new species having affinities with *T. biminiensis* also occurs on the southern coast of eastern Cuba. It may be known as

Typhlops contorhinus **new species (Figs. 8I, 9F)**

Holotype: MNHNCu 4552 (field tag number 191296), a male from 4.9 km S La Tinta, Guantánamo Province, Cuba, 5 meters elevation, collected on 29 June 1990 by Richard Thomas, S. Blair Hedges, Emilio Alfaro, and Daniel McCallister.

Diagnosis: A moderately large and slender species of the *T. biminiensis* group differing from all members of the species group in the Bahamas and Cuba in having a short rostral (Fig. 8), reflected in the high rostral indent (RI) value (Fig. 10F), and a large preocular apical diameter (Fig. 10C). The short rostral is also reflected in the width of the upper arm of the anterior nasal, which is relatively larger in *T. contorhinus* (ANT-

NAS/RW1 = 0.49) than other species in the group except *T. notorachius* and *T. anousius*. It further differs from *T. biminiensis* in having a rostral with an acuminate posterior edge, not broadly rounded, and a more slender body (TL/MBD 63 versus 39–51). It differs from *T. biminiensis*, *T. arator*, and *T. perimychus* in having a narrower rostral (Fig 10A) that is relatively broad on the apex of the snout (Fig. 8). From *T. perimychus*, it also differs in being larger (316 mm versus 280 mm TL), having more middorsal scales (502 versus 453–496), and a more slender body (TL/MBD 63 versus 41–59). In body shape, it is more slender (TL/MBD 63) than *T. notorachius*, *T. anousius*, and *T. arator* (Table 2). From *T. anousius*, it also differs in having scale row reduction at 31% TL rather than 2% TL. From *T. arator*, it further differs in having 24–22 scale rows rather than 26–24 rows and in having fewer middorsal scales (502 versus 578–579).

Description: Snout rounded, lobed. Rostral broad, nearly straight-sided in dorsal aspect, sides curving mesiad to apex (RW1/RL1 0.93), not flared on apex; moderate umbo; no labial flare. Anterior nasal width as a proportion of RW1 0.49. Upper wing of anterior nasals broad, preocular angle relatively small (98°), apex rounded; lower portion contacting labials 2 and 3 of upper labial series. OL 1/2 height, OS 0.24. Rostronasal pattern strongly divergent. Postocular very elongate by fusion (on each side) with a lower scale, extending well below bottom edge of ocular. First parietals relatively narrow and long (i.e., not transversely elongate), the width of two succeeding scale rows. Second parietals present and similar in size to the first. TL 316 mm. TL/TA 53. TL/MBD 63. Middorsal scales 502. Scale rows 24 reducing to 22 at 31% TL. Coloration bicolor with dorsal pigmentation (medium brown) ending abruptly along a midlateral or dorsolateral line by dropping out of pigmentation on individual scales, resulting in a jagged line of separation between pigmented and non-pigmented scales along almost all of the length; nine pigmented scale rows at midbody.

Distribution: Known only from the type locality, an otherwise xeric site along the Río Jauco in extreme eastern Cuba (Fig. 11).

Etymology: From the Greek, *kontos*, short, and *rhinos*, nose, an adjective meaning short-nosed.

The next new species having affinities with *T. biminiensis* occurs on the Maisi peninsula at the eastern end of Cuba. It may be known as

Typhlops anchaurus **new species (Fig. 8J)**

Holotype: MNHNCu 4553 (field tag number 190563), collected from within 1 km of Cueva de Agua (2.5 km airline NW Maisí), Guantánamo Province, Cuba on 31 July 1989 by Richard Thomas.

Diagnosis: A slender, moderate sized, and lightly pigmented species of the *Typhlops biminiensis* group distinguished from *T. biminiensis* in having a rostral with an acuminate posterior edge, not broadly rounded, and a more slender body (TL/MBD 63 versus 39–51). From *T. arator*, it differs in having 24–22 scale rows rather than 26–24 rows, in having fewer middorsal scales (514 versus 578–579), and in being more slender (TL/MBD 63 versus 51–55 in *T. arator*). From *T. perimychus*, it differs in having a greater number of middorsal scales (514 versus 453–496), a well-developed rostral protuberance (umbo), and a more slender body (TL/MBD 63 versus 41–59). From *T. anousius*, it differs in having scale row reduction at 31% TL rather than 2% TL and in having a relatively smaller upper arm of the anterior nasal (ANTNAS/RW1 = 0.36 versus 0.40–0.64 in *T. anousius*). The latter trait also distinguishes *T. anchaurus* from *T. notorachius* (0.42–0.53) and *T. contorhinus* (0.49). Additionally, *T. anchaurus* differs from *T. notorachius* in having a more slender body (TL/MBD 63 versus 45–57), and a well-developed umbo. From *T. contorhinus*, it also differs in having a relatively larger rostral (Fig. 10A), a smaller preocular apical diameter (Fig. 10C), relatively large eyes, and a smaller rostral indent (Fig. 10F).

Description: Snout tapering, somewhat pointed. Rostral broad and initially straight sided but curving smoothly towards apex (RW1/RL1 0.87), not flared on apex; umbo prominent and ventrally protuberant; no labial flare. Anterior nasal width as a proportion of RW1 0.36. Preocular angle 110°, apex rounded; lower portion contacting labials 2 and 3 of upper labial series on the left but supralabial 3 only on the right. OL 1/2 height, OS 0.23. Rostronasal pattern strongly divergent. Postocular low and relatively short, about 2 times higher than long. First parietal wide and wing-like, spanning 2. No second parietal. TL 240 mm. TL/TA 48. TL/MBD 63. Middorsal scales 514. Scale rows 24 reducing to 22 at 31% TL. Coloration bicolor but pigment very light, ending ventrad by dropping out of scales; seven pigmented scale rows along the body.

Distribution: Known only from the type locality at the extreme eastern tip of Cuba (Fig. 11).

Etymology: From the Greek, *anchauros*, greeting the dawn, in reference to the type locality at the extreme eastern tip of Cuba.

The last new species having affinities with *T. biminiensis* occurs in south-central Cuba. It may be known as

Typhlops satelles **new species (Fig. 8K)**

Holotype: SMF 61303, Rancho Luna, about 12 km airline S Cienfuegos, Cienfuegos Province, in south-central Cuba on 22 April 1966 by Z. Vogel.

Paratype: SMF 61304, same data as holotype.

Diagnosis: A slender and moderately large *Typhlops* of the *T. biminiensis* group. It differs from *T. biminiensis* in having a smaller rostral (Fig. 10A) with an acuminate posterior edge (Fig. 8K), a relatively short naris-eye distance (Fig. 10B), a more slender body (TL/MBD 62–75 versus 39–51), and scale row reduction at 11% TL instead of 50%. It differing from all other Cuban species of the group in having a more broadly rounded rostral scale in dorsal aspect that narrows less as it proceeds over the apex of the snout (Fig. 8K), and in its low rostral indent (Fig. 10F). Additionally, it differs from *T. perimychus* in having a greater number of middorsal scales (514–527 versus 453–496), scale row reduction at 11% TL instead of 50%, and a more slender body (TL/MBD 62–75 versus 41–59). From *T. arator* it differs in being more slender (TL/MBD 62–75 versus 51–55), having a shorter tail (TL/TA 61 versus 46–48), having scale row reduction at 11% TL instead of 34–41%, having 22–24 anterior scale rows instead of 26, having 22 posterior scale rows instead of 24, and having fewer middorsal scales (514–527 versus 578–579). From *T. anousius* it differs in being more slender (TL/MBD 62–75 versus 45–55), having scale row reduction at 11% TL instead of 2%, having a wider rostral scale (Fig. 10E), and having a relatively smaller upper arm of the anterior nasal (ANTNAS/RW1 = 0.32–0.33 versus 0.40–0.64). From *T. notorachius*, it differs in being more slender (TL/MBD 62–75 versus 45–47), having scale row reduction at 11% TL instead of 15–40%, and having a relatively smaller upper arm of the anterior nasal (ANTNAS/RW1 = 0.32–0.33 versus 0.42–0.53). From *T. contorhinus*, it differs in having scale row reduction at 11% TL instead of 31%, having a relatively smaller upper arm of the anterior nasal (ANTNAS/RW1 = 0.32–0.33 versus 0.49), and lacking a rostral umbo. From *T. anchaurus*, it differs in having scale row reduction at 11% TL instead of 31%, and lacking a rostral umbo.

Description: Snout rounded, somewhat down-turned with minimal umbo. Rostral broad and rounded in dorsal aspect, nearly as broad as long (RW1/RL1 0.98 in both specimens), with slight mucronation at tip; not flared on apex, apical width (RW2) 0.79–0.83 RW1; no labial flare, labial width (RW3) 0.69–0.76 RW1. Anterior nasal width as a proportion of RW1 0.32–0.33. Preocular angle 113–125°, apex not sharply angled; lower portion contacting labials 2 and 3 of upper labial series. OL 1/2 height, OS 0.20–0.28. Rostronasal pattern strongly divergent. Postocular 3.2–3.6 times higher than long. First parietal standard, spanning 2 scale rows. Second parietal present and similar in width to the first. TL to 350 mm. TL/TA 55–61. TL/MBD 62–75. Middorsal scales 514–527. Scale rows 24 reducing to 22 rows very far anteriorly at 11% TL or 22 rows not reducing. Coloration of holotype bicolor with dorsal pigmentation (pale brown) very restricted, so that viewed from above it appears as a narrow dorsal band 7 scale rows wide, ending along a jagged border by dropping out of pigmented scales. It is difficult to discern the pigment in the extremely desiccated paratype, but it appears to be the same as described for the holotype.

Distribution: Known only from the type locality, which is a public beach (0 m elevation) east of the inlet to the Bahia de Cienfuegos (Fig. 11).

Etymology: Satelles is Latin for guard or companion, a satellite, as *Typhlops satelles* may be regarded, also recalling the type locality.

Discussion

With the addition of these 11 new species, 40 species of *Typhlops* are now known from the West Indies. Based on these morphological data, previous morphological data for other species (Hedges & Thomas, 1991; Thomas, 1965;1968;1974;1976;1989), a phylogenetic framework based on morphology (Thomas, 1976;1989), and with some additional support from immunological (Hass, et al., 2001) and sequence analyses (S. B. Hedges, unpublished), two major divisions can be recognized: the *T. biminiensis* Group and a "Major Antillean Radiation." Within the latter, we provide names for eight species groups based on associations of species discussed above and in those studies.

The *T. hectus* Group (Hispaniola) consists of *T. agoralionis*, *T. hectus*, *T. sylleptor*, and *T. proancylops*. The *T. jamaicensis* Group (Jamaica and Hispaniola) is defined as including *T. capitulatus*, *T. gonavensis* Richmond, *and T. jamaicensis* Shaw. The *T. sulcatus* Group (Hispaniola) contains *T. sulcatus* Cope and *T. syntherus* Thomas. We define a *T. richardi* Group (Puerto Rico region, including Mona and Virgin Islands, and Caicos Islands) as consisting of *T. catapontus* Thomas, *T. granti* Ruthven and Gaige, *T. hypomethes* Hedges and Thomas, *T. monensis* Schmidt, *T. naugus* Thomas, elevated here to full species based on diagnostic traits in the original description (Thomas, 1965), *T. platycephalus* Duméril and Bibron, and *T. richardi* Duméril and Bibron. Our *T. dominicanus* Group (Lesser Antilles) contains *T. annae* Breuil, *T. dominicanus* Stejneger, *T. geotomus* Thomas, *T. guadeloupensis* Richmond, and *T. monastus* Thomas. We place *T. rostellatus* (Puerto Rico) in its own species group. The *T. pusillus* Group contains only *T. pusillus*, but that species is a complex of hidden species currently under examination (R. Thomas and S. B. Hedges, in preparation). The *T. lumbricalis* Group (Cuba, Hispaniola) contains *T. eperopeus*, *T. lumbricalis*, *T. schwartzi*, *T. tetrathyreus*, and *T. titanops*. The *T. biminiensis* Group (Cuba, Bahamas, Cayman Islands) contains *T. anchaurus*, *T. anousius*, *T. arator*, *T. biminiensis*, *T. caymanensis*, *T. contorhinus*, *T. epactius*, *T. notorachius*, *T. paradoxus*, *T. perimychus*, *T. satelles*, and *T. tasymicris* Thomas.

Discussion of detailed relationships and biogeographic inferences will be made elsewhere when DNA sequence analyses are presented. Nonetheless, the broad distribution of Hispaniolan species among the species groups of the Major Antillean Radiation suggests that this island was a center of evolution of the group. The position of *T. lumbricalis* (Cuba) nested within a clade of Hispaniolan species (*T. pusillus* and *T. lumbricalis* groups) suggests that it probably arose by dispersal from Hispaniola to Cuba. Likewise, the relationship of *T. jamaicensis* to two species that occur in southwestern Hispaniola (*T. capitulatus* and *T. gonavensis*), and considering the prevailing east-to-west ocean current flow, suggests that *T. jamaicensis* arose by dispersal from Hispaniola to Jamaica.

The geographic isolation of species on the Puerto Rican Bank suggests that they evolved during or subsequent to the glacial cycles of the Pleistocene (1.8–0.01 million years ago), during which there were extensive land connections at times of low sea level. The low immunological distances (one-way) between *T. platycephalus* and other species in this group (Hass, et al., 2001) are in agreement with such recent divergences. One-way immunological distances from *T. platycephalus* to members of other species groups in the Major Antillean Radiation (Hass, et al., 2001) are much larger. The average albumin immunological distance among the five clades at the base of the radiation is ~24 units, corresponding to an origin of those clades ~15 million years ago (middle Miocene). An early Cenozoic divergence estimate was obtained between *T. platycephalus* and a non-West Indian species, suggesting that the Major Antillean Radiation arose by an early dispersal from the mainland (Hass, et al., 2001; Hedges, 1996). However, one-way immunological distances are less reliable than reciprocal distances; the latter require the production and use of multiple antisera. Thomas (1989) suggested the possibility of an African connection for the Major Antillean radiation, based on possession of the characteristic preocular-ocular contact in an African species. Analyses of DNA sequences will be needed for additional insights into species relationships and to address broader questions concerning time of origin of the lineages in the Antilles and how they arrived in the context of Caribbean biogeography (Hedges, 1996; Hedges, 2001; Hedges, 2006; Iturralde-Vinent & MacPhee, 1999).

Acknowledgments

We thank the persons and institutions who assisted us in collecting and assembling the material used in this work, and each of the governments involved for permissions to collect and export specimens. In Cuba, we thank the National Museum of Natural History (Havana) and E. Alfaro, R. Arencibia, A. Perez-Asso, O. Perez-Beato, L. Diaz, A. Estrada, O. Garrido, L. L. Gonzalez, J. Moreno, J. Novo, and G. Silva. SBH thanks I. White for the opportunity to conduct fieldwork on the U. S. Naval base (Guantanamo Bay). In Haiti, we thank F. Sergile. In the Dominican Republic, we thank Y. Arias, H. Dominici, E. Fernandez, and S. Inchaustegui. On various trips where these snakes were collected we were assisted by C. A. Hass, M. Leal, D. McCallister, N. Plummer, and J. B. Pramuk. For loan of comparative material, we thank the Museum of Comparative Zoology at Harvard University (J. Cadle, J. Hanken, J. Rosado), National Museum of Natural History, Smithsonian Institution (T. Hartsell, R. Wilson, G. Zug,), the University of Kansas Natural History Museum (W. Duellman, J. Simmons, L. Trueb), and the Natural History Museum Senckenberg at Frankfurt (G. Köhler). This work as supported by grants from the National Science Foundation to SBH.

Literature cited

Breuil, M. (1999) Nouvelle espèce du genre Typhlops, (Serpentes, Typhlopidae) de l'île de Saint-Barthélemy, comparaison avec les autres espèces des Petites Antilles. *Bulletin Mensuel Société Linnéenne Lyon*, 68, 30–40.

Breuil, M. (2002) *Histoire naturelle des amphibiens et reptiles terrestres de l'archipel Guadeloupéen*. Muséum national d'Histoire naturelle, Paris, 339 pp.

Dixon, J.R. & Hendricks, F.S. (1979) The wormsnakes (Family Typhlopidae) of the Neotropics, exclusive of the Antilles. *Zoologische Verhandelingen*, 1–39.

Hass, C.A., Maxson, L.R. & Hedges, S.B. (2001) Relationships and divergence times of West Indian amphibians and reptiles: insights from albumin immunology. *In:* Woods, C.A. & Sergile, F.E. (Eds.) *Biogeography of the West Indies: Patterns and Perspectives.* CRC Press, Boca Raton, Florida, pp. 157–174.

Hedges, S.B. (1996) The origin of West Indian amphibians and reptiles. *In:* Powell, R. & Henderson, R.W. (Eds.) *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz.* Society for the Study of Amphibians and Reptiles, Ithaca, pp. 95–127.

Hedges, S.B. (2001) Caribbean biogeography: an outline. *In:* Woods, C.A. & Sergile, F.E. (Eds.) *Biogeography of the West Indies: Patterns and Perspectives.* CRC Press, Boca Raton, Florida, pp. 15–33.

Hedges, S.B. (2006) Paleogeography of the Antilles and the origin of West Indian terrestrial vertebrates. *Annals of the Missouri Botanical Garden*, 93, 231–244.

Hedges, S.B. & Thomas, R. (1991) Cryptic species of snakes (Typhlopidae: *Typhlops*) from the Puerto Rico Bank detected by protein electrophoresis. *Herpetologica*, 47, 448–459.

Iturralde-Vinent, M.A. & MacPhee, R.D.E. (1999) Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, 238, 1–95.

Leviton, A.E., Gibbs, R.H., Heal, E. & Dawson, C.E. (1985) Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*, 1985, 802–832.

Pough, F.H., Andrews, R.M., Cadle, J.E., Crump, M.L., Savitsky, A.H. & Wells, K.D. (2003) *Herpetology. Third Edition.* Prentice Hall, Upper Saddle River, New Jersey, 612 pp.

Powell, R., Henderson, R.W., Adler, K. & Dundee, H.A. (1996) An annotated checklist of West Indian amphibians and reptiles. *In:* Powell, R. & Henderson, R. (Eds.) *Contributions to West Indian Herpetology: a Tribute to Albert Schwartz*. Society for the Study of Amphibians and Reptiles, Ithaca, New York, pp. 51–93.

Richmond, N.D. (1955) The blind snakes (*Typhlops*) of Bimini, Bahama Islands, British West Indies, with description of a new species. *American Museum Novitates*, 1–7.

Schwartz, A. & Henderson, R.W. (1991) *Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history.* University of Florida Press, Gainesville, 720 pp.

Thomas, R. (1965) A reassessment of Virgin Islands *Typhlops* with the description of two new subspecies. *Revista de Biologia Tropical*, 13, 187–201.

Thomas, R. (1968) The *Typhlops biminiensis* group of Antillean blindsnakes. *Copeia*, 1968, 713–722.

Thomas, R. (1974) A new species of *Typhlops* (Serpentes: Typhlopidae) from Hispaniola. *Proceedings of the Biological Society of Washington*, 87, 11–18.

Thomas, R. (1976) *Systematics of Antillean blindsnakes of the genus Typhlops (Serpentes: Typhlopidae). Ph.D. dissertation*. Louisiana State University, Baton Rouge, 288 pp.

Thomas, R. (1989) The relationships of West Indian *Typhlops* (Serpentes: Typhlopidae) and the description of three new species. *In:* Woods, C.A. (Ed.) *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida, pp. 409–432.

Thomas, R., McDiarmid, R.W. & Thomapson, F.G. (1985) Three new species of threadsnakes (Serpentes: Leptotyphlopidae) from Hispaniola. *Proceedings of the Biological Society of Washington*, 98, 204–220.

Thomas, R. & Powell, R. (1994) *Typhlops pusillus*. *Catalogue of American Amphibians and Reptiles*, 595, 1–2.

Zug, G.R., Vitt, L.J. & Caldwell, J.P. (2001) *Herpetology. Second Edition.* Academic Press, San Diego, 630 pp.