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CRYPTIC SPECIES OF SNAKES (TYPHLOPIDAE: *TYPHLOPS*) FROM THE PUERTO RICO BANK DETECTED BY PROTEIN ELECTROPHORESIS

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ABSTRACT: An analysis of protein variation at 26 electrophoretic loci in the blindsnake *Typhlops richardi* inhabiting the Puerto Rico Bank revealed the presence of three cryptic species. One, *T. richardi*, is restricted to the Virgin Islands; the other two occur on Puerto Rico (and satellite islands) and are sympatric. The large and widely distributed Puerto Rican species takes the available name *T. platycephalus*. The small Puerto Rican species, known from northern and southeastern coastal localities and some satellite islands, is described herein as *T. hypomethes*. Except for body size, morphological differences distinguishing all three species are slight. *Typhlops richardi catapontus* from Anegada is raised to species level and *T. r. naugus* from Virgin Gorda is placed in its synonymy. Thus, the Puerto Rico Bank and adjacent Mona Island are inhabited by seven species of *Typhlops*: *T. catapontus*, *T. granti*, *T. hypomethes*, *T. monensis*, *T. platycephalus*, *T. richardi*, and *T. rostellatus*.

Key words: Serpentes; Typhlopidae; *Typhlops*; Caribbean; West Indies; Puerto Rico; Virgin Islands; Electrophoresis; Systematics

THE application of protein electrophoresis to systematic problems has been particularly rewarding in groups with conservative morphologies, such as amphibians. This technique is especially useful in the detection of cryptic species (e.g., Good, 1989; Highton and MacGregor, 1983; Karlin and Guttman, 1986; Larson and Highton, 1978). Among reptiles, burrowing forms also show subtle variation in external morphology, but there have been few molecular studies of intraspecific variation in those groups (Bezy et al., 1977; Hedges, 1989*a*). This is surprising considering the large size and wide distribution of some groups, such as the snake family Typhlopidae (140 species). This study is an example of the utility of protein electrophoresis in detecting cryptic species of burrowing reptiles, in this case blindsnakes of the genus *Typhlops* on the Puerto Rico Bank.

There are 17 species of *Typhlops* currently recognized in the West Indies (Thomas, 1989), and four of those occur in the Puerto Rico region: *T. monensis* Schmidt on Mona Island, *T. granti* Ruthven and Gaige and *T. rostellatus* Stejneger on Puerto Rico, and *T. richardi* Duméril and Bibron throughout the Puerto Rico Bank and on St. Croix and the Bahamas (Thomas, 1966, 1976). Four subspecies of *T. richardi* have been recognized in the past: *T. r. platycephalus* Duméril and Bibron on Puerto Rico, *T. r. catapontus* Thomas on Anegada, and *T. r. naugus* Thomas on Virgin Gorda (Thomas, 1966). However, the most recent taxonomic summary (Schwartz and Henderson, 1988) does not recognize subspecies within *T. richardi*. The finding of a population of unusually small *Typhlops* on the campus of the University of Puerto Rico (Río Piedras), otherwise very similar to *T. richardi*, prompted us to examine protein variation in *Typhlops* from the Puerto Rico Bank.

MATERIALS AND METHODS

Snakes were collected and brought to the laboratory alive for processing. Local abundance varied considerably, and thus sample size (1–14) depended upon availability. In the laboratory, they were killed by immersion in ice water, blood was taken for albumin immunological studies, and viscera (excluding gut contents) and skel-

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TABLE 1.—Protein loci and electrophoretic conditions.

Protein[1]	Locus	Enzyme Commission number[1]	Electrophoretic conditions[2]
1. Acid phosphatase	*ACP*	3.1.3.2	5
2. Aconitate hydratase	*ACON-1*	4.2.1.3	1
3. Aconitate hydratase	*ACON-2*	4.2.1.3	1
4. Adenylate kinase	*AK*	2.7.4.3	1
5. Aspartate aminotransferase	*AAT-1*	2.6.1.1	1
6. Creatine kinase	*CK-1*	2.7.3.2	6
7. Creatine kinase	*CK-2*	2.7.3.2	6
8. Glucose-6-phosphate isomerase	*GPI*	5.3.1.9	5
9. Isocitrate dehydrogenase	*ICD-1*	1.1.1.42	1
10. Isocitrate dehydrogenase	*ICD-2*	1.1.1.42	1
11. L-lactate dehydrogenase	*LDH-1*	1.1.1.27	3
12. L-lactate dehydrogenase	*LDH-2*	1.1.1.27	2
13. Lactoylglutathione lyase	*LGL*	4.4.1.5	6
14. Malate dehydrogenase	*MDH-1*	1.1.1.37	2
15. Malate dehydrogenase	*MDH-2*	1.1.1.37	2
16. Mannose-6-phosphate isomerase	*MPI*	5.3.1.8	5
17. Peptidase	*PEP-1*	3.4.13.11	4
18. Peptidase	*PEP-2*	3.4.13.11	4
19. Phosphoglucomutase	*PGM*	5.4.2.2	3
20. Phosphoglucose dehydrogenase	*PGD*	1.1.1.44	5
21. Protein 1	*PT-1*	—	4
22. Protein 2	*PT-2*	—	4
23. Protein 3	*PT-3*	—	3
24. Protein 5	*PT-5*	—	3
25. Pyruvate kinase	*PK*	2.7.1.40	1
26. Superoxide dismutase	*SOD*	1.15.1.1	3

[1] International Union of Biochemistry, Nomenclature Committee (1984).

[2] (1) Tris-citrate pH 8.0, 130 v, 6 h; (2) Tris-citrate pH 6.7, 150 v, 6 h; (3) Poulik, 400 v, approximately 7 h; (4) Lithium hydroxide, 400 v, approximately 8 h; (5) Tris-versene-borate, 250 v, 6 h; (6) Tris-HCl, 250 v, 4 h.

etal muscle (including some bone) were removed for electrophoresis. We preserved the remaining carcass in 10% formalin, transferred it later to 70% ethanol, and deposited it in the United States National Museum of Natural History (USNM).

We sampled the following populations: (1) 1.5 km W Playa de Tamarindo on the W shore of Bahia de la Ballena ($n = 6$); (2) 5.7 km WNW Sabana Grande ($n = 2$); (3) 12.3 km SSE Arecibo ($n = 10$); (4) 6 km (airline) SSE Dorado ($n = 5$); (5) Carolina, Barrio Cedros ($n = 1$); (6) 5 km S Mameyes ($n = 1$); (7) 3.5 km NW (airline) Mameyes, large form ($n = 1$); (8) Isla Vieques, Puerto Real ($n = 1$); (9) Río Piedras, on the campus of the University of Puerto Rico ($n = 14$); (10) 6.1 km W Playa de Vega Baja ($n = 3$); (11) Bosque de Aguirre and distal part of Peninsula de Jobos ($n = 4$); (12) Punta Tuna, approximately 3 km SSE (airline) Maunabo ($n = 1$); (13) 3.5 km NW (airline) Mameyes, small form ($n = 1$); (14) U.S. Virgin Islands, St. Thomas, Dorothea Estate, approximately 0.5 km S Dorothea Bay ($n = 2$); and (15) U.S. Virgin Islands, Bolongo ($n = 1$). The two other species of *Typhlops* from the Puerto Rico Bank, *T. granti* (Campamento Santiago, Bosque Estatal de Guanica, $n = 1$) and *T. rostellatus* [12.3 km (airline) SSE Arecibo, $n = 1$], were included for comparison. *Typhlops rostellatus* also was used to provide a root for the parsimony analysis. Its phylogenetic position outside of the other species from the Puerto Rico Bank is based on differences in scalation and hemipene morphology (Thomas, 1989) as well as albumin immunological distances (Hass and Hedges, unpublished data). Preparation of samples and electrophoretic methods followed procedures described elsewhere (Hedges, 1986). The 26 protein loci examined and electrophoretic conditions are listed in Table 1.

Allelic data were analyzed using two genetic distance methods. Nei's (1978) unbiased genetic distances were subjected to UPGMA (Sneath and Sokal, 1973) clustering. Cavalli-Sforza and Edwards (1967)

TABLE 2.—Nei's (1978) unbiased genetic distances above diagonal, Cavalli-Sforza and Edwards's (1967) chord distances below diagonal, and mean heterozygosities along diagonal.

	Population[1]							
	1	2	3	4	5	6	7	8
1. *platycephalus*	(0.12)	0.05	0.06	0.06	0.14	0.18	0.10	0.12
2. *platycephalus*	0.24	(0.04)	0.02	0.02	0.08	0.12	0.10	0.12
3. *platycephalus*	0.22	0.16	(0.08)	0.04	0.06	0.12	0.10	0.12
4. *platycephalus*	0.23	0.18	0.16	(0.07)	0.04	0.14	0.08	0.10
5. *platycephalus*	0.33	0.28	0.23	0.20	(0.00)	0.18	0.18	0.22
6. *platycephalus*	0.37	0.34	0.31	0.34	0.38	(0.12)	0.12	0.13
7. *platycephalus*	0.30	0.30	0.28	0.26	0.37	0.31	(0.04)	0.02
8. *platycephalus*	0.34	0.34	0.32	0.31	0.41	0.33	0.16	(0.08)
9. new species	0.40	0.38	0.37	0.41	0.50	0.42	0.40	0.40
10. new species	0.40	0.39	0.37	0.41	0.50	0.43	0.40	0.40
11. new species	0.38	0.37	0.35	0.40	0.48	0.41	0.39	0.39
12. new species	0.39	0.37	0.36	0.40	0.49	0.41	0.39	0.39
13. new species	0.40	0.39	0.37	0.41	0.50	0.43	0.41	0.41
14. *richardi*	0.56	0.56	0.54	0.54	0.59	0.52	0.47	0.48
15. *richardi*	0.54	0.55	0.53	0.53	0.59	0.50	0.45	0.46
16. *granti*	0.47	0.46	0.44	0.46	0.53	0.50	0.44	0.45
17. *rostellatus*	0.67	0.67	0.67	0.69	0.71	0.71	0.71	0.71

[1] See text for location of populations.

chord distances were used with the distance Wagner procedure (Farris, 1972) employing the multiple addition criterion (Swofford, 1981). A more complete discussion of these distances and methods is presented elsewhere (Hedges, 1986, 1989*b*). The genetic distance data were analyzed with BIOSYS-1 (Swofford and Selander, 1981).

Confidence estimates for groupings in the phylogenetic trees were obtained with the bootstrap method (Felsenstein, 1985). BIOSYS-1 was modified by S.B.H. to perform bootstrapping and generate 100 bootstrapped trees each for the UPGMA and distance Wagner analyses. During each cycle, loci were treated as characters and sampled randomly with replacement, a matrix of genetic distances was generated from the new sampling of loci, and a tree was constructed from the distance matrix. After 100 of these bootstrapped trees were generated by the program, the number (= percentage) of trees supporting each cluster was determined manually. Instead of presenting a majority-rule consensus tree of the results (Felsenstein, 1985), we present here the original genetic distance tree of all loci, with confidence limits indicated on each cluster. In this way, the confidence limits (>50%) and branch-length information are presented together.

The following abbreviations are used: HL (head length), HW (head width), MBD (midbody diameter), SVL (snout–vent length), TA (tail length), and TL (total length). Museum abbreviations follow standardized usage (Copeia 1985:802–832) except for ASFS (Albert Schwartz field series) and RT (Richard Thomas field series).

RESULTS

Five loci (*ACP*, *CK-1*, *ICD-2*, *PT-2*, and *SOD*) were monomorphic. Allelic variation among the 17 populations of *Typhlops* for the 21 variable loci is presented in Appendix I. Genetic distances and average heterozygosities are given in Table 2.

Both the phenogram (Fig. 1) and distance Wagner tree (Fig. 2) indicate the presence of three distinct clades among the populations of *T. richardi*. All populations from Puerto Rico and the adjacent island of Vieques form a single group. However, within that group, there are two distinct clusters, one representing a "small form" (five populations) and the other representing a "large form" (eight populations). In both trees *T. granti* is the sister species to the cluster of small and large Puerto Rican forms. The two populations from St. Thomas cluster, and are a sister group to the group containing *T. granti* and the small and large forms. *Typhlops rostella-*

TABLE 2.—Continued.

Population[1]								
9	10	11	12	13	14	15	16	17
0.19	0.19	0.17	0.18	0.19	0.47	0.43	0.30	0.77
0.17	0.17	0.14	0.16	0.18	0.49	0.44	0.28	0.78
0.18	0.18	0.15	0.16	0.18	0.46	0.42	0.27	0.79
0.23	0.22	0.20	0.21	0.23	0.44	0.41	0.31	0.87
0.36	0.36	0.34	0.35	0.37	0.55	0.54	0.43	0.96
0.25	0.25	0.23	0.24	0.26	0.40	0.37	0.37	0.93
0.22	0.22	0.20	0.21	0.23	0.32	0.28	0.28	0.95
0.21	0.21	0.19	0.20	0.22	0.33	0.29	0.29	0.94
(0.04)	0.05	0.01	0.06	0.01	0.44	0.40	0.24	0.70
0.21	(0.06)	0.03	0.09	0.06	0.44	0.43	0.20	0.65
0.13	0.17	(0.05)	0.04	0.01	0.42	0.38	0.20	0.65
0.22	0.26	0.19	(0.08)	0.06	0.44	0.39	0.24	0.67
0.13	0.21	0.12	0.22	(0.00)	0.43	0.38	0.26	0.69
0.54	0.54	0.53	0.54	0.53	(0.12)	0.02	0.46	0.98
0.52	0.53	0.52	0.52	0.51	0.14	(0.04)	0.44	1.05
0.42	0.40	0.41	0.42	0.43	0.55	0.54	(0.00)	0.77
0.64	0.63	0.64	0.64	0.64	0.71	0.73	0.66	(0.00)

tus was the most distant species in the phenogram.

In the phenogram (Fig. 1), bootstrap confidence estimates support the groups containing the small form, large form, and St. Thomas populations (80%, 95%, and 100%, respectively), as well as some other clusters. The placement of *T. rostellatus* as the most distant taxon is strongly supported (99%). The confidence estimate for the small form in the distance Wagner tree is equally as high (97%), but other clusters are not as strongly supported as those in the phenogram. The relationships of populations within the large and small forms differ slightly between the two trees (Figs. 1 and 2). Also, confidence estimates for groupings within the large and small forms are low, except for the cluster of populations 7 and 8.

DISCUSSION

The protein data clearly indicate the presence of three cryptic species among populations previously considered to be a single species, *Typhlops richardi*. Two of these occur on Puerto Rico: a large (approximately 280 mm SVL), widely dis-

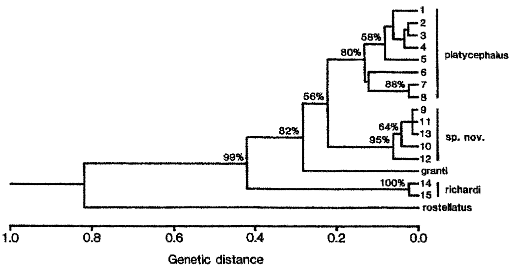

FIG. 1.—Phylogenetic tree of 17 populations of *Typhlops* from the Puerto Rico Bank constructed by the UPGMA Method using Nei's (1978) unbiased genetic distances. Numbers on tree are bootstrap confidence estimates (>50%) for groupings. Goodness-of-fit values are 0.96 (cophenetic correlation coefficient) and 14.9 (Prager and Wilson's [1976] *F*-value). Numbered localities (see text) are those populations previously placed under a single species, *T. richardi*.

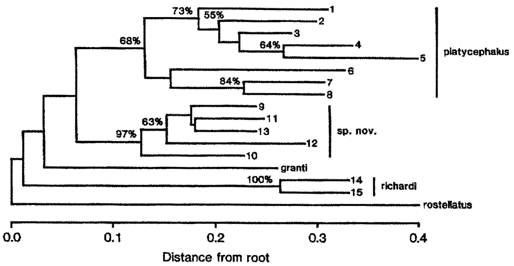

FIG. 2.—Phylogenetic tree of 17 populations of *Typhlops* from the Puerto Rico Bank constructed by the distance Wagner method using Cavalli-Sforza and Edward's chord distance and the multiple addition criterion, and rooted with *T. rostellatus*. Numbers on tree are bootstrap confidence estimates (>50%) for groupings. Goodness-of-fit values are 0.97 (cophenetic correlation coefficient) and 8.4 (Prager and Wilson's *F*-value).

tributed species which also occurs on Vieques and other satellite islands of Puerto Rico, and a small (approximately 190 mm SVL) species presently known only from northern and southeastern coastal areas, Vieques, and two other satellite islands off of eastern Puerto Rico. The large species usually is darker and often has a light tail band. Both are similar in scalation and cannot be separated by any single scale character or count, although there are subtle differences in head proportions (see below). They are sympatric along the northern coast of Puerto Rico and on Vieques. The third species is known only from the Virgin Islands and is similar in size to the large Puerto Rican species but usually lacks a tail band and has a narrower rostral scale.

Although the confidence limits for the large *Typhlops* from Puerto Rico are below 95%, the primary evidence that it and the small form are distinct species is their sympatry on Puerto Rico (and Vieques), and with no apparent hybridization. The Virgin Islands form is allopatric with the other two, but it is more distant (genetically) than those two species and *T. granti* (Figs. 1, 2), suggesting that it also is a distinct species. *Typhlops granti* is restricted to southwestern Puerto Rico and is sympatric with the large form. Additional evidence for the species-level status of these *Typhlops* is their level of genetic differentiation compared with other groups using Nei's genetic distances (Table 2). In a literature survey of over 8000 genetic distances from plant and animal groups, Thorpe (1982, 1983) found that 98% of intraspecific genetic distances are below 0.10 and 98% of interspecific distances are above 0.15. In this study, the small and large *Typhlops* from Puerto Rico are separated by an average Nei's D of 0.22, and both are separated from the Virgin Islands form by a D of 0.42. This level of differentiation provides additional support for their recognition as separate species.

The type locality of *T. richardi* is St. Thomas, U.S. Virgin Islands. Thus the name *richardi* applies only to the species represented by our populations on St. Thomas (localities 14 and 15). The name *platycephalus* Duméril and Bibron (revised type locality = Puerto Rico, see below) is available for one of the two Puerto Rican species. We have examined the type specimen of *T. platycephalus* (MNHN 1066), and it is a large animal (284 mm SVL) that agrees in other aspects with the large form. Therefore the name *T. platycephalus* clearly applies to the large and widespread Puerto Rican species. The small coastal species from Puerto Rico is described in the following taxonomic account.

Typhlops **hypomethes** sp. nov.

Holotype.—USNM 300574, an adult female, collected on the University of Puerto Rico Campus (faculty housing), Río Piedras, San Juan, Puerto Rico, 19 November 1986 by Richard Thomas.

Paratypes.—Puerto Rico: RT 10162-64, 7.0 km W Palmas Altas; RT 10082, Bosque de Cambalache, 10 km W Manatí; RT 8795, E end, Laguna Tortuguero; UPRRP 2204, Hato Tejas; UPRRP 4603, 4605, Bayamón; RT 6642, Cataño, near Isla de Cabras Causeway; ASFS V5943 (cleared and stained), USNM 300588–590, 3.5 km (road) W Playa de Vega Baja; RT 9161, Ocean Park, San Juan; RT 5635, 7039, 7053–56, 7059, 7082, 7109–10, 8118, 8141, 8143–44, 8282, 8775–76, 8829, 9043, 9045, 9121, 9137, 9374, 9406–08, 9425–27, 9429–30, 9557–58, 9560–69, 9574–78, 9627–35, 9638–40, 9650, 9674, 9676–77, 9679–80, 9865–66, 9895, 9909, 9969–70, 9973–76, 9983, UPRRP 4744, 4607, 10119–21, 10095, USNM 300575–582, University of Puerto Rico Campus, Río Piedras; RT 9673, Calle Sorbona, University Gardens, Río Piedras; UPRRP 3642, Río Piedras; RT 4885, Punta Vácia Talega; RT 6419–21, approximately 2 km W Punta Vácia Talega; UPRRP 2316, across Río Loíza from Central Loíza; USNM 300591, 3.5 km NW Mameyes; RT 6415, 2.5 km airline N Las Croabas, eastern shore, Cabezas de San Juan; RT 6417, Isla Palominos; UPRRP 3756, 3774, 3787, Isla Piñeros: RT 9194, Isla Vieques, limestone headland just east of Ensenada Sombe; RT 9322–23, 9325, Isla Vieques, the base of Cerro Martineau; 9652–53, Isla Vieques, vicinity of Monte Pirata; USNM 300587, Punta Tuna; RT 4106, approximately 2.5 km WSW Las Mareas (= approximately 1 km E Pozuelo), base of Península de Jobos; RT 9577–78, USNM 300583–586, Bosque de Aguirre, distal part of Península de Jobos; RT 8602, Cerro del Muerto, 1.5 km ESE Las Ollas.

Diagnosis.—A small, relatively slender, round-snouted species of *Typhlops* having the preocular in contact with only the 3rd of the upper labials; a moderate, slightly obovate to oval rostral with no apical flare; reduced prootic lappet (single 5th cranial nerve foramen), triradiate pelvic moieties, attenuate hemipenes, bicolor pigmentation (light gray-brown) with frequent piebalding ("dropping out" of pigmented scales), and no tail band.

Description (following format of Thomas, 1989).—(1) Head narrow but not tapering, snout rounded on apex (not ogival). (2) Rostral moderate in dorsal aspect (rostral width/rostral length = 0.49–0.60, $\bar{x}$ = 56, n = 7), labial flare slight, no apical flare but expansion reaching widest point dorsoposterior to apex and tapering slightly towards posterior point (weakly obovate to oval; rostral papilla lanceolate). (3) Preocular subtriangular, angle 65–80 deg ($\bar{x}$ = 73.6, n = 15), contacting only the 3rd of the upper labials. (4) Ocular roughly 60–70% as long as high; sinuosity slight, 0.05–0.17. (5) Rostronasal pattern divergent. (6) Postoculars two (cycloid), occasionally one. (7) First parietal standard, width spanning two scale rows. (8) Second parietal present and equal to first or undifferentiated (isomorphic with following scales). (9) TL to 270 mm. (10) TL/TA = 35–47. (11) TL/MBD = 41–56 ($\bar{x}$ = 45.6, n = 23). (12) Middorsals = 363–407 ($\bar{x}$ = 387, SE = 1.99, n = 27). (13) Scale rows 22 reducing to 20 at 42–49% of SVL (not counting irregular reductions). (14) Color pale gray-brown on dorsalmost 9–11 scale rows; many specimens with scattering of unpigmented scales, especially on the head and neck, producing a piebald appearance; no specimens with well-formed unpigmented tail band, although some have an unpigmented notch or weak band; transition to unpigmented venter is a combination of ventrad fading (reduced pigment density) and dropping out of individual scales producing a jagged edge. (15) Rectal caecum present. (16) Hemipenes attenuate. (17) Cranium broad, width across prefrontals about 92% width across prootics. (18) Premaxilla broad, about 44% of width across prefrontals, straight anteriorly, not protuberant; posteroventral edges transverse, making a curved but right angle juncture with blade; blade hastate (slightly constricted basally); median ventral eminence low, rounded. (19) Nasals without lateral angle. (20) Septomaxilla with hook, tapered anteriorly. (21) Frontal–parietal suture transverse, slightly sinuous. (22) Frontal without bladelike or wedgelike ventromedial processes. (23) Optic foramen canalicular. (24) Postorbital process of parietal moderate. (25) Parietal without temporal ridges. (26) Trigeminal foramen: tongue of prootic abuts parietal; lappet of prootic extremely reduced; no secondary foramen (Thomas, 1989). (27) Supraoccipitals unfused, in broad median contact. (28) Exoccipitals not fused with prootics. (29) Angular moderate (not sliverlike). (30) Dorsal process of quadrate not hooked. (31) Atlantal hypapophysis small, knoblike, axial hypapophysis long, carinate (= 2 fused); total hypapophyses = 3. (32) Hyoid of two ossified ceratohyals nearly in contact at their anterior ends and joined by a very small Y-shaped cartilaginous basihyal. (33) Pelvic moieties tripartite (attenuate, cartilaginous pubis and ilium and rodlike ossified ischium); hypoischium not seen, possibly lost in preparation. (34) Eye moderately prominent, set into fleshy orbit, 42–57% diameter of subconical, lightly pigmented fleshy orbit, lens just beneath ocular surface; no bulge in ocular.

Data for holotype.—An adult male with partly everted hemipenes; TL = 201 mm, TA = 5 mm, HL = 5.8 mm, HW = 2.8 mm, MBD = 5.1 mm; middorsal scales = 377; reduction from 22 to 20 scale rows occurring 94 and 96 mm posterior to snout; postoculars = 2/2; parietals = 1/1.

Distribution.—The eastern periphery of Puerto Rico (Fig. 3); known from 7.0 km W Palmas Altas and the Bosque de Cambalache east along the north coast and around the eastern end of the island to nearly midway along the south coast (Cerro del Muerto). Most of the localities are coastal, the interiormost ones being Hato Tejas, Bayamón, Río Piedras, and Trujillo Alto. The range may extend somewhat far-

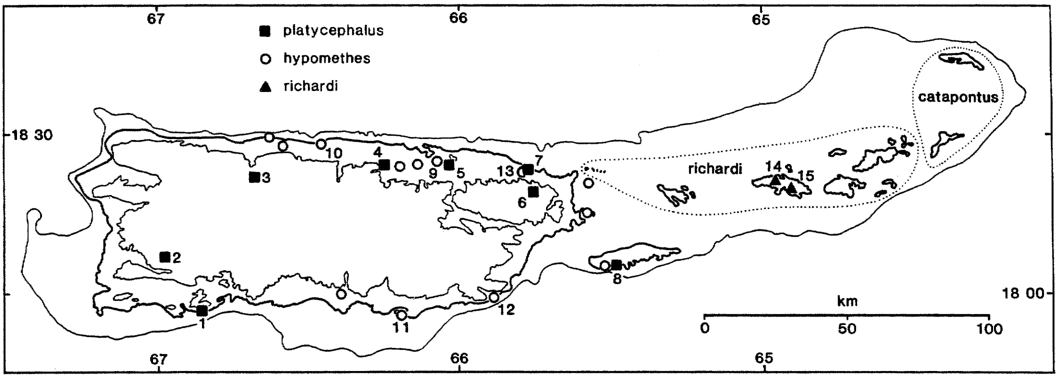

FIG. 3.—The Puerto Rico Bank, showing localities of *Typhlops* sampled in this study. Open circles = *T. hypomethes* (including all known localities), solid squares = *T. platycephalus*, and solid triangles = *T. richardi*. The solid narrow lines = −100 m (surrounding the bank) and +100 m (within Puerto Rico). The ranges of *T. richardi* (excluding Bahamas and St. Croix) and *T. catapontus* are indicated.

ther west along both coasts but probably does not go west of Arecibo in the north or Ponce in the south. Also occurs on the eastern islands of Palominos, Piñeros, and Vieques.

Comparisons.—The pertinent comparisons of the new species are with the other members of the Puerto Rico group of *Typhlops* (*catapontus*, *granti*, *monensis*, *platycephalus*, and *richardi*; Fig. 4) with which it shares the major morphological feature of attenuate hemipenes. *Typhlops granti* is the most extreme of this group morphologically: it is smaller, more slender (TL/MBD 54–60), has few scale rows (18–16), a truncate snout, and broader rostral. *Typhlops monensis* has both low longitudinal counts (302–345) and fewer scale rows (20–18); in details of head scalation it more closely resembles *platycephalus*. Among the other species, the major differentiating features are head size, snout shape, and rostral shape. *Typhlops hypomethes* cannot be distinguished from the sympatric *platycephalus* in middorsal scales, nor in scale rows or reduction level, although it is more variable in reduction level. From *platycephalus*, *hypomethes* differs in its smaller size and narrower head (Fig. 5). Its snout is rounded, whereas that of *platycephalus* is narrower (depressed) and more pointed; the rostral scale of *hypomethes* does not widen on the apex of the snout and then narrow dorsally, as does that of *platycephalus* (Fig. 6); rather, the scale reaches its widest point dorsal to the anterior nasal–postnasal suture and then narrows gradually towards its posterior tip; the result is a weakly obovate scale in dorsal view (Fig. 6). The rostral of *platycephalus* typically becomes very broad over the apex of the snout (widest point at the anterior nasal–postnasal suture), narrows, then expands before the tip giving it a guitar shape. There is variation such that some rostrals narrow monotonically towards the tip, and a few are very similar to the oval rostral of *hypomethes*. Aside from small head size, one of the best features for field identification with the naked eye or low magnification is the shape of the pigmented papillas of the rostral and postnasal scales (Fig. 6); in *platycephalus*, the rostral papilla is wide anteriorly with the pale glandular margins of the scale diverging; the rostral papilla of *hypomethes* is narrower anteriorly, then narrowing posteriorly to a thin spire, with glandular margins curving mesially. A deeply pigmented parenthesis of the postnasal papilla encloses the rostral papilla in a pincerlike fashion. The rostral scale of *hypomethes* is flat on the apex and does not protrude, as it does in adult *platycephalus*, so the head shape in dorsal aspect is broadly rounded, that of *platycephalus* "ogival" (Fig. 6). Juvenile *platycephalus*, however, have rounded snouts, but the rostral shape difference is still evident in its narrowing just posterior to the apex of the snout. *Typhlops hypomethes* is similar to *richardi* in its rounded snout and obovate

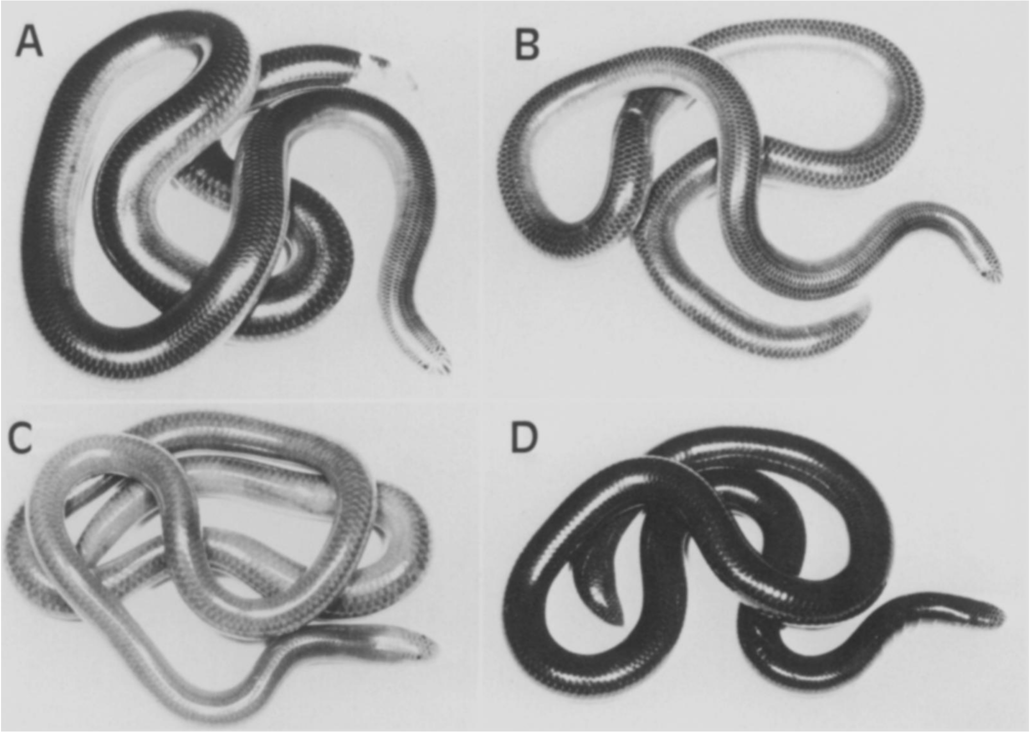

FIG. 4.—The four species of *Typhlops* from the main island of Puerto Rico. (A) *T. platycephalus*, 12.3 km (airline) SSE Arecibo; (B) *T. hypomethes*, Bosque de Aguirre and distal part of Península de Jobos; (C) *T. granti*, Bosque Estatal de Guánica, Campamento Santiago; and (D) *T. rostellatus*, 12.3 km (airline) SSE Arecibo.

to oval rostral shape; the main rostral shape difference is the noticeable labial flare in *richardi* and its lack in *hypomethes* (Fig. 6). From *richardi, hypomethes* differs also in its smaller size, smaller head (Fig. 5), and higher middorsal scale counts, although *richardi* is variable geographically in this regard. In skeletal characters, *hypomethes* differs from *platycephalus* in that the lappet of the prootic is vestigial, resulting in a single foramen for the trigeminal nerve; in *platycephalus* the lappet is fused with the tongue thereby isolating a secondary foramen; in *richardi*, the lappet is reduced and does not contact the tongue, but the two projections approximate one another enough so that a secondary foramen appears as a diverticulum. The premaxilla of *hypomethes* has a basally constricted (spearlike) blade that meets the posteroventral edge at a right angle; the blade of both *richardi* and *platycephalus* are broad and triangular, that of

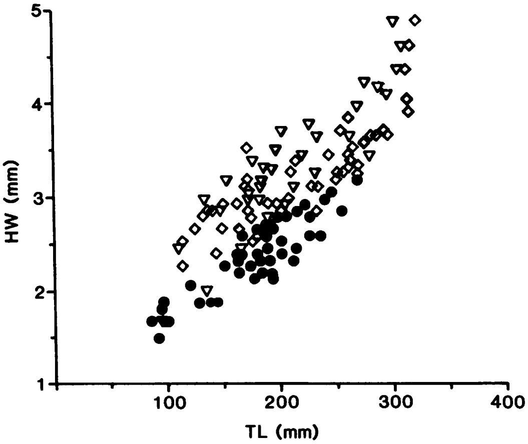

FIG. 5.—Graph of headwidth (HW) vs. total length (TL) in some *Typhlops* from the Puerto Rico Bank. Filled circles, *T. hypomethes*; open squares, *T. platycephalus*; triangles, *T. richardi* and *T. catapontus*.

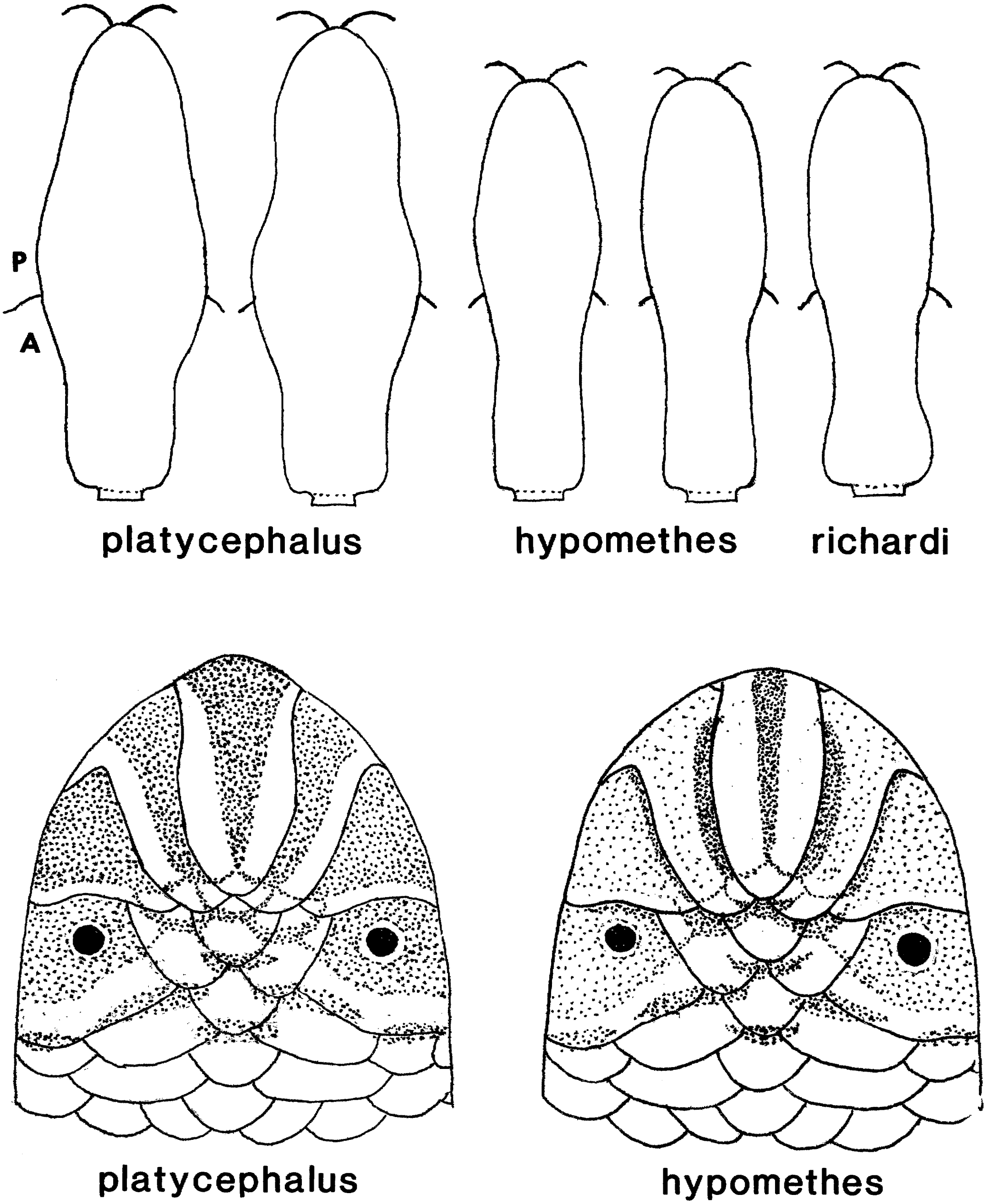

FIG. 6.—Above, common rostral shapes of *T. platycephalus*, *T. hypomethes*, and *T. richardi* (drawn as though flattened); lower edge (dotted line) is the labial border, P is the postnasal, and A is the anterior nasal; below are semidiagrammatic representations of head scalation and coloration in *T. platycephalus* and *T. hypomethes*.

richardi meeting the posteroventral edge of the premaxilla in a broadly curving juncture. The median eminence of the premaxilla is prominent in *richardi*, low and rounded in *platycephalus* and *hypomethes*. The hyobranchium of *hypomethes* has a very small Y-shaped cartilaginous basihyal; that of *richardi* is small but not so reduced, whereas that of *platycephalus* is well-developed. The hypapophysis of the atlas is small and knoblike in *hypomethes* but tablike (dorsoventrally flattened) in *richardi* and *platycephalus*; there are two unfused hypapophyses on the axis of *platycephalus* and *richardi*; in *hypomethes*, they are fused producing a prominent bladelike structure. These osteological comparisons are based on examination of one cleared and stained specimen each of *hypomethes* and *richardi*, and three specimens of *platycephalus*. The stability of the character states is inferred from the examination of 55 cleared and stained specimens of West Indian *Typhlops* (Thomas, 1976).

From *T. catapontus*, *hypomethes* is distinguishable by its one-step scale row reduction. *Typhlops catapontus* reduces from 22 to 20 scale rows far anteriorly at about 10–30% of the SVL and then has a second reduction step from 20 to 18 rows posterior to midbody (60–70% SVL); *catapontus* is also broader headed and larger than *hypomethes*. Piebalding on the head and anterior body, present in about 70% of the *hypomethes*, is virtually absent in *platycephalus*, *richardi*, and *catapontus*, although *catapontus* has fewer pigmented scale rows.

Comments.—We consider *Typhlops richardi* to occupy all but the easternmost of the Virgin Islands, Virgin Gorda and Anegada, extending west through Culebra and its cays (known from cayos Luís Peña and Norte). The snakes from Cayo Diablo and Surprise Cay (both close to one another in the string of cays called La Cordillera just east of Puerto Rico) we provisionally refer to *richardi* because of their large size and head width; the populations on these cays need to be more thoroughly sampled to evaluate their taxonomic status. Similar comments apply to the Vieques *Typhlops* identified as *platycephalus*. We use the name *Typhlops catapontus* for the populations on Anegada and Virgin Gorda, provisionally relegating *richardi naugus* to its synonymy. A more exhaustive study of variation in the *Typhlops* of the islands east of Puerto Rico is needed.

Although *hypomethes* resembles *richardi* in snout and rostral shape, it is close to *platycephalus* in certain other features: middorsal counts and the occurrence of tail banding (even though infrequent), suggesting, as do the allozyme data, that *hypomethes* and *platycephalus* share a more recent common ancestor with one another than with any of the other species.

Typhlops platycephalus was originally described (Duméril and Bibron, 1844) as having come from Martinique. Stejneger (1904) deduced that the type material of the Puerto Rican *Diploglossus pleei*, *Anolis cristatellus*, *Anolis pulchellus*, and *Typhlops platycephalus* were transshipped by Plée through Martinique and thus mistakenly ascribed to that island when the species were described (Duméril and Bibron, 1837, 1844). Since neither Stejneger (1904) nor Ruthven and Gaige (1935) appear to have examined the types, we borrowed the holotype of *T. platycephalus* and syntype of *T. richardi*. The latter was described as having come from St. Thomas, Virgin Islands, and, although there has never been any reason to question its provenance, we can confirm that it agrees in size, proportions, rostral shape, and scale counts with the St. Thomas *richardi* (TL = 172 mm, TA = 4.5, HL = 6.2, middorsal scales = 332, scale rows reduce from 22–20 at 32% SVL, reduction to 18 rows at 95% SVL). The holotype of *platycephalus* agrees with the larger of the Puerto Rican species in details of rostral shape, size (TL = 291 mm, TA = 7.0), middorsal scales (365), reduction (22–20 at 51% SVL), and HL (6.2 mm). It does not have a tail band, however, which indicates that it came from eastern, southern, or interior Puerto Rico.

Etymology.—We use *hypomethes* by analogy with the Greek promethes, forethinking, and epimethes, afterthinking, to mean below thinking, a double allusion to having been passed over (not thought about), and to the occurrence of the topotypical population on a university campus.

Specimens examined.—*Typhlops platycephalus*: MNHN 1066 (holotype), approximately 200 specimens from the main island of Puerto Rico; UPRRP 3602, Isla Palominos; RT 7107, Isla Vieques, Puerto Real; 9625, Isla Vieques, near Isabel II (Santa Maria); RT 9651, 9654, Isla Vieques, vicinity of Monte Pirata; RT 9913, Isla Vieques, Tablón, Camp Garcia; RT 9324, 10127–28, Isla Vieques (no other data). *Typhlops richardi*: MNHN 3220 (syntype) *Typhlops* cf. *richardi*: UPRRP 3946, La Cordillera, Surprise Cay; UPRRP 3532–33, RT 6334–35, La Cordillera, Cayo Diablo; UPRRP 5059, Cayo Norte (near Culebra).

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APPENDIX I

Allelic Variation in Typhlops *from the Puerto Rico Bank at 21 Polymorphic Loci*

Locus	Population[1]																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
ACON-1	b (0.58) c (0.42)	b (0.25) c (0.75)	b (0.35) c (0.65)	c	b	c	b	b	c	c	c	c	b	b	b	a	c
ACON-2	c	c	c	c	c	c	c	c	c	c	c	c	c	b	b	a	c
AK	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b
AAT-1	a	a	a	a	a	a	a	b	a	b	a	a	b	b	b	a	a
CK-2	b	b	b	a	b	a	b	b	a	b	a	a	b	a	a	a	a
GPI	e	d (0.25) e (0.75)	e	c (0.33) e (0.67)	e	a (0.25) e (0.75)	e	e	e	e	e	c (0.13) e (0.87)	e	e	e	b	b
ICD-1	a (0.08) b (0.92)	b	b	b	b	b (0.57) c (0.43)	b	b	b	b	b	b	b	b	b	b	b
LDH-1	a	a	a	a	a	a	a	a	a	a	a	a	a	c	c	a	b
LDH-2	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a
LGL	a	a	a	a	a	a	a	a	a	a (0.5) b (0.5)	a	a	a	b	b	a	c
MDH-1	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	c
MDH-2	a (0.92) b (0.08)	a (0.5) b (0.5)	a (0.6) b (0.4)	a	a(0.4) b(0.6)	a	b	a	a	b	a	a	a	a	a	a	a
MPI	a (0.25) b (0.75)	b	a (0.3) b (0.7)	b (0.83) c (0.17)	a(0.5) b(0.5)	b	a	b	b	a (0.5) b (0.5)	b	b	b	b	b (0.5) c (0.5)	b	c
PEP-1	d (0.58) e (0.34) f (0.08)	d (0.5) e (0.5)	d (0.95) e (0.05)	b	d(0.6) e(0.4)	b	d	c (0.5) d (0.5)	d	d	a	b	d	d	d	d	g
PEP-2	b (0.42) e (0.58)	e	b (0.55) e (0.45)	b	b(0.1) e(0.9)	b	e	b (0.5) c (0.5)	b	b (0.5) f (0.5)	b	b	b (0.5) e (0.5)	b (0.5) d (0.5)	b (0.5) d (0.5)	b	a
PGM	e	e	e	a (0.83) e (0.17)	e	e	e	e	e	e	e	e	e	e	d (0.5) e 0.5)	c	b
PGD	b	b	b	b	b	b (0.96) c (0.04)	b	b	b	b	b (0.5) c (0.5)	b (0.75) c (0.25)	b	b	b	b	a
PT-1	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	b	b
PT-3	b (0.83) c (0.17)	b	b	b (0.83) e (0.17)	b	b (0.29) e (0.71)	b	b	e	b	b (0.5) e (0.5)	b (0.5) e (0.5)	b	d	d	b	a
PT-5	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a
PK	a (0.67) b (0.33)	a (0.5) b (0.5)	a (0.15) b (0.85)	a	a(0.7) b(0.3)	a	b	a	a	a	a	a	a	a	a	a	c

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[1] See text for location of populations.