A NEW SPECIES OF BLIND SNAKE, TYPHLOPS MARXI, FROM THE PHILIPPINES (SERPENTES: TYPHLOPIDAE)

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ABSTRACT. - A new species, *Typhlops marxi*, is described from northwestern Sámar Island in the Philippines. It is placed in a species group of its own due to its unusual combination of features that do not indicate affinity with any known group: 30 midbody scale rows, a laterally pointed snout with horizontal cutting edge, a supralabial imbrication pattern type of T–0, and type B foramina in a multicameral tracheal lung. Three new systematic characters are introduced from the ophidian respiratory system: the cardiac lung, morphological lung types (unicameral, paucicameral and multicameral), and lung foramina types (A–G).

INTRODUCTION

The number of valid scolecophidian species inhabiting the Philippine Islands is currently a matter of debate. The last complete review of the fauna was Taylor's (1922) monograph on Philippine snakes in which he recognized fourteen species (Table 1). Since then four additional species have been described, two by Savage (1950), *Typhlops hypogius* and *T. hedraeus*, and two by Wynn & Leviton (1993). Although they did not cover the entire Philippine herpetofauna, Brown & Alcala (1970) listed the taxa known from the seven largest islands. McDowell (1974) revised the New Guinea and Solomon Island Typhlopidae and included discussion of most of the Philippine species, of which five were synonymized (*dendrophis, longicaudus, mindanensis, rugosus* and *suluensis*) and four suggested to be synonymous with other taxa (*hedraeus, hypogius, jagorii* and *luzonensis*; see Table 1). Hahn (1980) followed the rearrangements of McDowell (1974) with the exception of *Typhlops hypogius* and *T. luzonensis*, which he retained as valid species. Alcala (1986) listed thirteen Philippine species as valid but did not recognize *T. hedraeus* or *T. manilae*. In the most recent study of Philippine typhlopids, Wynn & Leviton (1993) recognized six species (*Ramphotyphlops braminus, R. cumingii, R. olivaceus, Typhlops hedraeus, T. ruber* and *T. ruficaudus*), tentatively synonymized *Typhlops canlaonensis* with *T. ruficaudus*, and described two new species, *Typhlops castanotus* and *T. collaris*. The status of *Typhlops manilae* was not discussed, so currently there are eight or nine recognized species of blind snakes inhabiting the Philippine Islands.

While examining the scolecophidian collection in the Field Museum of Natural History in 1988, I found a single specimen of typhlopid originating from Sámar Island in the Philippines

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Table 1. History of species recognition, generic placement and orthography of Philippine scolecophidians. Generic abbreviations: *R.* = *Ramphotyphlops*, *T.* = *Typhlops*, *Ty.* = *Typhlina* (=*Ramphotyphlops*).

Species	Taylor 1922	Brown & Alcala 1970	McDowell 1974	Hahn 1980	Alcala 1986	Wynn & Leviton 1993
1. *braminus*	*T. braminus*	*T. braminae*	*Ty. bramina*	*Ty. bramina*	*T. braminae*	*R. braminus*
2. *castanotus*						*T. castanotus*
3. *canlaonensis*	*T. canlaonensis*	*T. canlaonensis*	*T. canlaonensis*	*T. canlaonensis*	*T. canlaonensis*	= *T. ruficaudus*
4. *collaris*						*T. collaris*
5. *cumingii*	*T. cumingii*	*T. cumingi*	*Ty. cumingii*	*Ty. cumingii*	*T. cumingi*	*R. cumingii*
6. *dendrophis*	*T. dendrophis*	*T. dendrophis*	= *Ty. cumingii*	= *Ty. cumingii*		= *R. cumingii*
7. *hedraeus*			= ? *T. ater*	= ? *T. ater*		*T. hedraeus*
8. *hypogius*			= ? *T. ruber*	*T. hypogius*	*T. hypogia*	= *T. ruber*
9. *jagorii*	*T. jagorii*	*T. jagori*	= ? *T. ruficauda*	= ? *T. ruficaudus*	*T. jagorii*	= *T. ruficaudus*
10. *longicaudus*	*T. longicauda*	*T. longicauda*	= *Ty. cumingii*	= *Ty. cumingii*	*T. longicauda*	= *R. cumingii*
11. *luzonensis*	*T. luzonensis*	*T. luzonensis*	= ? *T. ruber*	*T. luzonensis*	*T. luzonensis*	= *T. ruber*
12. *manilae*	*T. manilae*			*T. manilae*		
13. *mindanensis*	*T. mindanensis*	*T. mindanensis*	= *Ty. cumingii*	= *Ty. cumingii*	*T. mindanensis*	= *R. cumingii*
14. *olivaceus*	*T. olivaceus*		*Ty. olivacea*	*Ty. olivacea*	*T. olivacea*	*R. olivaceus*
15. *ruber*	*T. ruber*	*T. ruber*	*T. ruber*	*T. ruber*	*T. ruber*	*T. ruber*
16. *ruficaudus*	*T. ruficauda*	*T. ruficauda*	*T. ruficauda*	*T. ruficaudus*	*T. ruficauda*	*T. ruficaudus*
17. *rugosus*	*T. rugosa*	*T. rugosa*	= *Ty. cumingii*	= *Ty. cumingii*	*T. rugosa*	= *R. cumingii*
18. *suluensis*	*T. suluensis*		= *Ty. olivacea*	= *Ty. olivacea*	*T. suluensis*	*R. olivaceus*

which could not be identified with any known species. It appears to represent a taxon new to science and is here named *Typhlops marxi*.

Typhlops marxi, new species
(Figs. 1–2)

Holotype – female (FMNH 96520), Tarabucan (12°13'N, 124°35'E), four miles southeast of spur of Sigarag Mountains (which are 13 miles south of Catarman), Matuguinao Municipality, extreme northern Western Sámar Province, northwestern Sámar Island, northeastern Visayas Group, east-central Philippines, coll. D. S. Rabor (Philippine Zoological Field Work Expedition, no. 1041), v.1957.

Material examined.– *Ramphotyphlops albiceps* (FMNH 180003, 180004, 180007; TNRC 123, 185; SLS 196), *R. braminus* (FMNH 53251; MCZ 172796, 175924; UMMZ 167976, 167977), *R. broomi* (MCZ 10224), *R. cumingii* (CAS 25483; FMNH 41092, 53221), *R. erycinus* (MCZ 49619), *R. infralabialis* (MCZ 65991; MVZ 40753), *R. ligatus* (CAS 135108), *R. lineatus* (FMNH 131235, 197951; MCZ 177345), *R. nigrescens* (FMNH 97892; MCZ 129883; SDSU uncat.), *R. olivaceus* (FMNH 131588; MCZ 45757), *R. polygrammicus* (MCZ 74162, 135506), *R. proximus* (CAS 84075), *R. solomonis* (MCZ 65996, 145955, 175090, 175099), *R. subocularis* (MCZ 66013, 175091; NMBA 11706, 11710), *R. wiedii* (FMNH 97882), *R. willeyi* (MCZ 110258), *Typhlops acutus* (FMNH 8651), *T. ater* (FMNH 142108; MCZ 33505; USNM
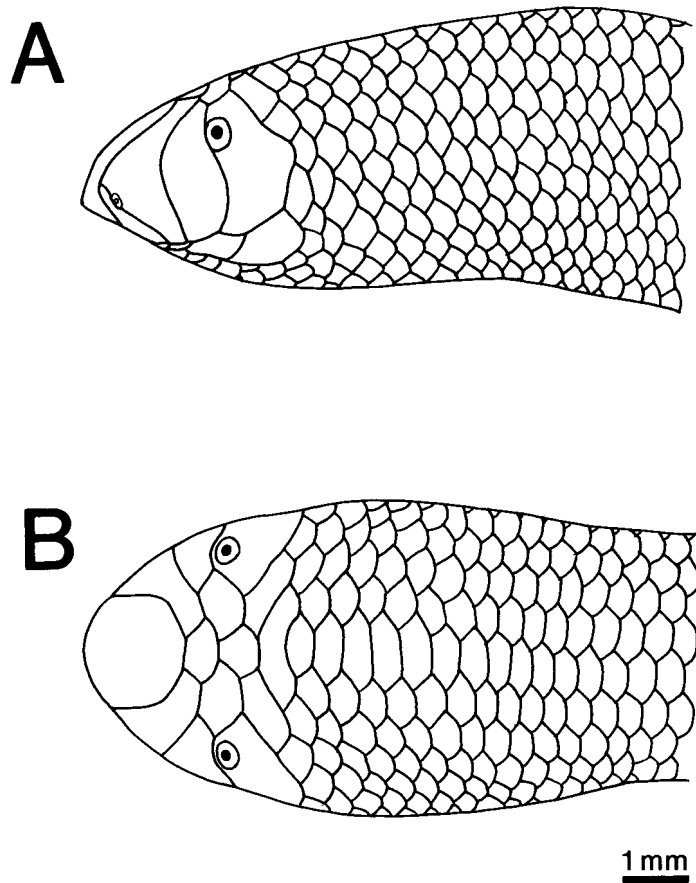

Figure 1. Lateral (A) and dorsal (B) view of head of holotype of *Typhlops marxi* (FMNH 96520) showing outline of scales.

43455; ZMA 17737), *T. boettgeri* (FMNH 73112, 73114; MNHN 1901.177; UMMZ 129031), *T. bothriorhynchus* (UF 48813), *T. caecatus* (MCZ 55381), *T. castanotus* (CAS 27942; MCZ 25594), *T. collaris* (UF 54186, 68443), *T. comorensis* (CAS 142915–16), *T. cuneirostris* (MCZ 74451–52), *T. decorsei* (MNHN 1950.210), *T. depressiceps* (MCZ 145954), *T. domerguei* (UMMZ 197249), *T. grandidieri* (MNHN 1905.271), *T. hedraeus* (MCZ 17578; USNM 229285), *T. khoratensis* (FMNH 189933; TNRC uncat.), *T. kraalii* (ZMA 14225), *T. lankaensis* (FMNH 100134), *T. microcephalus* (UMMZ uncat.), *T. mucronatus* (MCZ 33504; ZMH 3970, 3972), *T. ocularis* (UMMZ 197250), *T. pammeces* (MCZ 5229), *T. ruber* (FMNH 53223; MCZ 79698), *T. ruficaudus* (CAS 21066, UF 54652), *T. tenebrarum* (FMNH 120237), *T. violaceus* (FMNH 124231; ZMH 3967), *T. zenkeri* (MCZ 13242).

Diagnosis.– *Typhlops marxi* can be distinguished from all other Philippine scolecophidians by unique combination of 30 midbody scale rows, snout having a horizontal transverse edge, and type T-0 supralabial imbrication pattern. In addition, it is unusual in presence of V-shaped transversely enlarged interparietal and multicameral tracheal lung with type B foramina.

Description.– Holotype is subadult female with snout-vent length of 169 mm and total length of 179.5 mm. Midbody diameter 4 mm, body width contained in total length 45 times. Tail length 10.5 mm, representing 5.9% total length. Midtail diameter 3 mm, tail 3.5 times as long as wide. Longitudinal scale row formula 28–30–26, counted 15 scales posterior to mental, at midbody, and 10 scales anterior to anal shields. There are 525 transverse scale rows (total middorsal count between rostral and terminal spine) and 36 subcaudal scales. Five anal scales present. In lateral profile, terminus of tail exhibits downward curvature and sharp, posteroventrally directed terminal spine.
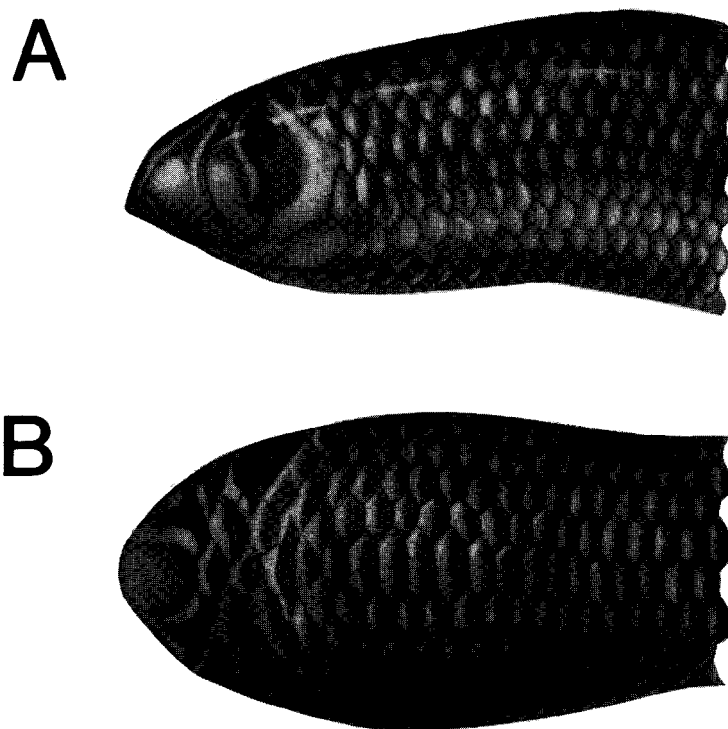

Figure 2. Lateral (A) and dorsal (B) view of head of holotype of *Typhlops marxi* (FMNH 96520).

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Head slightly wider than neck, bluntly pointed and weakly trilobed when viewed from above, with rostral projecting slightly beyond curvature of head. In lateral profile, snout wedge-shaped with two transverse edges: a slightly flattened, nearly vertical anterodorsal edge and more prominent, nearly horizontal anteroventral edge. Rostral shield 2/5 diameter of head, slightly broader than long with parallel sides in dorsal view, not reaching interocular level. Nostril near rostral border, oriented along 45° angle, directed laterally, and inferior in position. Nasal completely divided; inferior nasal suture contacts second supralabial near its junction with first supralabial while superior nasal suture directed medially and contacts rostral just dorsal to nostril. Postnasal, with slightly concave caudal border, larger than preocular but smaller than ocular, extending beyond posterior edge of rostral but separated on midline by slightly enlarged prefrontal. Frontal smaller than prefrontal. Supraocular enlarged, 1.5 times the width of prefrontal and twice the width of frontal, with lateral edge wedged between preocular and ocular. Parietal transversely enlarged (apparently from fusion of two scales) and obliquely oriented, slightly less in width than rostral with lateral border extending down behind ocular to level of eye. Posterior to frontal and elongated parietals is median, azygous enlarged interparietal (presumably from fusion of interparietal with scales on either side), slightly wider than rostral and twice the width of prefrontal.

Four supralabials present, fourth largest and about twice the size of third, third twice the size of second, and second larger than first. Supralabial imbrication pattern is type T–0 as posterodorsal borders of all supralabials are overlapped by ventral borders of nasal, preocular, and ocular (Wallach, 1993). Formula for right side of head is N1/SL1, PreOc/SL2, Oc/SL3, Oc/SL4; on left side it is N1-N2/SL1, PreOc/SL2, Oc/SL3, Oc/ SL4. On left side the suture between first and second supralabial joins prenasal-postnasal junction and suture between second and third supralabial joins preocular near nasal-preocular junction. Preocular narrower than postnasal and ocular in contact with second and third supralabials. At level of eyes posterior edge is concave while below eye it is convex. Ocular wider than postnasal and preocular, presenting triangular caudal margin with rounded apex (suggestive of fusion of median postocular with ocular), bordered posteriorly by three postoculars (between parietal and fourth supralabial). Mental shield separates infralabials at apex of U-shaped mandibular symphysis. Eye visible and moderate in size with faintly discernible pupil; anteriorly it contacts preocular border while dorsally it is close to supraocular border. Tongue lacks lateral papillae.

After preservation in alcohol overall coloration of dorsum is light brown and venter is yellowish-cream. Chromatophore pigmentation of dorsal body scales varies from posterior 2/3 scale (on cranial part of body) to posterior 3/4 scale (on caudal portion of body). Thus basal 1/3 to 1/4 of dorsal scales is unpigmented. Snout and subcaudals are unpigmented with chromatophores and light yellow in coloration. Pigmentation of dorsum involves 16 middorsal rows anteriorly, 14 rows at midbody, and 12 rows posteriorly. Conversely, unpigmented venter involves 12 rows anteriorly, 16 rows at midbody, and 14 rows posteriorly. Cephalic glands restricted to sutures of head shields, and while distinct on head dorsum are indistinct ventrolaterally.

Internal anatomy.– In following discussion of viscera, lengths and midpoints (MP) of organs and certain gaps and intervals between them (Wallach, 1985, 1991) are presented as percent snout-vent length (% SVL). Gap is defined as distance between any two organs or points (i.e., liver–gall bladder gap is measured from posterior tip of liver to anterior tip of gall bladder) whereas interval is distance from anterior tip of craniad organ to posterior tip of caudad organ

(i.e., liver–gall bladder interval is measured from anterior tip of liver to posterior tip of gall bladder). Thus interval includes lengths of two organs plus gap between them. As some of pulmonary terminology used here is new, a brief description is presented of variation in lung morphology. A more detailed analysis of snake lungs is in preparation by author.

Right lung (RL) is present in all snakes, but left lung (LL) is reduced in size relative to right and may be present or absent (Butler, 1895). Left lung is universally absent in five families (Anomochilidae, Anomalepididae, Leptotyphlopidae, Tropidophiidae and Acrochordidae), lacking in most species of three other families (Typhlopidae, Hydrophiidae and Viperidae), and absent in various species of many of remaining snake families (pers. obs.). Tracheal lung (TL), located craniad of heart along trachea (Cope, 1894), is characteristic of six families (Anomalepididae, Typhlopidae, Tropidophiidae, Acrochordidae, Hydrophiidae and Viperidae) in addition to a number of colubrid subfamilies or tribes (i.e., Xenodermatinae, Pareatinae, Dipsadini, Homalopsinae and Lycophidini). Any snake may thus possess one (RL), two (RL + LL, RL + TL) or three (RL + LL + TL) different lungs. Since diameter of heart is nearly equal to that of body cavity in Scolecophidia, there is an abrupt reduction in width of tracheal lung of Typhlopoidea at cranial border of heart, followed by narrow section of lung that lies dorsolaterally along right side of heart, after which there is gradual expansion in lung diameter with beginning of right lung at caudal tip of heart. This short section of respiratory system (usually 3–5% SVL) is here termed cardiac lung (CL) and represents a fourth lung type whose importance is discussed below. Cardiac lung is defined as constricted portion of lung connecting tracheal lung to right lung, adjacent to heart and equal to it in length. Those few African and Asian species of Typhlopidae retaining vestigal left lung (at least two *Rhinotyphlops* and 11 *Typhlops*; Brongersma, 1958, and pers. obs.) thus possess four lung types (RL + LL + TL + CL).

Lungs of snakes can be arranged into three morphological types following classification system established by Duncker (1978) for amniotic vertebrates: unicameral, paucicameral, and multicameral. Unicameral (U) lung essentially tubular or fusiform organ with large hollow, axial cavity in open communication with lumen of trachea. Paucicameral (P) lung partly divided by transverse septa that form distinct lateral pockets or shallow cells, each of which is in open contact with tracheal lumen. Multicameral (M) lung composed of separate, independent chambers or sacs whose lumina communicate solely with tracheal lumen by way of individual foramina (usually one per chamber) in tracheal membrane. Majority of snakes (more than 90% of all species) have unicameral lungs. Without exception, all left lungs are unicameral; in addition, most tracheal lungs and right lungs are also unicameral in structure. Duncker (1978) and Perry (1983) erroneously claimed that all snakes possessed unicameral lungs; Perry (1989) cited a personal communication from V. Wallach and questionably acknowledged the presence of ophidian multicameral lungs. Personal observation has revealed that in addition to unicameral lungs, snakes of families Anomalepididae, Typhlopidae, Acrochordidae, Elapidae, and Colubridae may also exhibit paucicameral or multicameral tracheal lungs. Furthermore, cardiac lung and right lung of Anomalepididae and Typhlopidae may be multicameral, paucicameral and/or unicameral. Structure of tracheal lung, cardiac lung and right lung in any species of Typhlopoidea may be identical (i.e., U + U + U, respectively) or different (M + P + U, respectively). Within a specific lung, organization may be uniformly one type or composed of two or even three structural types. Thus, tracheal lung may be entirely U, P, or M or may consist of different regions such as U + P, U + M, P + M, or U + P + M, always with one type predominating along majority of lung's length. In spite of its short length, cardiac lung may be U, P, M, U + P, U + M, P + M, or U + P + M, making it a valuable systematic character. Likewise, right lung may be U, P + U, M + U, or M + P + U. Disregarding greatly reduced cardiac lung,

development and vascularity of lungs are always most complex and robust towards cardiac region, so unicameral or paucicameral portions of mainly multicameral tracheal lungs are craniad while cranial sections of right lungs may be multicameral or paucicameral but caudal portions are always unicameral.

With exception of larynx, cartilaginous rings of trachea in snakes are incomplete, forming C- or U-shaped structures in cross-section that are joined by intervening membrane of variable width and thickness (Kardong, 1972). Tracheal membrane, stretching between tips of incomplete rings, perforated in multicameral lungs by eight to 80 more or less equally spaced foramina that vary in size and position along membrane, and which allow passage of air from tracheal lumen into vascularized tracheal chambers. Foramina are classified according to relationship to border between tracheal membrane and distal tips of tracheal rings. Tips of rings may terminate at tracheal border, forming straight edge, or they may project freely beyond border into tracheal lumen as free tips, forming dentated edge. Intermediate between these two extremes is serrated tracheal border formed from rings whose tips barely project beyond border's edge. At least nine different types of foramina have been observed in snakes, six of which are found in scolecophidians. Foramina are identified by lightly stretching tracheal membrane until natural configuration is achieved as in inflated condition. Type A foramina largest, equal in width to tracheal membrane with edges in contact with both of membrane's borders. Since trachea normally opens laterally with distal tips directed to right side of snake, borders of membrane are usually dorsal and ventral in position. Type B foramina moderate to large in size, in contact with ventral (but not dorsal) tracheal border. Type C foramina smaller than type A, centered along membrane's longitudinal midline and not in contact with either border. Type D foramina similar to type B except that they only contact dorsal border. Type E consists of duplex arrangement: a large (or primary) foramen located medially along the membrane with smaller (or secondary) foramen lateral to it. Type F (intercalary or tertiary) foramina small and irregular, wedged between any of the above types. Type G foramina minute, located between bronchial cartilages in intrapulmonary bronchus. Several other types are known but only types A–G found in the Typhlopidea.

In *Typhlops marxi*, tracheal lung (23.1% SVL, MP = 21.6%) occupies right side of anterior body cavity, width varying from 0.33 body diameter cranially to 0.67 caudally. Multicameral and weakly vascularized, it contains 37 separate, hollow chambers, their inner walls invested with pulmonary blood vessels in irregular pattern. Wall of lung thin and transparent, internal vascular structure visible from exterior. Tracheal membrane avascular, transparent and perforated by 37 large type B foramina, each opening into single vascularized air chamber. Trachea (36.1% SVL, MP = 19.2%) has approximately 336 rings (or 93 per 10% SVL) that lack free tips but form serrated edge along tracheal border. Located along left lateral side of body, it is visible ventrally along entire length of tracheal lung. Tracheal membrane narrow in comparison to width of tracheal rings (tracheal membrane/tracheal ring ratio 0.4 at midlung and 0.6 posteriorly). Tracheal entry into right lung terminal as in all scolecophidians. Cardiac lung (4.1% SVL) unicameral and weakly vascularized. Right lung (13.6% SVL, MP = 44.1%) short and very narrow (0.25 body diameter cranially to 0.1 body diameter caudally). It is unicameral throughout length and weakly vascularized with single tier of faveoli along its anterior 60% but reticulated with a fine network of blood vessels along posterior 40%. Caudal tip located at 51% SVL. Respiratory system (tracheal lung, cardiac lung and right lung) 40.8% SVL (MP = 30.5%). Moderate intrapulmonary bronchus (IPB) present (8.3% SVL), extending 60.9% length of right lung. As in most typhlopids there is no left lung, left bronchus, or left orifice.

Heart moderate in length (4.1 % SVL, MP = 35.2%) but positioned far caudad with long snout–heart interval (37.3% SVL, MP = 18.6%). Cranial tip of liver overlaps ventricle of heart by 1.2% SVL (i.e., heart–liver gap = –1.2%). Junctions of left and right systemic arches with aorta are 3.6% and 4.4% SVL craniad of ventricular apex, respectively. Moderate-sized liver multisegmented and convoluted throughout entire length (24.9% SVL, MP = 49.1%). Left liver lobe (LL, 20.7% SVL) extends craniad of right lobe by 1.2% SVL while right liver lobe (RL, 23.7% SVL) extends caudad of left lobe by 4.1% SVL, the LL/RL length ratio 87.5%. Gall bladder (1.2% SVL, MP = 65.7%) immediately anterior to pancreas, both organs equal in size. Both liver–gall bladder gap (3.6% SVL, MP = 63.3%) and liver–gall bladder interval (29.6% SVL, MP = 51.5%) short. As in all typhlopids, left oviduct missing. Right ovary (4.7% SVL, MP = 75.1%) longer than left ovary (2.7% SVL, MP = 78.0%). There are no developing follicles in ovaries; this observation plus size of specimen suggest that it is immature. Right adrenal gland (0.6% SVL, MP = 77.8%) equal in size to left adrenal (0.6% SVL, MP = 79.6%). Left kidney (4.7% SVL, MP = 85.2%) slightly longer than right kidney (4.1% SVL, MP = 82.5%), an unusual but occasional occurrence in snakes; both organs overlap for 1/4 their total length. Each kidney possesses single renal artery, is not lobed but covered with multiple fine transverse creases, and is positioned far anterior in body cavity with kidney–vent interval (anterior tip of right kidney to vent) of 19.5% SVL (MP = 90.2%) and kidney–vent gap (posterior tip of left kidney to vent) of 12.4% SVL (MP = 93.8%). Large rectal caecum (3.6% SVL, MP = 88.8%) present, its diameter three times that of adjacent small intestine.

Etymology.– It gives me great pleasure to name this species in honor of Hymen Marx, retired Curator of the Division of Amphibians and Reptiles, Field Museum of Natural History, Chicago, Illinois, USA. He has made significant contributions to our knowledge of the world's snake fauna and evolution of character states in higher snakes, but is especially known for his work on the relationships of snakes of the family Viperidae. I am personally indebted to him for his generosity and assistance over the years in entrusting me to dissect snakes in the Field Museum's collection. A significant portion of my data on the internal anatomy of snakes is derived from FMNH specimens. My friendship with Hy has been a truly unique and unforgettable experience.

DISCUSSION

Comparisons with other species.– *Typhlops marxi* differs from all known Philippine typhlopids by the unique combination of a snout pointed in lateral profile, a transverse horizontal edge to the rostral, 30 midbody scale rows, a type T-0 supralabial imbrication pattern, and type B tracheal foramina. The high number of midbody scale rows easily distinguishes *Typhlops marxi* from the three scolecophidians known from Sámar Island (Alcala, 1986): *Ramphotyphlops braminus* with 20 rows, *R. olivaceus* with 20–22 rows, and *Typhlops ruber* with 26 rows.

Typhlops marxi differs from *R. braminus* in the shape of the snout, both dorsally and laterally (pointed vs. rounded), midbody scale rows (30 vs. 20), total middorsals (525 vs. less than 365), SIP type (T-0 vs. T-III), contact of superior nasal suture with rostral (inferior, not visible from above vs. dorsal, visible from above), origin of inferior nasal suture (second supralabial vs. preocular), dorsal rostral shape (broader than long with parallel sides vs. twice as long as broad with an anterior constriction), lateral tongue papillae (absent vs. present), proportional tail length (long vs. short), tracheal foramina number and type (37 type B vs. 17–22 type D), and ventral coloration (unpigmented vs. lightly pigmented).

From *Ramphotyphlops cumingii*, with which it shares the greatest resemblance, *T. marxi* differs in midbody scale rows (30 vs. 24–28), SIP type (T–0 vs. T–III), size of interparietal (transversely enlarged vs. not enlarged), type of tracheal foramina (type B vs. type C), structure of the cardiac lung (unicameral vs. multicameral with 7–9 foramina), and structure of the right lung (unicameral vs. multicameral with 3–8 foramina).

Typhlops marxi can be separated from *R. olivaceus* by its rostral shape (broader than long vs. longer than broad), midbody scale rows (30 vs. 20–22), the SIP type (T–0 vs. T–III), lateral tongue papillae (absent vs. present), type of tracheal foramina (type B vs. type C), structure of the cardiac lung (unicameral vs. multiicameral with 3–9 cells), and structure of the right lung (unicameral vs. multicameral with 2–3 cells).

Typhlops marxi differs from *T. castanotus* in midbody scale rows (30 vs. 26–28), total middorsals (525 vs. fewer than 340) and subcaudals (36 vs. fewer than 15), lateral snout shape (pointed vs. rounded), dorsal rostral shape (broader than long vs. longer than broad), number of postoculars (three vs. two), tail length proportions (long vs. short), SIP type (T–0 vs. T–III), dorsal pigmentation (light vs. dark), type and number of tracheal foramina (37 type B vs. 67 type C), tracheal lung type (multicameral vs. paucicameral), right lung type (unicameral vs. paucicameral), and rectal caecum (well developed vs. absent).

From *Typhlops collaris*, *T. marxi* can be separated by midbody scale rows (30 vs. 26–28), total middorsals (525 vs. fewer than 460) and subcaudals (36 vs. fewer than 15), lateral snout shape (pointed vs. rounded), dorsal rostral shape (broader than long vs. longer than broad), proportional tail length (long vs. short), SIP type (T–0 vs. T–III), tracheal foramina number and type (37 type B vs. 7–21 type C), and rectal caecum (well developed vs. absent).

Typhlops marxi can be distinguished from *T. hedraeus* by midbody scale rows (30 vs. 18), total middorsals (525 vs. fewer than 400) and subcaudals (36 vs. fewer than 20), distribution of cephalic glands under head shields (restricted to scale margins vs. widely dispersed under shields), lateral snout shape (pointed vs. rounded), SIP type (T–0 vs. T–II), relative nasal width (slightly wider than ocular vs. wider than both preocular and ocular), structure of the tracheal lung (multicameral vs. unicameral), and rectal caecum (well developed vs. absent).

From *Typhlops manilae*, the only Philippine species not available for examination as it is still known only from the holotype, *T. marxi* differs in midbody scale rows (30 vs. 28), subcaudals (36 vs. 12), subocular shield (absent vs. present), lateral shape of snout (pointed vs. rounded), position of nostrils (inferior vs. lateral), superior nasal suture (complete vs. incomplete), shape of rostral (broader than long, not reaching level of eyes vs. longer than broad, reaching level of eyes), parietal shields (enlarged vs. not enlarged), relative nasal width (narrower than ocular vs. wider than ocular), proportional tail length (long vs. short), and dorsal coloration (light brown vs. dark brown).

Typhlops marxi is separable from *T. ruber* by midbody scale rows (30 vs. 26), a total middorsals (525 vs. fewer than 360) and subcaudals (36 vs. fewer than 15), lateral snout shape (pointed vs. rounded), SIP type (T–0 vs. T–III), dorsal rostral shape (broader than long vs. longer than broad), tail length proportions (long vs. short), dorsum pigmentation (light vs. dark), number and type of tracheal foramina (37 type B vs. 25–29 type C), structure of the cardiac lung (unicameral vs. multicameral with 4–6 foramina), and structure of the right lung (unicameral vs. multicameral with 5–10 foramina).

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From *Typhlops ruficaudus*, the only Philippine species with 30 midbody scale rows, *T. marxi* differs in the lateral shape of the snout (pointed vs. bluntly rounded), SIP type (T–0 vs. T–III), total middorsals (525 vs. fewer than 420) and subcaudals (36 vs. fewer than 15), dorsal rostral shape (broader than long vs. longer than broad), proportional tail length (long vs. short), dorsum pigmentation (light vs. dark), tracheal foramina type and number (37 type B vs. 21–23 type C), structure of the cardiac lung (unicameral vs. multicameral with 6–9 foramina), structure of the right lung (unicameral vs. multicameral with 4–5 foramina), and the rectal caecum (well developed vs. absent).

Generic status.– As the holotype and only known specimen is a female, it is not possible to determine the generic allocation with certainty. Three genera are currently recognized in the Typhlopidae: *Ramphotyphlops*, *Rhinotyphlops* and *Typhlops*. Since *Rhinotyphlops* is endemic to Africa and extreme southwestern Asia, it is not considered further. The only definitive character presently known to distinguish *Ramphotyphlops* from *Typhlops* is the presence in male *Ramphotyphlops* of retrocloacal sacs in the posterior abdominal cavity (Robb, 1966a-b; McDowell, 1974). (See note added to proof on page 110).

Several other characters, while present in most of the species of one genus, have exceptions occurring in the other that invalidate their use as reliable diagnostic features. These include the following characters: (1) solid protrusible hemipenes, (2) tail length/width ratios, (3) superior nasal suture, (4) lateral tongue papillae, and (5) supralabial imbrication pattern. A more variable character is a pointed snout.

Before discussing the characters above, there is a species whose allocation to *Ramphotyphlops* is questionable. Hahn (1980) transferred *Typhlops albiceps* to *Ramphotyphlops* without comment. In the only male *R. albiceps* available to me, a 126 mm juvenile from Thailand (TNRC 185), I was unable to locate retrocloacal sacs but did observe testes and a pair of wide, straight hemipenes. The Southeast Asian distribution of *R. albiceps* is outside the range of all other known species of *Ramphotyphlops*. I suspect that *albiceps* may be a *Typhlops*; examination of a mature male could resolve the dilemma.

In resurrecting the genus *Ramphotyphlops*, Robb's (1966b) diagnostic character was the solid, awn-like protrusible hemipenis that was identifiable, in specimens with retracted organs, by some degree of helical coiling in the tail. McDowell (1974) reported one exceptional species, *Typhlina (=Ramphotyphlops) cumingii*, to exhibit a straight hemipenis (although it may possess a Z-shaped flexure) in conjunction with small, nearly spherical retrocloacal sacs. *Ramphotyphlops cumingii* has a long tail that apparently eliminates the need for coiling, even though both the distal awn and proximal sheath are more than half the length of the tail (McDowell, 1974). Robb (1966b) reported cloacal pouches and a coiled hemipenis in *Typhlops lineatus* and transferred it to *Ramphotyphlops*. McDowell (1974) remarked that the retrocloacal sacs in *Typhlina (=Ramphotyphlops) lineata* were very short. Apparently small retrocloacal sacs and minimal hemipenial coiling are primitive conditions in *Ramphotyphlops*. A. H. Wynn brought to my attenton a 210 mm male from Java (USNM 25351) that possesses short retrocloacal sacs plus a hemipenis with a single coil. Two other males from Java (FMNH 131235, 234 mm, and MCZ 177345, 226 mm), however, possess narrow, straight hemipenes; in at least one (MCZ 177345), small retrocloacal sacs were observed after reexamination of the specimen. Unless two cryptic species are involved on Java, the hemipenis exhibits intraspecific variation in *R. lineatus*. Although approximately the same size, the smallest individual of the three specimens possesses the coiled hemipenis while the two larger specimens have a straight organ, thereby eliminating ontogeny as a causative factor. Ontogenetic variation does occur in the hemipenial coiling of

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an undescribed species of the *R. subocularis* group from Bougainville Island. The number of coils in seven males ranges from 3–7, distributed as follows by total length of specimen: 167 mm (3), 178 mm (3), 252 mm (5), 257 mm (7), 274 mm (7), 292 mm (7), and 301 mm (6). Hemipenial coiling is thus variable in some species of *Ramphotyphlops*.

Robb (1966b) pointed out that all the *Ramphotyphlops* she examined, with the exception of *R. lineatus*, possessed a long tail whose length was at least twice that of its width (TL/TW = 2.0–3.0), whereas Australasian *Typhlops* (including *R. lineatus*) possessed a short tail whose length was equal to or less than its width (TL/TW ≤ 1.0). She stated that the Philippine *T. ruficaudus* was long tailed, but this was probably due to a misidentification as *T. ruficaudus* (and the entire *ruficaudus* species group) is short tailed. Thus, within the Australasian region, relative tail proportions provide a clue to generic boundaries although the *Typhlops ater* species group possesses a tail of intermediate proportions (TL/TW = 1.1–3.7). Even though *T. marxi* is represented by a female, it has a very long tail (TL/TW = 3.5), suggestive of the genus *Ramphotyphlops*.

When McDowell (1974) hypothesized that *Typhlops braminus* was a parthenogenetic species lacking male individuals, he faced the difficult task of inferring whether it was more closely related to *Typhlops* or *Ramphotyphlops*. Without the diagnostic male reproductive structures, the choice remains an educated guess. Based upon a similarity to *Ramphotyphlops erycinus* with 20 midbody scale rows, 300 total dorsals, complete division of the nasal with superior suture extending onto dorsum of head, narrow rostral, and lateral tongue papillae, McDowell (1974) transferred *Typhlops braminus* to the genus *Typhlina* (=*Ramphotyphlops*), a move followed by all subsequent authors. Extension of the superior nasal suture, parallel to the rostral, onto the dorsum of the snout is characteristic of the entire *Ramphotyphlops polygrammicus* species group (*erycinus, kimberleyensis, ligatus, micrommus, nigrescens, polygrammicus, proximus, troglodytes*, and *wiedii*). In a few other species of *Ramphotyphlops* the superior nasal suture is just barely visible from above (*batillus, broomi, diversus*, and *leucoproctus*). In most of the species of all the other species groups of *Ramphotyphlops*, the superior nasal suture is not visible from above; whether the suture is complete or incomplete, it does not extend onto the dorsum of the snout.

Certain species of *Typhlops* resemble *Ramphotyphlops braminus* and may be members of the *braminus* group (*caecatus, comorensis, domerguei, jerdoni, khoratensis, lankaensis, leucomelas, malcolmi, pammeces, tenebrarum, veddae, violaceus*, and *zenkeri*). Most share with *R. braminus* the following characters: a T–III supralabial imbrication pattern, 20 midbody scale rows, a low number of middorsals (280–330), and a superior nasal suture visible from above. In addition, several have the inferior nasal suture contacting the preocular. Table 2 compares *R. braminus* with those species sharing certain similarities. The majority of the species are from Sri Lanka and southern India, the probable region of origin of *R. braminus*. Loveridge (1957) placed *capensis* in the synonymy of *braminus* while Roux-Estève (1974, 1980) assigned *caecatus* and *zenkeri* of Africa and *domerguei* of Madagascar to the *braminus* group. Hahn (1977) refuted Roux-Estève's placement of *caecatus* and *zenkeri* in the *braminus* group due to convergence of scale characters and the hypothesis that the closest relatives of *R. braminus* are Asian. If McDowell was correct in allocating *braminus* to *Ramphotyphlops*, then probably at least some of the above species also belong with *braminus* in that genus, but it is premature to make such changes at this time since the male reproductive structures are unknown for most of the species. A. H. Wynn and C. Gans are currently investigating some members of this group but their studies are not yet completed. Within *Typhlops* a dorsally visible superior nasal suture is known only in various New World species of that genus. In *T. marxi* the superior nasal suture is not visible dorsally so it is uninformative.

McDowell (1974) reported that presence of lateral papillae on the tongue of *Ramphotyphlops* distinguished that genus from *Typhlops*. He noted tongue papillae, outside of *Ramphotyphlops*, only in *Typhlops acutus* of India. In addition to *albiceps* and *lineatus* I have observed lingual papillae in *T. boettgeri, T. decorsei, T. microcephalus,* and *T. mucronatus* from Madagascar, *T. bothriorhyncus* from Myanmar, and two undescribed species of *Typhlops* from Madagascar and Hong Kong. As *Typhlops marxi* lacks lateral tongue papillae, the evidence is negative but suggestive of *Typhlops*.

Table 2. Characters of *Ramphotyphlops braminus* and possible relatives. Abbreviations: LSR – longitudinal scale rows at midbody; TSR – transverse scale rows between rostral and terminal spine; SNS – superior nasal suture (O = not visible dorsally, S = short extension dorsally, L = long extension dorsally); INS – inferior nasal suture (SL = contacts supralabial 1 or 2, PO = contacts preocular); SIP – supralabial imbrication pattern.

Species	Distribution	LSR	TSR	SNS	INS	SIP
braminus	Tropicopolitan	20	290–364	L	PO	T–III
lankaensis	Sri Lanka	20	229–261	L	PO	T–III
leucomelas	Sri Lanka	22	325	L	SL2	T-III
malcolmi	Sri Lanka	20	273–282	L	SL2	T–III
tenebrarum	Sri Lanka	20	312–329	L	SL2	T–III
veddae	Sri Lanka	20	295–309	L	SL2	T–III
violaceus	Sri Lanka	20	245–308	L	PO	T–III
pammeces	Southern India	20	328–400	L	SL2	T–III
jerdoni	Eastern Himalayas	22	260–313	L	SL2	T–III
khoratensis	Thailand	20	315–328	O	PO	T–III
capensis	Madagascar	20	498	S	SL2	T–III
domerguei	Madagascar	22	252–262	S	SL2	T–III
comorensis	Comoro Islands	20	384–411	S	SL2	T–III
conradi	Sulawesi, Indonesia	20	398	S	SL2	T–III
erycinus	Australia	20	315–335	L	SL1	T–III
caecatus	Ghana, Côte d'Ivoire	18–20	282–334	S	SL2	T–III
zenkeri	Cameroon	18	250–281	S	PO	T–III

Whereas all *Typhlops* possess either a type T–0, T–I, T–II, T–III, or T–V supralabial imbrication pattern (SIP), nearly every species of *Ramphotyphlops* exhibits a type T–III pattern, the sole exception being *R. subocularis* (*sensu stricto*) with a type T–0 (Wallach, 1993). The presence of a T–0 SIP in *R. subocularis* is surely a uniquely derived feature of that species from the Bismarck Archipelago. All of the other members of McDowell's (1974) *R. subocularis* group of Papua New Guinea and the Solomon Islands (*R. infralabialis, R. solomonis* and *R. willeyi* plus the types of *T. adamsi, T. bergi,* and *T. keasti*) have a T–III pattern. Among Philippine typhlopids, all possess either a type T–II or T–III SIP, so the type T-0 pattern of *Typhlops marxi* must be a uniquely derived feature within the Philippine fauna. A T–0 pattern is present also in most *Rhinotyphlops*, some African *Typhlops, Typhlops grandidieri* of Madagascar, and the Indian *Typhlops acutus*. This character is suggestive of placement in *Typhlops*; it would unequivocally eliminate *Ramphotyphlops* as a possibility were it not for the exceptional *R. subocularis*.

A snout with a laterally pointed profile and a horizontal cutting edge to the rostral is present in 50% of *Ramphotyphlops* species and 80% of *Rhinotyphlops* species, but it is rare (5%) among *Typhlops* species (*acutus, cuneirostris, decorsei, depressiceps, grandidieri, ocularis* and *unilineatus*). This character suggests affinity with *Ramphotyphlops*.

Since the generic boundaries of *Ramphotyphlops* are not precisely known, the extent of its geographical range is uncertain. Excluding *Ramphotyphlops albiceps* plus the introduced parthenogenetic *R. braminus*, the genus extends from Malaysia and the Philippines southward throughout Indonesia, Papua New Guinea and Australia, thence eastward through the Solomon Islands and New Caledonia to Fiji (McDowell, 1974; Hahn, 1980). *Typhlops*, with a much wider distribution, occurs sympatrically with *Ramphotyphlops* in Malaysia, the Philippines, Indonesia and Papua New Guinea. Since both genera are represented not only in the Philippines but also on Sámar Island, distribution provides no evidence of generic affinity.

Most *Ramphotyphlops* species have from 18–24 midbody scale rows; only the Philippine *R. cumingii* (24–28 rows) and the *R. subocularis* group (26–36 rows) possess more rows at midbody. However, no fewer than nine species of *Typhlops* (six African, one Indian, one Southeast Asian, and one Philippine) have 30–44 midbody scale rows. Midbody scale rows are suggestive of *Typhlops*. At least 16 species of *Ramphotyphlops* and 17 species of *Typhlops* have more than 500 longitudinal scale rows so this character is uninformative.

McDowell (1974) used the disposition of the cephalic gland lines to distinguish *Ramphotyphlops* from the *Typhlops ruficaudus* species group. He reported that in the *ruficaudus* group the nasal-preocular gland line contacts the preocular-ocular line posteroventral to the nostril while in *Ramphotyphlops* the nasal-preocular gland line is well separated from the preocular-ocular line. However, Wynn & Leviton (1993) have pointed out that contact of the gland lines occurs only in species having contact between the postnasal and third supralabial. Their examination of *T. luzonensis* (of the *ruficaudus* group) revealed that the gland lines do not fuse when the preocular overlaps the second supralabial; in fact, the gland lines are separated by a distance equal to the width of the overlap of the preocular and the second supralabial. Since the gland lines are not discernible ventrolaterally in *T. marxi*, analysis of this character is moot.

Typhlops marxi shares with *Ramphotyphlops subocularis* a long tail, pointed snout and lack of tongue papillae plus an SIP type not present in any other species of *Ramphotyphlops* and which would otherwise provide strong support for the inclusion of *marxi* in *Typhlops*. *Typhlops marxi* differs from *R. subocularis*, however, in midbody scale rows (30 vs. 34–36), subcaudals (36 vs. fewer than 26), rostral shield (broad vs. narrow), suboculars (none vs. 4–5), subpreocular (absent vs. present), paired supranasals (absent vs. present), superior nasal suture (complete vs. incomplete), postoculars (3 vs. 4–5), mandibular symphysis (U-shaped vs. V-shaped), liver (multisegmented and convoluted vs. straight and unsegmented), cardiac lung (unicameral vs. multicameral), right lung (short, narrow and unicameral vs. long, wide and multicameral), and distribution (Philippine Islands vs. Bismarck Archipelago, Papua New Guinea).

In addition to being restricted to northeastern Papua New Guinea (Bismarck Archipelago and Bougainville Is.) and the Solomon Islands, all members of the *subocularis* group possess the following characteristics that differ remarkably not only from *marxi* but from most other Typhlopidae. Both the ocular and preocular have been divided so that 2–6 small suboculars and 1–2 subpreoculars are present below the former two shields. A pair of prefrontals or supranasals

are usually present. The rostral shield is reduced; it is very narrow (1/10–1/5 head width) and extends only halfway to the level of the eyes. The symphysis of the lower jaw is V-shaped rather than U-shaped as in all other Scolecophidia (McDowell, 1974). The liver is straight and unsegmented as in the Alethinophidia in contrast to the multisegmented, usually convoluted liver of other scolecophidians (Underwood, 1967). The cardiac lung is multicameral (with 3–12 foramina). The right lung is enlarged; its length nearly equal to that of the tracheal lung, its diameter 1/2–3/4 of the body width, and it is multicameral (with 5–14 foramina) for more than half its length. These characters provide additional support for the idea of S. B. McDowell that the *subocularis* group might represent a separate genus.

A comparison of tracheal foramina type distribution in more than 100 typhlopid species reveals the following relative frequencies: 31 *Ramphotyphlops* species (65% A, 16% C, 16% D, 3% E), 17 *Rhinotyphlops* (41% C, 35% A, 12% D, 6% B, 6% E), 33 Old World *Typhlops* (44% A, 28% C, 22% D, 3% B, 3% E), and 23 New World *Typhlops* (65% B, 22% C, 4% A, 4% D, 4% E). Type B foramina are unknown among *Ramphotyphlops* and present only in one *Rhinotyphlops (crossi)* and one Old World *Typhlops (bibronii)* species. However, type B foramina are characteristic of the majority of New World *Typhlops*, being present in *capitulatus, dominicanus, granti, hectus, jamaicensis, monastus, platycephalus, richardii, sulcatus, tetrathyreus,* and *titanops* of the *lumbricalis* species group, *brongersmianus* and *reticulatus* of the *reticulatus* group, and *biminiensis* and *caymanensis* of the *tenuis* group. The type B foramina of *T. marxi,* unknown among all but two Old World Typhlopidae, suggest a relationship to New World *Typhlops*.

CONCLUSIONS

The above evidence demonstrates that *marxi* cannot be unequivocally allocated to either *Typhlops* or *Ramphotyphlops* and that it is not closely related to any Philippine species. The few characters that it shares with *Ramphotyphlops subocularis*, such as the T–0 supralabial imbrication pattern, and which prevent its unquestionable assignment to *Typhlops*, carry no weight in contrast to the distinctive suite of features that separate the *subocularis* group from all other scolecophidians. The type B tracheal foramina of *T. marxi* are unique among Australasian scolecophidians, and are known only in one *Rhinotyphlops* and one *Typhlops* species from Africa, plus the majority of New World (especially Caribbean) species of *Typhlops*.

Therefore, in view of this and due to the uncertainty regarding the male reproductive structures, a conservative approach is adopted and the new species is provisionally referred to the genus *Typhlops*. Its systematically isolated position, with no apparent affinity to Australasian taxa, argues for placement in the *Typhlops marxi* species group as the sole member. Further study and additional specimens may shed light upon the relationships of *Typhlops marxi*. Four scolecophidian species groups are now recognized as having representatives inhabiting the Philippines (McDowell, 1974; Wynn & Leviton, 1993): *T. hedraeus* of the *ater* group with rounded snout, 18 scale rows, moderate tail, and T–II SIP; *R. braminus* of the *braminus* group with rounded snout, dorsally visible nasal suture, 20 scale rows, short tail, and T–III SIP; *R. cumingii* and *R. olivaceus* of the *multilineatus* group with pointed snout, 24–28 scale rows, long tail, and T–III SIP; *T. castanotus, T. collaris, T. ruber* and *T. ruficaudus* of the *ruficaudus* group with rounded snout, nasal suture invisible dorsally, 26–30 scale rows, short tail, and T–III SIP. To those can be added *T. marxi* of the *marxi* group with pointed snout, 30 scale rows, long tail, and T–0 SIP.

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NOTE ADDED TO PROOF

Alphin & Donnellan (1993) reported absence of retrocloacal sacs in two males each of *Ramphotyphlops endoterus* and *R. hamatus*, presumed to be a secondary loss. If confirmed then this character is no longer unequivocally diagnostic for *Ramphotyphlops*. However, the single male *R. hamatus* available to me (Western Australian Museum R66323 from SSE Banjawarn, 12 km (=Eastern region, B in fig. 3 of Alphin & Donnellan, 1993: 249)) possesses a hemipenis with five and a half coils and small retrocloacal sacs 1.8% SVL.