A new species of blindsnake, genus *Ramphotyphlops* (Typhlopidae, Squamata), from northwestern Western Australia, with a redescription of *R. hamatus*, Storr 1981

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Abstract

Ramphotyphlops pilbarensis sp. nov. is described from scattered localities in arid northwestern Western Australia. The species is morphologically most similar to *R. hamatus*, with which it was previously confused, and to *R. endoterus*, but differs from these taxa in various meristic and qualitative scalation features. Genetic data suggest a distant relationship amongst the three species. The importance of accounting for sexual dimorphism in typhlopid systematics is emphasized.

Introduction

Blindsnakes of the family Typhlopidae are one of the least studied components of the Australian herpetofauna. The last comprehensive revision of the group was by Waite (1918), who recognised a total of nineteen species. Since that time, additional species have been described by Kinghorn (1929, 1942), Loveridge (1945), Robb (1972) and Storr (1981, 1983, 1984), the latter describing nine new taxa from western and central Australia. Currently a total of thirty one species is recognised (Cogger 1986).

Typhlopid snakes are remarkably uniform in body form and scalation, and thus present relatively few characters of systematic value. For these reasons, the true number of species may be seriously underestimated by morphological criteria alone. Recently, we undertook an electrophoretic study designed to test for sibling species in the widespread but variable "species" *Ramphotyphlops australis* (Gray, 1845). The results of this study (to be published separately) not only confirmed the presence of at least two species within "*australis*", but also revealed *R. hamatus* Storr, 1981, for which several specimens were included as one of several outgroups, to comprise two, genetically very distinct taxa. Subsequent examination of voucher material confirmed the presence of two, morphologically distinct species within *R. hamatus*, one of which is described as new in this paper. Four specimens fo the new species (those pre R80000) were included by Storr (1981) among the paratype series of *R. hamatus*. The composite nature of Storr's description, together with the presence of hitherto undescribed sexual

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dimorphism in this (and other) typhlopid species, warrants its redescription. The new species is compared in detail with each of *R. hamatus* and *R. endoterus* Waite, 1918.

Methods

Individual typhlopid body scales are more easily distinguished along the pigmented, dorsal surface than along the unpigmented venter and for this reason, vertebral scale counts (from immediately behind the frontal to a point opposite the vent) were taken in preference to the more traditional ventral counts. Where both counts are available (the latter from Storr's unpublished data sheets), the vertebral and ventral counts typically differ by \pm 5-10, which is consistent with the combined repeatability of the two measurements. Subcaudal counts are taken ventrally and do not include the terminal, spine-bearing scale. Body diameter is the average of body width and depth, measured at or near midbody. The sex of all specimens was determined by examination of the reproductive tract; meristic and mensural data are presented separately for each sex and for a combined sample which includes those animals with indistinct or damaged gonads. Specimens in the collection of the Western Australian Museum are indicated by an R prefix; those in the South Australian Museum are prefixed with SAMR.

Allozyme electrophoresis of liver homogenates was performed on "Cellogel" (Chemetron, Milan) according to the methods of Richardson *et al.* (1986). The enzymes examined are listed at the end of the paper with their Enzyme Commission numbers and abbreviations.

Systematics

Ramphotyphlops pilbarensis sp. nov. Figures 1.2

Holotype

R90864 in the Western Australian Museum, adult male, pit-trapped on 26 September 1988 by J. Dell at Site WS2, Woodstock Station, Pilbara region in 21°36'42"S 118°57'20"E. Liver sample preserved in -80°C ultrafreeze at W.A. Museum.

Paratypes

R10897 (M) Muccan HS; R13055 (M), R13056, R73521, R90643 (F), R90864 (M) Woodstock Station; R83772 (F) 25 km WNW Balfour Downs; R108813 (M) 20 km E South Hedland.

Diagnosis

A moderately large, moderately elongate blindsnake with prominent beaked snout, 22 midbody scale rows and nasal cleft intersecting preocular. Distinguishable from other *Ramphotyphlops* with 22 midbody scale rows as follows: from *R. hamatus* by more numerous vertebrals (Q > 400 v. < 400; \Im usually > 380 v. usually < 380), relations of nasal cleft (from second supralabial in *R. hamatus*) and more anteriorly placed nostril; from *R. australis* (sensu Storr 1981) by more prominently beaked snout, relations of nasal cleft (from second supralabial in *R. australis*) and more numerous vertebrals (*australis* Q < 365; $\Im < 330$); from *R. endoterus* by longer snout, more elliptical rostral, more anteriorly placed nostril and less numerous vertebrals (*endoterus* Q > 426; $\Im >$

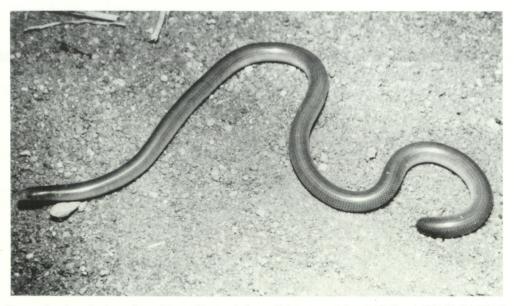


Figure 1 A male *Ramphotyphlops pilbarensis* from 20 km east of South Hedland (WAM R108813), photographed in life by B.Maryan.

416). Distinguishable from the superficially similar R. unguirostris in having fewer midbody scale rows (22 v. 24) and in the relations of the nasal cleft (to first supralabial in R. unguirostris).

Description

SVL: \bigcirc 312-362 (N=2, X=337±35.4) 3 225-260 (4, 239±15.2) all specimens 110-362 (N=8). Tail: \bigcirc 7.7-8.8 (2, 8.3±0.8) 3 8.9-9.7 (4, 9.3±0.4). Tail as % of total length: \bigcirc 2.37-2.41 (2, 2.4±0.02) 3 3.6-3.8 (4, 3.8±0.1); Diameter: \bigcirc 6.4-7.0 (2, 6.7±0.4) 3 5.1-5.7 (4, 5.3±0.3). Number of times diameter repeated in total length: \bigcirc 45.7-57.9 (2, 51.8±8.7) 3 42.3-50.4 (4, 46.6±3.6).

Head moderately elongate and moderately depressed. Rostral "beak" prominent, rounded in dorsal outline, with slight to moderate bilateral indentations on each side of rostral scale; extended backward by low ridge to near posterior margin of preocular; margin of beak acute but usually lacking a distinct "cutting edge" or any ventral emargination. Nostrils inferior, situated about 3/4 way from eye to tip of snout; shielded above by posterolateral continuation of rostral beak. Eyes moderately large and distinct.

Rostral (from above) elliptical, longer than wide, about 2/3 as wide as snout, and extending back about 4/5 way to eyes; rostral margins on undersurface of snout converging to rear; lingual groove weakly developed. Nasals narrowly to widely separated behind rostral; nasal cleft crosses preocular/nasal suture well above level of supralabials, then runs to second supralabial; not continued beyond nostril. Preocular

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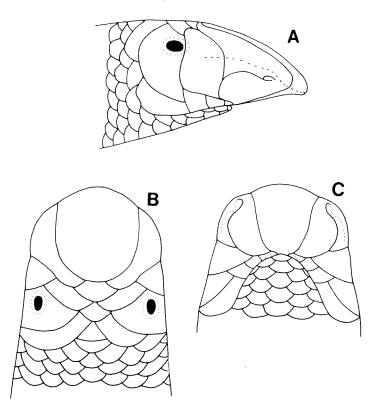


Figure 2 Head scalation of the holotype of *Ramphotyphlops pilbarensis* in A, lateral, B, dorsal and C, ventral views.

narrow, less than half width of ocular. Prefrontal larger than frontal, these scales in narrow contact; frontal slightly smaller than interparietal. Supraoculars subequal to prefrontal, narrowly excluded from median contact. Scales of first postocular row usually fused into elongate "nuchals" of 2-4 scale rows width. Supralabials 4, increasing in size from first to last; first contacts rostral and nasal; second abuts nasal and preocular; third is deeply wedged between preocular and ocular. Mental no larger than postmental scales; infralabials 3, third covered by last supralabial.

Scales rows 22 at midbody (N=8) and on neck (8). Vertebrals: \bigcirc 400-425 (2; 412.5±17.7); \bigcirc 372-391 (4, 384.0±8.3); all specimens 363-425 (8). Subcaudals: \bigcirc 15-16 (2; 15.5±0.7); \bigcirc 17-22 (4; 20.0±2.5); all specimens 15-22 (N=8).

Colour (in preservative) of dorsal and upper lateral surfaces pale purplish-brown; of lower surface (9-11 scale rows wide) cream; boundary between these zones usually diffuse, owing to presence of some partially pigmented scales, but jagged and sharp in some areas of most specimens. Snout pale, with diffuse pigmentation. Tongue (protruding on R10897) bifid for 1.4 mm; with 2-3 lateral papillae just proximal to furcation.

Inverted hemipenis (as revealed by dissection of R10897) helically coiled, with 3 complete turns. Noninversible portion of hemipenis extremely elongate, 'flagellum'-like, protuding from cloacal aperture in R90864.

Retrocloacal sacs (sensu McDowell 1974) of males very elongate, extending forward 15.7 mm (a total of 29 scales) from the vent in R90864.

Individual and ontogenetic variation.

In R83772 the rostral beak bears a sharp cutting edge; this is interrupted at the level of each rostral/nasal suture, and lacks any distinct emargination. In the two immature specimens (R13056 and R73521) the rostral beak is less prominent and less acutely angled than in adults. Immature pattern as for adults but dorsum paler.

Details of holotype.

SVL: 232 mm; Tail: 9.1 mm; Vertebrals: 372; Subcaudals: 19; Diameter: 5.7 mm.

Distribution and habitat

Known from scattered localities in the catchments of the Yule and de Grey Rivers, northwestern Western Australia; from Woodstock Station in the northeast Pilbara, north to Muccan on the De Grey River, and southeast to Balfour Downs on the southern margin of the Great Sandy Desert (see Figure 2).

Detailed habitat data are available for two specimens (R90643 and R90864), both pit-trapped at How *et al.*'s (1991) Site WS2 on Woodstock Station. This site is described as follows: "*Acacia pyrifolia*, 2-3 m tall, 3% canopy cover, *Hakea suberea*, 2-3 m tall, <0.5% canopy cover and *Acacia* sp. 2-3m tall, <0.5% canopy cover over *Triodia* spp.(2) c. 0.5m tall, 80% canopy cover. Soil coarse sandy loam with granite bedrock at 30-40 cm. Site was burnt in January 1990." Site WS2 was further characterized by an abundance of meat ant (*Iridomyrmex*) nests (J.Dell, *pers.comm*.).

Etymology

After the region in which it occurs, and with the aim of drawing attention to the largely unheralded level of faunistic endemism of the Pilbara region.

Ramphotyphlops hamatus, Storr 1981 Figure 4

Material

Specimens marked with asterisk were included in electrophoretic study; sex indeterminate unless stated. R81525 (F) White Cliffs Homestead; R56072 (F), R58925 (F), R69572 (F) Marandoo; R67920 (F), R66323 (M); R66322 (M), R67919 (F) 31-36 km SE Mt Meharry; R92998 (M) 6 km WSW Mt Newman; R26304 (F) Newman; R13359 Jiggalong; R15113 (M) Ullawarra Station; R34570 50 km E Carnarvon; R37049 (M) Callagiddy Station; R62373 (M) Mt Narryer Station; R82734 19 km N Nerren Nerren HS; R62870 (M) 21 km SSE Mt Keith; R69294 (M), R69329, R69306 (M), R74795 (M), R69226 (F), R69242 (F) 9.5-12.5 km SSE Banjawarn; R62871 (F) 10km NW Erlistoun; R69193 (F) 18.5 km ENE Yuinmery HS; R97337 (F) Mullewa; R1733 (M) Newmarracarra via Geraldton; R32368 Geraldton; R28312 (F) Canna; R34684 (F) 7 km E Oudabunna HS; R13686 (F) Morawa; R12653 (F) Paynes Find; R72900 (M) 2.5 km N Mt.Linden; R45699 (F) Three Springs; R24789 (F) Caron; R73357 (F) 11.5 km WNW Mt Manning Range; SAMR29495* (F) Leonora; R10044 (F) Pithara; R24984 (F) Mollerin; R7025 Boulder; R21568 (F) Merredin; R97470* (M) 9.5 km NE Kellerberin.

Description

SVL: Q 85-377 (23, 253.3±61.8) O 110-273 (15, 214.9±51.2) all specimens 85-377 (44). Tail: Q 2.6-8.8 (23, 8.2±1.6) O 4.5-11.0 (15, 7.9±2.1). Tail as % of total length: Q 1.7-3.2 (23, 2.4±0.4) O 2.3-4.1 (15, 3.6±0.5); Diameter: Q 2.3-7.8 (23, 5.6±1.3) O 2.4-6.9 (15, 4.8±1.3). Number of times diameter repeated in total length: Q 28.7-58.7 (23, 46.6±6.9) O 38.1-57.8 (15, 47.3±5.9).

Head moderately elongate, not markedly depressed (see Figure 4). Rostral beak prominent, rounded in dorsal outline, with slight to very slight indentations at lateral margins of rostral; extended backward by low ridge to near posterior margin of preocular; margin of beak acute, that portion of beak on rostral scale with a distinct, emarginated cutting edge. Nostrils inferior, situated about 2/3 way from eye to tip of snout; shielded above by posterolateral continuation of rostral beak. Eyes moderately large and distinct.

Rostral (from above) subovate, slightly longer than wide, about 3/4 as wide as snout, and extending back 4/5 way to eye; lateral margins of rostral on undersurface of snout convergent to rear; rostral without lingual groove. Nasals narrowly to widely separated behind rostral; nasal cleft passes well forward of preocular/nasal suture, usually runs to second supralabial near contact with first supralabial (occasionally to the inter-labial suture); not continued beyond nostril. Preocular about 2/3 width of ocular. Prefrontal larger than frontal, these scales in narrow contact; frontal smaller than interparietal. Supraoculars subequal to prefrontal, narrowly excluded from median contact. "Nuchals" usually one per side. Supralabials four, morphology as in *R. pilbarensis*. Mental larger than postmental scales; infralabial row as in *R. pilbarensis*.

Scales rows 22 (N=46) at midbody and on neck (N=10). Vertebrals: \bigcirc 343-396 (23; 370.4±16.2); 3 330-367 (15; 350.3±10.0); all specimens 330-396 (N=44). Subcaudals: \bigcirc 12-16 (23; 13.3±1.2); 3 12-18 (15; 15.8±1.7); all specimens 12-18 (44).

Dorsal and upper lateral surfaces (in preservative) pale to dark purplish-brown; lower surfaces cream, usually 9-11 scale rows in width (but as few as 3 in some specimens); primary boundary usually jagged and sharp, owing to bordering scales being either wholly dark or immaculate; most specimens with some outlying, all dark scales. Snout variably pale or dark.

Immature specimens with paler upper colouration but with same basic patterning as adults.

Tongue (protruding on R69329, R12653) bifid for 1.5 mm; with 2-3 lateral papillae just proximal to furcation.

Inverted hemipenis (as revealed by dissection of R72900) helically coiled, with 3 turns; apical, noninversible "flagellum" elongate.

No trace of retrocloacal sacs in two adult males examined (R72900 and SAMR29495), despite presence of sperm in efferent ducts.

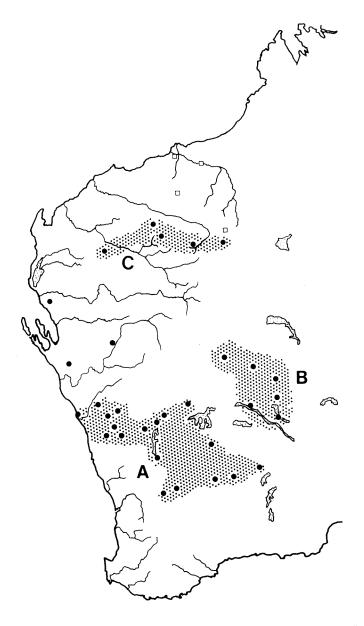


Figure 3 Map of Western Australia showing specimen locations for *Ramphotyphlops pilbarensis*(□) and *Ramphotyphlops hamatus*(•). For analysis of geographic variation, the sample of *R. hamatus* is arbitrarily divided into three geographic regions: A, "Southwestern"; B, "Eastern"; and C, "Northern".

Distribution and geographic variation

Widespread through southern arid and semi-arid regions of Western Australia, from various localities in the Hamersley Range south to Kellerberrin in the Wheatbelt and Woolgangie in the southern Goldfields (see Figure 3). The easternmost records are from the Laverton district in the eastern Goldfields. With the exception of one specimen (R34570) from Grey's Plains (southeast of Carnarvon), all specimens are from localities above 200 m in elevation.

Specimens from the eastern and northern part of the range are longer on average and have higher vertebral scale counts than those from the southwestern region. Using the arbitrary geographic groupings shown on Figure 3, vertebral counts of female R. *hamatus* are 343-375 (N=13) for area A, 374-383 (4) for Area B, and 383-396 (5) for area C. Males show similar though less pronounced trends. There are no obvious trends in either subcaudal counts, diameter or tail length.

With the presently available material, it is unclear whether these geographic differences are representative of gradual clines or of abrupt shifts in population meristics. In either case, it is clear from the limited genetic data (see below) that *R. hamatus* from Kellerberrin (in area A) and from Leonora (in area B) are genetically very similar. For this reason, we are relatively confident that *R. hamatus* as currently comprised represents a single species with at best, weakly differentiated regional populations.

Habitat

Habitat notes are available for 12 specimens scattered throughout the species range; it has been collected in "mallee woodland over spinifex (e.g., R67920, R66322)", in "mid-dense mulga woodland" (R66323), in "samphire" (R74795) and in "bowgada and minner-richie (*Acacia* spp.) at the foot of a breakaway" (R96639). Three specimens were located under rocks; one was dug from an abandoned ant nest.

Electrophoretic distinction between R. pilbarensis, R. hamatus and R. endoterus

Only a small number of specimens were available for electrophoretic analysis, two of R. *pilbarensis* from Woodstock Station, one of R. *hamatus* from each of Kellerberrin and Leonora, and one of R. *endoterus* from Yulara in South Australia. Table 1 shows the allelic profiles of the these samples for 35 presumptive gene loci.

Ramphotyphlops pilbarensis and R. hamatus have fixed differences (i.e., they fail to share alleles) at 12 loci: Est-1, Est-2, Got-1, Hbdh, Mdh-1, Np, Ntak, PepA, Pgam, Pgk, Pgm-2 and Sordh. This amounts to 35% fixed difference overall between the allopatric samples.

Ramphotyphlops pilbarensis and R. endoterus have fixed differences at 11 loci (31% of loci scored): Acon-2, Adh, Gdh, Got-1, Gpi, Hbdh, Mdh-1, Np, Ntak, PepA and Pgam.

The degree of genetic differentiation among these species exceeds that usually found among widely separated populations of a single biological species (Avise 1975; Richardson *et al.* 1986). However, in the absence of sympatric comparisons, the genetic Table 1 Allele frequencies, expressed as a percentage, in four populations of Ramphotyphlops. Alleles are designated alphabetically, with a being the most cathodally migrating allele. Where enzymes are encoded by more than one locus, the loci are designated numerically in order of increasing electrophoretic mobility. Where allele frequencies are not given, the frequency is 100%. Sample sizes are given in brackets at the head of each column. Population 1 is R. pilbarensis from Woodstock Reserve, W.A.; population 2 is R. hamatus from Kellereberin, W.A.; population 3 is R. hamatus from Leonora, W.A.; population 4 is R. endoterus from Kulnara, S.A. The following 21 loci were invariant among the listed populations: Acon-1, Acp. Enol, Fum, Gapd, Gda, Glo, Got-2, Gpi, Lap, Ldh-1, Mdh-2, Mpi, Ndpk-1, Ndpk-2, Pk, Pgm-1, Sod and Tpi.

	POPULATION					
I	LOCUS	1	2	3	4	
		(2)	(1)	(1)	(1)	
1	4con-2	a	a	а	b	
/	4 <i>da</i>	b	b	b	b(50)	
					a(50)	
•	4 <i>dh</i>	b	b(50)	b(50)	b	
			a(50)	a(50)		
	Est-1	a	b	b	а	
	Est-2	b	а	а	b	
1	Fdpase	а	b	а	а	
(Gdh	а	а	а	b	
(Got-1	b	а	а	b	
(Gpi	b	b	b	а	
I	Hbdh	а	b	b	с	
1	Mdh-I	а	b	b	b	
1	Vp	а	b	b	b	
1	Vtak	а	b	b	b	
1	Pep-A	а	d(50)	d	b	
	-		c(50)			
1	Pgam	b(75)	c	с	с	
		a(25)				
1	Pgk	c(25)	а	а	b	
	-	b(75)				
1	^p gm-2	d(25)	а	а	b	
	-	c(50)				
		b(25)				
2	Sordh	b	а	а	c(50)	
					b(50)	

data are merely suggestive and would not constitute sufficient grounds for the recognition of a new species.

A phylogenetic analysis undertaken as part of a wider allozyme electrophoretic study (incorporating several populations of R. australis and R. bituberculatus; the latter employed as an outgroup) suggests that R. hamatus as formerly construed is polyphyletic; i.e. each of R. hamatus and R. pilbarensis are most closely related to part of R. australis as it is currently construed (Aplin and Donnellan in prep.). Interestingly, these data also hint at special cladistic affinity between R. endoterus and R. hamatus.

The two populations of R. hamatus have a single fixed difference at the Fdpase locus. This may be indicative of a low level of genetic differentiation between the Wheatbelt and the Eastern Goldfields populations of R. hamatus, or may it be due to the small sample sizes, one in each case. Additional sampling is required to clarify this point.

Summary of morphological differences between R. pilbarensis, R. hamatus and R. endoterus

Ramphotyphlops pilbarensis is most readily confused with each of *R. hamatus* and *R. endoterus*. All three are moderately elongate snakes with 22 scales at midbody and a pronounced rostral beak. Nevertheless, each is readily identified by a combination of meristic and discrete characters.

Ramphotyphlops pilbarensis differs most strikingly from R. hamatus in the relations of the nasal cleft: this intersects the preocular/nasal suture in R. pilbarensis yet passes well forward of this suture in R. hamatus (compare Figures 1 and 3). Other differences include the more anterior placement of the nostril in R. pilbarensis, the more acutely pointed (from above) snout of R. hamatus, and the presence of a distinct emargination of the rostral beak in R. hamatus alone. The two species are closely similar in snout-vent length and body proportions, with females substantially longer and stouter than males in both R. hamatus and R. pilbarensis. Females of each species likewise show no difference in tail length, however the tail of male R. pilbarensis appears to be slightly longer on average than that of male R. hamatus.

Vertebral and subcaudal counts also show strong sexual dimorphism in each of the two species. In this case however, there is also a clear separation **between** the species for **each sex**, *R. pilbarensis* with higher vertebral and subcaudal counts than *R. hamatus*. Given that the two species do not differ in absolute size, the body scales of *R. pilbarensis* are thus relatively foreshortened, resulting in a greater number of scale whorls for a given length of snake. Unfortunately, the degree of difference is not sufficient to make this a viable means of identification, there being only 20-30 additional whorls in a snake of 200-300 mm SVL (i.e., one extra whorl per cm).

Ramphotyphlops pilbarensis and R. endoterus are similar in many respects including the relations of the nasal cleft (contacting the preocular in both species), the absence of any emargination around the rostral beak, and overall size and proportions. Ramphotyphlops endoterus differs from R. pilbarensis in having a relatively shorter snout, a more nearly ovate rostral shield (as viewed from above; see Figure 24 in Waite 1918), higher vertebral counts (Q 436-447 v. 400-425; \Im 416-445 v. 372-387; values for R. endoterus from unpublished observations on material in W.A. and S.A. Museums), and lower subcaudal counts (Q 10-16 v. 15-16; \Im 15-18 v. 19-22).

The hemipenis of *R. endoterus* (based on R17782 and R22096) is essentially similar to that of the other species, having a long apical flagellum and three helical coils in the inverted condition. Male *R. endoterus* appear to lack retrocloacal sacs. In this regard it is similar to *R. hamatus* and differs from *R. pilbarensis*.

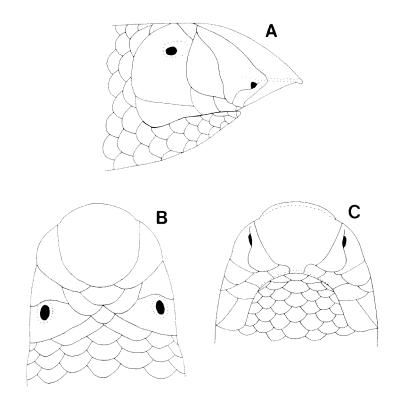


Figure 4 Head scalation of the holotype of *Ramphotyphlops hamatus* in A, lateral, B, dorsal and C, ventral views.

Discussion

The presence in the new species of both a helically coiled hemipenis bearing a long, noninversible portion, and well-developed retrocloacal sacs support its inclusion within *Ramphotyphlops* as defined by Robb (1966; see also McDowell 1974, as *Typhlina*). More suprising is the finding that retrocloacal sacs are absent in at least some individuals of the species *hamatus* and *endoterus*, this despite the presence in both of a hemipenis of the *Ramphotyphlops* type. Since retrocloacal sacs are widely distributed among Australo-papuan typhlopids (Robb 1966; McDowell 1974) their absence in the latter two species, if confirmed, is most likely due to secondary loss. However, much additional work on the reproductive anatomy of these taxa is required before any firm conclusions should be drawn.

The present study raises a number of additional points of general relevance to the systematics of Australian typhlopid snakes. The first is that the level of meristic variation in species of *Ramphotyphlops* has been overestimated in earlier studies, owing to the presence of significant sexual dimorphism, the presence of some composite taxa, and the presence of significant geographic variation in some values. In the case of *R. hamatus*, Storr reports a combined sex, species-wide range of 338-394 for ventrals and 11-22 for subcaudals. Our data indicate that males of this species have significantly narrower ranges for both vertebrals (330-367) and subcaudals (12-18), while females show a narrower range for subcaudals (12-16) but an equivalently wider range for vertebrals (343-396). As indicated above, female vertebral counts show marked geographic variation and actual populational ranges may be considerably narrower; viz. ranges of 343-375 (N=13), 374-383 (4) and 383-396 (5) for the southwestern, eastern and northern regions respectively. Clearly then, analyses based on known-sex samples should yield better taxonomic discrimination among species of *Ramphotyphlops*, particularly where comparisons are between geographically restricted samples.

A high level of sexual dimorphism was recorded by Laurent (1964) and Roux-Esteve in African typhlopids (*Typhlops* and *Rhinotyphlops*) and is evident in meristic data supplied by McDowell (1974) for various Indonesian and Melanesian typhlopids (*Typhlops* and *Ramphotyphlops*). From our ongoing studies of Australian *Ramphotyphlops*, we can confirm the presence of marked dimorphism in at least 6 species (*hamatus, pilbarensis, pinguis, australis sensu* lato; the latter taxon probably a composite of 3 species). We suggest that marked sexual dimorphism will be a major component of meristic variation in many if not all Australian typhlopids, and urge that all future taxonomic work on the group be based on "known sex" comparisons.

A second general point concerns the taxonomic utility of certain features which have in the past been used to distinguish between species of *Ramphotyphlops*. Tail length and body diameter are two characters which feature in many of the original descriptions of Australian typhlopids and in Boulenger's (1893) key to "*Typhlops*". Tail length is often referred to either in relation to overall body length or in relation to tail breadth. As shown in this study, tail length is both absolutely and relatively longer in male than in female *Ramphotyphlops*, presumably as a means of accomodating the elongate hemipenes. Moreover, because males are actually smaller overall, this translates into an even greater dimorphism in relative length. The length to width ratio is also affected in the same way as males have a longer tail but are narrower bodied (and tailed) overall. Body diameter is often cited in relation to body length (i.e. the diameter goes 30-40 times in the total length). Although in *R. hamatus* diameter is also sexually dimorphic when taken as an absolute, this is offset by the greater length of females. Hence the ratio of body length to body diameter appears not to differ significantly between the sexes.

One character which appears to have been downplayed by recent workers is the relations of the nasal cleft. This character features prominently in Boulenger's key to the blindsnakes of the world, and provides the first triplet in Waite's (1918) key to Australian typhlopids. Cogger (1986 and earlier editions), however, cautioned against strong reliance on this character for identification, and suggested that it "is much more variable

than has generally been conceded". Storr (1981) employed the relations of the nasal cleft as a terminal key character, but noted variation in this character in three taxa: *R. australis, R. hamatus* and *R. grypus.* Interestingly enough, two of these taxa are now known to be composites, and at least in the latter case, the differing relations of the nasal cleft actually represents the single most effective means of distinguishing *R. pilbarensis* from *R. hamatus.* This is not to say that this character is invariant or that it will always reliably discriminate between species, but rather that the level of variability of any given characters can only be determined in the context of a well-resolved taxonomy based on other characters. In the case of anatomically conservative groups such as typhlopid snakes, biochemical techniques including allozyme electrophoresis hold great potential for the initial discrimination of morphologically cryptic species.

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APPENDIX I

Proteins examined, Enzyme Commission numbers, and Abbreviations

Aconite hydratase (ACON, E.C. 4.2.1.3), acid phosphatase (ACP, E.C. 3.1.3.2) alcohol dehydrogenase (ADH, E.C. 1.1.1.1), enolase (ENOL, E.C. 4.2.1.11), esterase (EST, E.C. 3.1.1.1), fructose-diphosphotase (FDPASE, E.C. 3.1.3.11), fumarate hydratase (FUM, E.C. 4.2.1.2), glyceraldehyde-phosphate dehydrogenase (GAPD, E.C. 1.2.1.2), guanine deaminase (GDA, E.C. 3.5.4.3), glutamate dehydrogenase (GDH, E.C. 1.4.1.2), lactoylglutathione lyase (GLO, E.C. 4.4.1.5), aspartate aminotransferase (GOT, E.C. 2.6.1.1), glucose phosphate isomerase (GPI, E.C. 5.3.1.9), 3-hydroxybutyrate dehydrogenase (HBDH, E.C. 1.1.30), lucine amino peptidase (LAP, E.C. 3.4.1.1), lactate dehydrogenase (LDH, E.C. 1.1.1.27), malate dehydrogenase (MDH, E.C. 1.1.1.37), mannosephosphate isomerase (MPI, E.C. 5.3.1.8), Nucleoside diphosphate kinase (NDPK, E.C. 2.7.4.6), purine-nucleoside phosphorylase (NP, E.C. 3.4.-.-), phosphgycerate mutase (PGAM, E.C. 2.7.5.3), phosphgycerate kinase (PGK, E.C. 2.7.2.3), superoxide dismutase (SOD, E.C. 1.15.1.1), L-iditol dehydrogenase (SORDH, E.C. 1.1.1.4), triose-phosphate isomerase (TPI, E.C. 5.3.1.1).

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