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An extended description of the Pilbara Death Adder, *Acanthophis wellsi* Hoser (Serpentes: Elapidae), with notes on the Desert Death Adder, *A. pyrrhus* Boulenger, and identification of a possible hybrid zone

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Abstract – An extended description is provided for the Pilbara Death Adder, *Acanthophis wellsi*, based on material from throughout the Pilbara region and adjacent Cape Range Peninsula, Western Australia. *Acanthophis wellsi* was formerly confused with the Desert Death Adder, *A. pyrrhus*, but differs from this highly distinctive species in features of head scalation and hemipenial morphology as well as meristic parameters. Possible hybrids between the two species are identified from the Giralia – Cane River area where their distributions interdigitate. Several populations of *A. wellsi* show a striking pattern polymorphism involving melanism of the head and transverse body bands.

A pilot genetic analysis of a small number of individuals suggests that all of the species of *Acanthophis* are closely related. *Acanthophis wellsi* appears to be closest genetically to *A. pyrrhus*, but this may not denote a special cladistic affinity. A cladistic analysis of morphological characters identifies *A. wellsi* as a relatively plesiomorphic species, perhaps closest in overall body form to the common ancestor of all *Acanthophis* species.

INTRODUCTION

Australasian elapid snakes of the genus *Acanthophis*, commonly known as Death Adders, are found in most parts of Australia and New Guinea and west to the Indonesian island of Ceram. Despite a high level of public and scientific interest in these snakes, little basic taxonomic research has been undertaken on the group. Storr (1981) recognised three closely related species in Western Australia, which he tentatively identified as *A. antarcticus* (Shaw and Nodder), *A. praelongus* Ramsay and *A. pyrrhus* Boulenger. Unfortunately, Storr's plea for a thorough, Australia-wide revision of the group has not been taken up, with the result that his taxonomic concepts remain largely untested outside of Western Australia. Barnett and Gow (1992), Mitschin and Davis (1992), Ball (1993) and Hoser (1995) all alluded to the presence of additional undescribed species of *Acanthophis* in Australia. McDowell (1984) and O'Shea (1996) both commented on the confused state of taxonomy of New Guinean Death Adders.

The nomenclature of *Acanthophis* has been impacted by two works published by 'amateur' herpetologists in unrefereed contexts. Wells and Wellington (1985) proposed four additional species of *Acanthophis* in their essentially self-published "Classification of the Amphibia and Reptilia of Australia". Three of these proposed taxa (*armstrongi, lancasteri, schistos*) were based solely on Storr's (1981) figures and descriptions of each of the three Western Australian populations; these are *nomina nuda* because they do not include or point to previously published differential diagnoses. The fourth Wells and Wellington name, *A. hawkei*, proposed for the 'Barkly Adder', minimally satisfies the conditions for 'availability' as set out by the International Code of Zoological Nomenclature (1985). However, the taxon has not been adequately diagnosed and for the present is best treated as a junior synonym of *A. antarcticus*.

More recently, Hoser (1998) described five new species and one new subspecies of *Acanthophis* in an "overview" of Death Adders, published in *Monitor*, the jounal of the Victorian Herpetological Society. Hoser's nomenclature is a mixture of invalid usage based on unavailable Wells and Wellington names, together with several new names which minimally satisfy the terms of availability as defined by the ICZN (1985). One of the available Hoser names is applicable to a distinctive taxon from the Pilbara region of Western Australia, which the present authors had submitted for publication earlier in 1998. The status of Hoser's other proposed new taxa (*bottomi, crotalusei, cummingi, woolfi*) is currently uncertain and we recommend that these taxa not be taken into general usage until such time as the systematics of the genus is investigated in greater detail. Hoser's continued use of the Wells and Wellington *nomina nuda* "*armstrongi*", "*lancasteri*"

and *"schistos"* also introduces a further element of confusion into the taxonomy of this group.

In this paper we provide an extended description of the Pilbara Death Adder, which now bears the name *Acanthophis wellsi* Hoser (herein emended from *A. wellsei* Hoser). We also give an extended description of *A. pyrrhus* based on material from throughout its range, and present preliminary genetic evidence concerning the level of differentiation among the various species of *Acanthophis*. Finally, we identify a possible zone of hybridization between *A. wellsi* and *A. pyrrhus* based on morphological criteria.

MATERIALS AND METHODS

Specimens in the following collections were examined: Western Australian Museum (WAM); South Australian Museum (SAM); Queensland Museum (QM); and Northern Territory Museum (NTM). Specimens in the Australian Museum (AM) were examined on our behalf by Dr G.M. Shea of Sydney University. The sex of many specimens could be determined by examination of gonads; however, a significant number are either badly damaged or immature, and could not be reliably sexed. Specimens were judged to be 'adult' if they showed signs of reproductive maturity (i.e., enlarged ovarian follicles, elongate or expanded oviduct in females; enlarged testis, convoluted efferent duct in males).

The following standard measurements and counts were taken on all specimens: snout-vent length (SVL); tail length (TailL); ventral scale count [VSC; counted by the method of Dowling (1951)]; and midbody scale count (MSC). The subcaudal scales in *Acanthophis* consist of an anterior series of undivided scales, followed by a series of paired scales which grade onto the characteristic 'caudal lure' with its small spine. The undivided subcaudal scales (USC) and divided subcaudal scales (DSC) were counted separately. All measurements are given in mm.

Mensural and meristic data are presented by sex for each species, and for a 'pooled' sample which includes any unsexed individuals. The extent of sexual dimorphism and regional differentiation within each of *A. wellsi* and *A. pyrrhus* were explored using One-Factor ANOVA; results with $p < 0.05$ are treated as 'significant'. The hemipenis was studied in its everted condition in three specimens of *A. wellsi*; and in its retracted condition by dissection of one specimen each of *A. wellsi* and *A. pyrrhus*.

A series of animals from the Giralia – Cane River area of Western Australia are identified as possible hybrids between *A. wellsi* and *A. pyrrhus*. The mensural and meristic data for these specimens are presented separately, both on account of their intrinsic interest, and also to avoid any blurring of the distinction between the two parental taxa.

Frozen liver samples suitable for allozyme electrophoresis were available from seven individuals of *A. wellsi*, six individuals of *A. antarcticus* derived from four populations, and one individual of each of *A. pyrrhus* and *A. praelongus*. Two individuals of *Echiopsis curta* (Schlegel) and one each of *Notechis scutatus* (Peters) and *N. ater* (Krefft) were also included as outgroups for cladistic analysis and to provide a broader perspective on interspecific and intergeneric genetic differentiation among the live-bearing Australian elapids, the evolutionary lineage to which *Acanthophis* most likely belongs (Greer 1998). Full locality details for all specimens employed in both the morphometric and genetic studies are provided in the Appendix.

Allozyme electrophoresis of liver homogenates was conducted on cellulose acetate gels ('Cellogel', Chemetron) according to the methods of Richardson *et al.* (1986). The proteins and enzyme products of a presumptive 39 loci were scored. The proteins stained, the abbreviations used and the Enzyme Commission numbers are: aspartate aminotransferase (AAT, EC 2.6.1.1), aconitase hydratase (ACOH, EC 4.2.1.3), aminoacylase (ACYC, EC 3.5.1.14), adenosine deaminase (ADA, EC 3.5.4.4), adenylate kinase (AK, EC 2.7.4.3), aldehyde dehydrogenase (ALDH, EC 1.2.1.5), carbonate dehydratase (CA, EC 4.2.1.1), enolase (ENO, EC 4.2.1.11), esterase (EST, EC 3.1.1.?), fructose-bisphosphatase (FBP, EC 3.1.3.11), fumarate hydratase (FUMH, EC 4.2.1.2), glyceraldehyde-3-phosphate dehydrogenase (GAPDH, EC 1.2.1.12), guanine deaminase (GDA, EC 3.5.4.3), glutamate dehydrogenase (GDH, EC 1.4.1.3), glycerol-3-phosphate dehydrogenase (G3PDH, EC 1.1.1.8), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), alanine aminotransferase (GPT, EC 2.6.1.2), glutathione redustase (GSR, EC 1.6.4.2), L-iditol dehydrogenase (IDDH, EC 1.1.1.14), isocitrate dehydrogenase (IDH, EC 1.1.1.42), cytosol aminopeptidase (LAP, EC 3.4.11.1), L-lactate dehydrogenase (LDH, EC 1.1.1.27), lactoylglutathione lyase (LGL, EC 4.4.1.5), malate dehydrogenase (MDH, EC 1.1.1.37), mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), nucleoside-diphosphate kinase (NDPK, EC 2.7.4.6), dipeptidases (PEP-A, EC 3.4.13.?), tripeptide aminopeptidase (PEP-B, EC 3.4.11.?), proline dipeptidase (PEP-D, EC 3.4.13.?), phosphoglycerate mutase (PGAM, EC 5.2.4.1), phosphogluconate dehydrogenase (PGDH, EC 1.1.1.44), phosphoglycerate kinase (PGK, EC 2.7.2.3), phosphoglucomutase (PGM, EC 5.4.2.2), superoxide dismutase (SOD, EC 1.15.1.1) and triose-phosphate isomerase (TPI, EC 5.3.1.1). Alleles are designated in order of cathodal mobility (i.e., *a* signifies least cathodal migration).

SYSTEMATICS

Acanthophis wellsi Hoser, 1998 (emended name)

Acanthophis wellsei Hoser, 1998: 37–39, figs pp. 34, 38 (Type locality: Wittenoom Gorge, Blue Asbestos Mine, Western Australia).

Holotype

WAM R8886, immature animal of uncertain sex, collected by K.H. Burton at the Blue Asbestos Mine, Wittenoom Gorge, Western Australia, Australia in 22°15'S, 118°23'E. The specimen was accessioned on 26th November 1945.

Paratypes

Australia: Western Australia: WAM R21538 from Wittenoom Gorge; R17121 and R18493 from Wittenoom; WAM R67921 from 31 km SE Mt Meharry; WAM R56097 from Marandoo. Full locality details are provided in the Appendix.

Revised diagnosis

A relatively elongate, slender-bodied *Acanthophis*, usually with reddish ground colour, superficially similar to *A. pyrrhus* but differing in having prefrontals usually undivided (always divided in *A. pyrrhus*), less strongly keeled prefrontal scales, less rugose supraocular scales, smooth scales on flanks (keeled in *A. pyrrhus*) and more boldly patterned supralabial, infralabial and mental scales. Further differing from *A. pyrrhus* in having lower modal midbody scale count (19 vs 21), significantly lower ventral (123–141 *vs* 136–158) counts, and usually lacking any dark tipped scales along the posterior margin of each transverse dark band.

Differs from *A. antarcticus* in more slender build and having lower modal midbody scale count (19 vs 21), more numerous ventral scales [110–124 in *antarcticus*; data from Storr (1981)] and usually more subdued dorsal patterning.

Differs from *A. praelongus* in lacking strong lateral flanges on the supraocular scales (weakly developed in Cape Range population of *A. wellsi*), and having lower midbody scale counts (modal count 19 vs 23) and usually more subdued dorsal patterning.

Description

Summary mensural and meristic data are given in Table 1, together with details of statistical tests for sexual dimorphism.

Table 1 Summary mensural and meristic data for *Acanthophis wellsi*, presented separately for male and female specimens and then for a 'pooled' sample which includes unsexed specimens. Results of One-way ANOVA are shown for each primary parameter. A significant level of sexual dimorphism is observed only in number of undivided subcaudal scales, with Tail Length approaching significance.

Parameter	Sex	N	Mean ± SD (Range)	ANOVA results
Snout-Vent Length	M	12	365.8 ± 47.50 (260–435)	F = 0.180, df = 24, p = 0.675
	F	13	355.8 ± 66.74 (237–443)	
	all	40	328.8 ± 85.41 (141–443)	
Tail Length	M	12	71.8 ± 10.26 (54–84)	F = 3.953, df = 24, p = 0.058
	F	13	62.3 ± 13.17 (41–78)	
	all	40	62.2 ± 17.98 (28–90)	
Total Length	M	9	435.1 ± 63.27 (317–511)	F = 0.162, df = 22, p = 0.691
	F	13	422.8 ± 76.56 (290–520)	
	all	35	378.1 ± 111.57 (170–520)	
Tail Length as % of Total Length	M	9	16.3 ± 2.07% (13–18%)	
	F	13	14.9 ± 2.42% (11–18%)	
	all	35	16.0 ± 2.00% (11–19%)	
Ventral body scales	M	12	133.5 ± 3.32 (126–138)	F = 0.318, df = 24 p = 0.578
	F	13	134.5 ± 5.52 (123–141)	
	all	40	133.9 ± 4.05 (123–141)	
Subcaudal scales	M	7	49.9 ± 3.13 (46–55)	F = 3.274, df = 16, p = 0.090
	F	10	46.8 ± 3.62 (41–52)	
	all	29	47.3 ± 4.01 (41–55)	
Undivided subcaudal scales	M	11	28.6 ± 4.30 (24–39)	**F = 13.93, df = 25, p = 0.001**
	F	15	21.1 ± 4.45 (11–28)	
	all	44	25.9 ± 5.54 (11–39)	
Divided subcaudal scales	M	11	21.3 ± 4.43 (13–28)	F = 2.358, df = 25, p = 0.138
	F	15	23.7 ± 3.75 (19–34)	
	all	43	21.6 ± 4.85 (6–34)	
Total ventral scales	M	6	183.7 ± 5.85 (175–191)	F = 2.233, df = 13, p = 0.161
	F	8	178.5 ± 6.78 (168–188)	
	all	23	180.4 ± 5.81 (168–191)	

SVL 141– 443 (n=40). Mean SVL for adult males (342.3) and for adult females (364.4) not significantly different. TailL 24–94 (n=40); or 11.5–19.3% of total length. Mean TailL of males (68.0) significantly higher than that of females (61.6).

Ventral scales 123–141 (n=40); mean ventral count of females (135.3) significantly higher than that of males (132.2). Subcaudal series consists of proximal undivided series, followed by divided series which terminate in weakly 'caudal lure' and spine. Combined subcaudal count is 43–63 (n=44), mean subcaudal count significantly higher in males (49.8) than females (44.4). Undivided subcaudals 13–39 (n=43), mean USC significantly higher in males (29.2) than females (21.1). Divided subcaudals 6–34, mean DSC not differing between sexes. Caudal 'lure' not markedly compressed and lacking any obvious specialization of scales except for presence of terminal spine. Tail tip usually white (71%; n=34), less often entirely dark (26%) or banded (3%).

Body scales in 17–21 rows at midbody, modal 19 (82%; n=43). Keeling of body scales most prominent on upper four dorsal scale rows; more lateral scale rows weakly keeled or smooth.

Head pear-shaped, broadest across rear, narrowing abruptly onto facial region (Figure 2b,c). Snout relatively deep and foreshortened.

Head scalation mildly rugose. Prefrontals generally undivided, one per side. Frontal and parietal scales with subdued, irregular sculpting. Single supraocular scale with subdued, irregular sculpting but lacking lateral flange. Preocular always single. Suboculars usually 2 (93%, n=43), occasionally 3 (7%). Postoculars usually 2 (93%, n=43), occasionally 1 (7%). Numerous temporal scales usually arranged in 3+4+5 or 3+3+5 pattern. Primary temporals usually 3 (91%, n=43), occasionally 2 (7%) or 4 (2%). Secondary temporals usually 4 (58%) or 3 (30%), occasionally 5 (12%). Tertiary temporals usually 5 (86%), occasionally 4 (5%) or 6 (9%). Uppermost temporal scales with distinct keels; lower temporal scales smooth.

Rostral scale relatively high and narrow. Upper labials always 6 (n=43), fifth and sixth largest of series. 'Temporolabial' scale (*sensu* McDowell 1970) here counted with secondary temporal series.

Main features of head and body pattern can be seen in Figures 1a–c and 2. Animals exist in two main colour phases – 'typical' and 'melanistic' – but some other variants including rare 'weakly-banded' individuals, are known. The 'melanistic' sample includes individuals of both sex as well as immature animals. The Primary description is of the 'typical' colour phase (Figure 1a); variants are noted as appropriate.

Body and tail are conspicuously banded in all but a few specimens. Bands are usually two longitudinal scales in width (occasionally 1 or 3), alternating between pale brick red to pale yellowish brown and darker reddish-brown to brown. There are usually 40–43 dark bands on the body, with a further 15 or so on tail. Conspicuous black spotting occurs across both anterior and posterior margins of dark bands on neck, but is generally confined to posterior margin of bands on mid- to lower body and on tail. In rare exceptions (e.g., WAM R125733) spotting is present across the anterior margin of bands throughout the entire length of the snake.

Crossbands become diffuse on lower flanks, giving way to two rows of black spots; these are strongest on the neck and weaken posteriorly. The lower row of spots is positioned on the outer margin of the ventral scales. Ventral scales are otherwise immaculate.

Head reddish-brown, often slightly darker than body; pigment extending over temporal scales and upper labials almost to oral margin. Lower labials usually with distinct, centrally located 'spots' of same colour; these are weak or absent in some individuals. Mental scale and adjacent chinshields usually with conspicuous 'inverted-V' mark; this is weakly developed in some specimens.

'Melanistic' individuals (Figure 1b) usually with black head and crossbands on yellowish-brown ground colour. Black spotting is usually discernible across anterior margins of dark bands. Facial pattern as in 'typical' phase. Some individuals (e.g., WAM R125736) have chocolate-brown head and pale chocolate-brown crossbands on pale orange-brown ground colour.

Occasional individuals are plain brick red and have faintly indicated crossbands (Figure 1c); black spotting is restricted to the few anteriormost crossbands in the neck region.

The hemipenis in its everted state is deeply divided, each of the separate 'horns' terminating in a rounded, flattened cupula. The spermatic sulcus bifurcates at the pont of division of the organ and extends onto both horns. The base of the organ is longitudinally ribbed, but the horns are conspicuously and uniformly spinose up to the terminal cupula. In its retracted condition, the hemipenis extends to just past the posterior margin of subcaudal 12. The organ and spermatic sulcus divide at the posterior margin of subcaudal 6 and the terminal cupula takes the appearance of a 'flounce'.

Details of Holotype

The holotype is in a poor state of preservation, especially in the posterior third of the body, and is badly faded. The tail tip including the caudal lure is missing. The following mensural and meristic data can be documented: SVL 215; TailL 35 (incomplete); MBS 19; VTC 132; USC 29; temporals 3+3+5; preocular 1; suboculars and postoculars 2. Indistinct cross bands are visible. The supralabials and temporals are extensively pigmented and the infralabials are prominently marked.

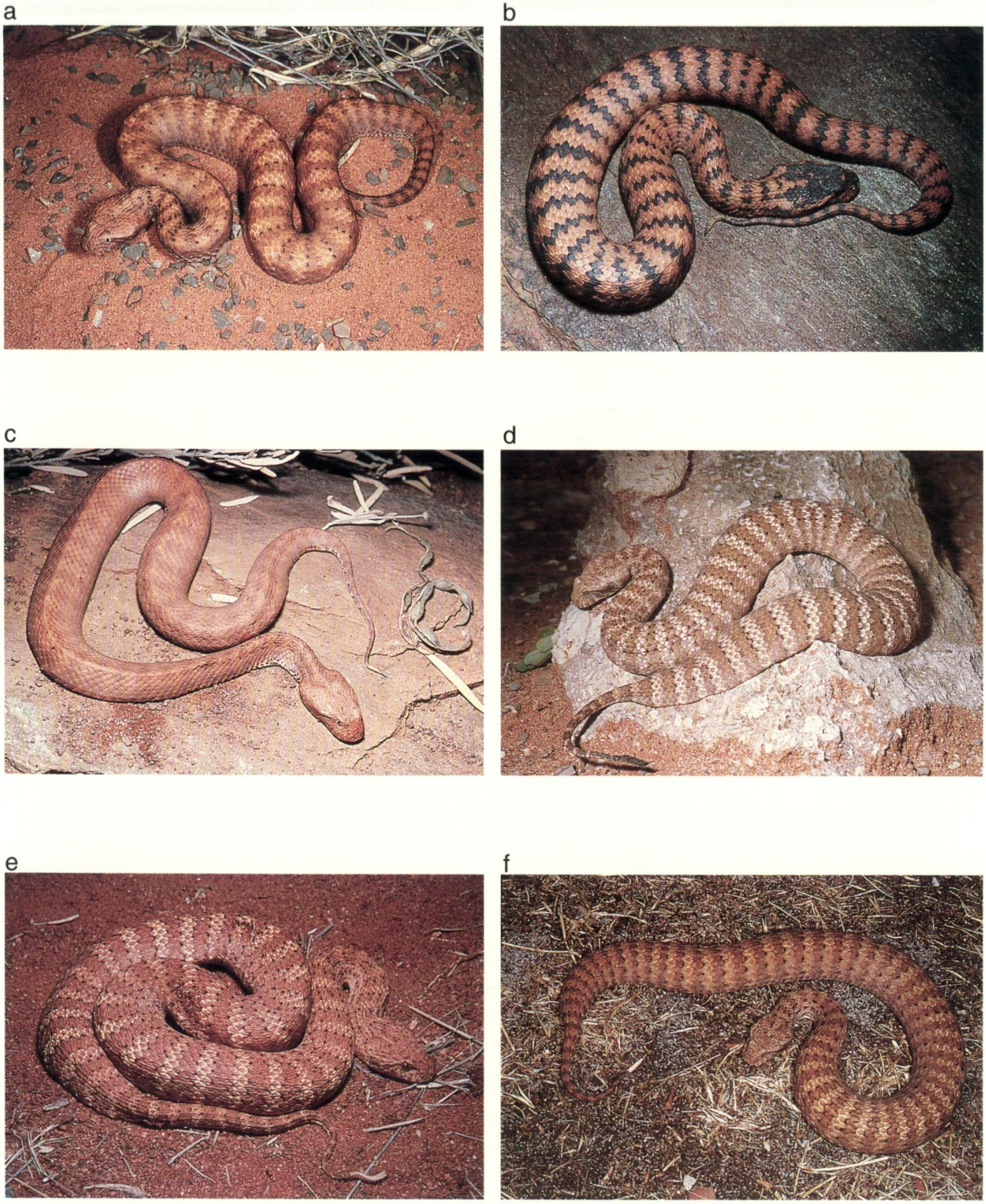

Figure 1 Photographs of various individuals of *Acanthophis wellsi* and *A. pyrrhus* from Western Australia, illustrating extent of inter- and intra- specific variation in morphology and colour pattern. Taxon and locality details as follows: a, *A. wellsi*, 'typical' colour phase from 26 km ENE Mardie Homestead (photograph B. Maryan); b, *A. wellsi*, 'melanistic' colour phase from Pannawonica (photograph B. Maryan); c, *A. wellsi*, 'weakly banded' colour phase from Pannawonica, WAM R113167 (photograph R.E. Johnstone); d, distinctive, pale form of *A. wellsi* from Yardie Creek, Cape Range Peninsula (photograph D. Knowles); e, *A. pyrrhus* from Ord Ranges (photograph B. Maryan); f, possible hybrid *A. wellsi* X *A. pyrrhus* from 4.5 km N Cane River (photograph B. Maryan).

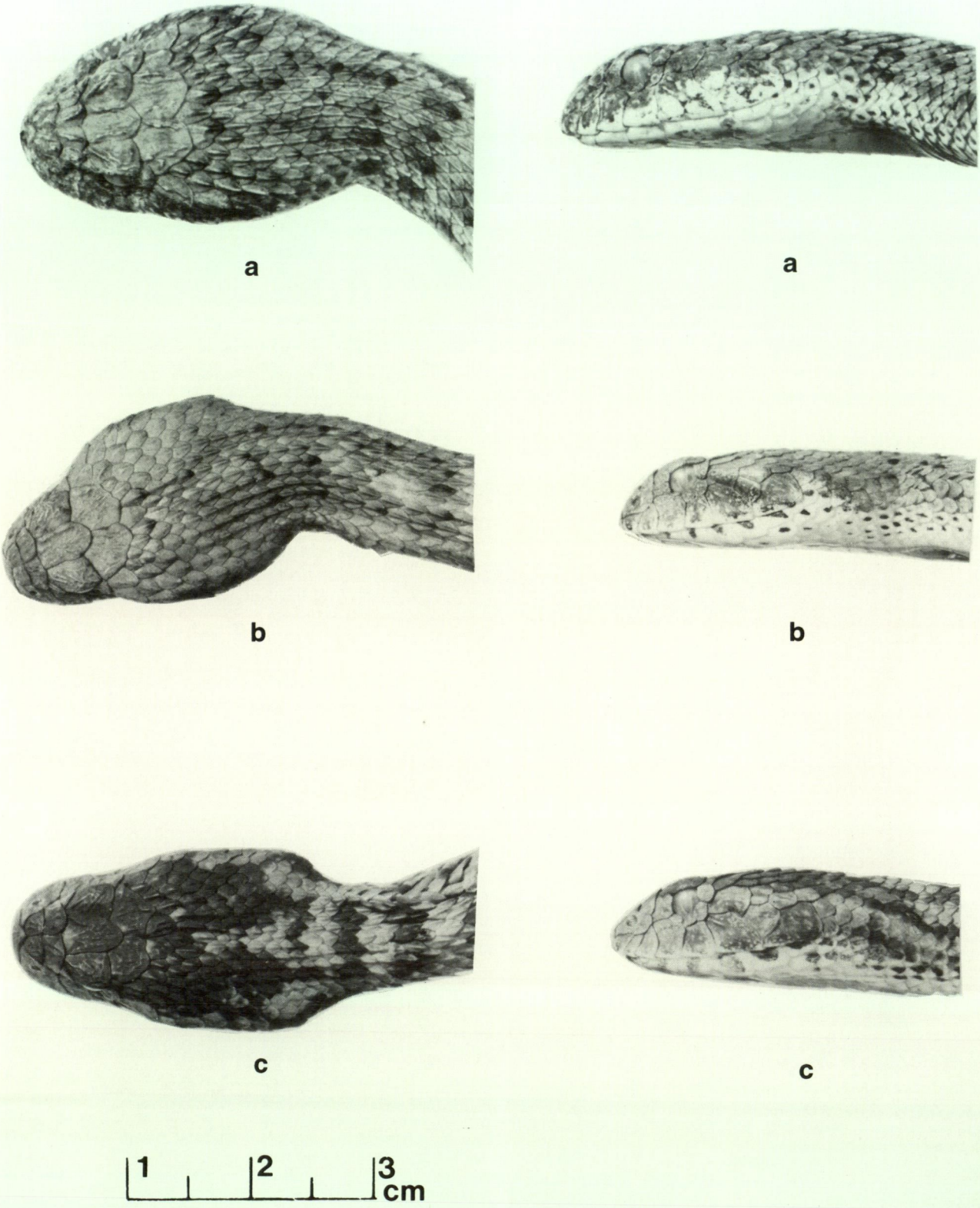

Figure 2 Head scalation and patterning of a, *A. pyrrhus* (WAM R79139), b, *A. wellsi* 'typical' colour morph (WAM R80443) and c, *A. wellsi* 'melanistic' colour morph (WAM R113166), all shown in dorsal and lateral views.

Taxonomic remarks

Wells and Wellington (1985) evidently had some grounds for suspecting that the Pilbara adders were distinct from *A. pyrrhus*. However, they erred in their systematic treatment of the species on two counts. Firstly, *Acanthophis armstrongi* Wells and Wellington, 1985, proposed for adders of the "Pilbara and Kimberley regions of Western Australia", is a *nomen nudum* due to a lack of adequate diagnosis of the taxon (they refer to Storr's

Table 2 Allele profiles for four melanistic (M) and two typically-patterned (T) individuals of *Acanthophis wellsi* from the vicinity of Pannawonica, west Pilbara. All other loci examined were invariant. The two morphs show no differential assortment of alleles and the combined sample is consistent with a single population in Hardy-Weinberg equilibrium.

Regno	Morph	Sex	Aat-2	Acoh-2	Acyc	Gpt	Gsr-1	PepB	PepD	Pgdh	Pgm-1
113374	M	F	de	c	b	a	a	d	c	a	d
113114	M	F	d	ac	bc	ab	ab	ad	c	a	d
113166	M	F	de	ac	b	a	b	ad	c	a	b
113167	M	F	de	ac	b	a	b	d	bc	ab	b
113377	T	M	d	c	b	a	ab	d	bc	ab	cd
113378	T	F	d	c	b	a	b	bd	bc	a	d

description and Figure 3 for diagnostic characters, yet Storr did not compare the Pilbara *'pyrrhus'* with any other population of this species). And secondly, the proposed holotype of *A. armstrongi* (WAM R61537) is not an individual of the true Pilbara Adder, *A. wellsi*. In reality, it is either a true *A. pyrrhus*, as restricted herein, or an individual of hybrid origin. If the latter diagnosis is correct (see below for further discussion), then the name *armstrongi* would be additionally unavailable under the terms of Article 23h of the International Code for Zoological Nomenclature (3rd Edition, 1985), which states that animals of hybrid origin are not permissible as holotypes of new taxa.

Ball (1993: 5) reported the Pilbara Adders as a "suspected new species" and noted that taxonomic work was ongoing at the Western Australian Museum. Hoser (1997) initally applied the name *"armstrongi"* to the Pilbara Adders, but was subsequently informed that the Wells and Wellington name was based on an individual of *A. pyrrhus*. In describing *A. wellsi*, he erroneously implied that Aplin had decided against naming the Pilbara Adder (Hoser 1998: 38). The name *wellsi* only minimally satisfies the requirements of the ICZN (1985) but is adopted here in the interests of nomenclatural stability.

Genetic comparisons

The Pannawonica population of *A. wellsi* (WE1) consists of two 'typical' and four 'melanistic' phase individuals (Table 2). This sample does not show any differential assortment of alleles by colour phase and is consistent with a single population in Hardy-Weinberg equilibrium.

Table 3 shows the allelic profiles of 36 presumptive loci for eight *Acanthophis* populations and the four outgroup samples. The following loci were invariant: ENO, FBP, GPI, G3PDH, IDH-2, LAP, LDH-1, LDH-2, MDH-1, MDH-2, NDPK, PGK and TPI.

The single sample of *A. wellsi* from Cleaverville (WE2), on the northern margin of the species' distribution, shares all of its known alleles with the larger Pannawonica series, hence it can be regarded as part of the same population.

The single available sample of *A. pyrrhus* comes from near Yuendumu in the Northern Territory. It differs from the sample of *A. wellsi* in being homozygous for a distinct allele (c) at *PepA*, heterozygous with two distinct alleles (b,e) at *PepB*, and heterozygous with one shared (a) and one distinct (b) allele at *Acoh-1*.

The single available sample of *A. praelongus* (from northeastern Queensland) is somewhat better differentiated from *A. wellsi*. It is homozygous for distinct alleles at four loci (*Aat-2, Ada, Est, Mpi*), and is heterozygous with one shared and one distinct allele at each of *Gda* and *Gpt*.

The four populations of *A. antarcticus* are all well-differentiated from *A. wellsi*, but show considerable intraspecific variation (discussed further below). The *A. antarcticus* sample as a whole shows 'fixed' allelic differences from *A. wellsi* at two loci (*Ada* and *Est*), with other distinct alleles in various homozygous and heterozygous combinations at three others (*Gpt, Idh-1* and *Pgm-1*). A similar level of distinction is observed from each of *A. pyrrhus* and *A. praelongus*. *Acanthophis pyrrhus* is distinct from *A. antarcticus* at *Est* and *PepB*, while *A. praelongus* is distinct from *A. antarcticus* at *Aat-2* and *Mpi*. Not surprisingly, the larger sample of *A. antarcticus* also provides many unique alleles (e.g., at *Acoh-2, Acyc, Gda, Gpt, Idh-1, PepD, Pgdh* and *Pgm-1*).

The genetic data are summarised as a matrix of percent 'fixed' difference (i.e., loci which lack any shared alleles) in Table 4.

Distribution and geographic variation

Acanthophis wellsi is known from widely scattered localities throughout the Pilbara region, from Robe River and Pannawonica at the western end of the Hamersley Range to the Burrup Peninsula in the north and east through the Chichester Ranges to Carawine Gorge on the Oakover River (Figure 5). An apparently isolated population occurs on the Cape Range peninsula.

Table 3 Allele profiles for various populations and individual specimens of *Acanthophis,* representing each of the four species, and for two species of *Notechis* and for *Echiopsis curta.* Sample codes are as follows: AB1-AB2: *Acanthophis wellsi;* PY1: *A. pyrrhus;* AN1-AN4: *A. antarcticus;* PR1: *A. praelongus;* E1-E2: *E. curta;* N1: *Notechis scutatus;* N2: *N. ater.*

Locus	WE1 (6)	WE2 (1)	PY1 (1)	AN1 (1)	AN2 (2)	AN3 (2)	AN4 (1)	PR1 (1)	E1 (1)	E2 (1)	N1 (1)	N2 (1)
Aat-1	a	a	a	a	a	a	a	a	b	b	a	a
Aat-2	e(25) d(75)	e(50) d(50)	d	d	d	d	d	c	a	b(50) a(50)	a	a
Acoh-1	a	a	b(50) a(50)	a	a	a	a	a	d(50) b(50)	b	c	c
Acoh-2	c(75) a(25)	c	c	c	c	b	c	c	d	d	e	e
Acyc	c(8) b(92)	b	b	b(50) a(50)	b(50) a(50)	b(25) a(75)	b(50) a(50)	b	c(50) b(50)	b	b	b
Ada	c	-	-	b	b	b	b	b	b	b	a	a
Ca	b	b	b	b	b	b	b	b	a	a	a	c
Est	b	b	b	a	a	a	a	a	c(50) a(50)	c	a	a
Fumh	b	b	b	b	b	b	b	b	a	a	a	a
Gapdh	b	b	b	b	b	b	b	b	a	a	a	a
Gda	b	-	b	b	b	b	b	c(50) b(50)	a	a	a	a
Gpt	c(8) a(92)	a	a	e	e	c(25) b(75)	e	e(50) a(50)	f	f	d	f
Gsr-1	d(67) b(33)	b	b	d	b	d	d(50) b(50)	d(50) b(50)	d	d(50) b(50)	a	e(50) c(50)
Gsr-2	b	b	b	b	b	b	b	b	c(50) a(50)	a	a	a
Iddh	a	a	a	a	a	a	a	a	b	b	c(50) b(50)	b
Idh-1	a	a	a	b	b	c(25) b(75)	a	a	a	a	a	a
Lgl	b	b	b	b	b	b	b	b	a	a	b	b
Mpi	b	b	b	b	b	b	b	a	c	c	c	c
PepA	b	b	c	b	b	b	b(50) a(50)	-	d	d	d	d
PepB	d(75) a(17)	d(50) c(50)	e(50) b(50)	d	d	d	d	d	d	g(50) d(50)	f	i(50) h(50)
PepD	c(75) b(25)	b	b	c(50) b(50)	c(25) b(75)	b	c	c	a	a	a	a
Pgam	b	b	b	b	b	b	b	b	a	a	a	a
Pgdh	b(17) a(83)	a	a	a	a	a	a	b(50) a(50)	a	a	a	a
Pgm-1	d(92) c(8)	d	d	d	b	d	b	d(50) a(50)	f(50) d(50)	e(50) d(50)	b	d
Pgm-2	b	b	b	b	b	b	b	b	a	a	a	a
Sod	a	a	a	a	a	a	a	a	b	b	b	b

Unfortunately, sample sizes are inadequate to attempt any statistical analysis of geographic variation, owing to the confounding effect of sexual dimorphism. Specimens of *A. wellsi* from throughout the Pilbara region appear to be fairly uniform in size and meristic parameters. However, the sample of female specimens from the isolated Cape Range population (n=5; see Table 5) could be compared with that from the Pilbara region proper (n=10). This comparison demonstrates that the Cape Range population differs from that of the Pilbara in having significantly lower ventral counts and a relatively longer tail. The Cape Range specimens also differ from other *A. wellsi* in having distinctly

Table 4 Matrix of percent 'fixed' genetic difference between each of the species and populations. A genetic difference between two samples is regarded as 'fixed' if they lack any allele in common. The small samples available for analysis mean that many of the values will be an overestimate of the true level of 'fixed' genetic difference between the populations from which they are drawn.

	WE1 (6)	WE2 (1)	PY1 (1)	AN1 (1)	AN2 (2)	AN3 (2)	AN4 (1)	PR1 (1)	E1 (1)	E2 (1)	N1 (1)	N2 (1)
WE1	-											
WE2	0	-										
PY1	3	5	-									
AN1	0	11	16	-								
AN2	13	11	16	5	-							
AN3	10	14	18	5	10	-						
AN4	10	11	16	5	3	13	-					
PR1	11	11	14	8	11	16	8	-				
E1	51	51	53	49	54	49	49	45	-			
E2	51	49	50	51	54	51	51	47	0	-		
N1	54	51	53	54	51	54	49	50	23	26	-	
N2	51	49	50	51	54	51	51	47	21	23	13	-

flared supraocular scales (less pronounced than those of *A. praelongus*), more strongly developed dorsal keeling on scale rows 1–4, and in being considerably paler, with grey crossbands on a cream ground colour. One specimen (WAM R93212) from Vlaming Head at the extreme north end of the peninsula has bilaterally divided prefrontal scales, but without the associated strong keeling typical of *A. pyrrhus*. These differences suggest that the Cape Range population of *A. wellsi* is genetically isolated from that of the Pilbara region, but the differences may also relate to differences in substrate between the two areas (limestone and sand *vs* iron-rich rocks and skeletal soils). The Cape Range population may warrant subspecific distinction from typical *A. wellsi*; however, it would be prudent to first determine the level of genetic divergence between them.

Melanistic individuals are known from within each of the three sub-regions as defined above; i.e., from Mt Meharry in the southern Hamersley Range (WAM R67921); from Pannawonica on the

Table 5 Comparison of geographically discrete Pilbara and Cape Range populations of *Acanthophis wellsi*. Statistical comparisons are limited to female samples due to small number of available males from the Cape Range population. Significant interpopulational differences are observed in ventral scale counts. The relative tail length values do not overlap between the two small samples, with Cape Range population females having proportionally longer tails. Mensural data are also presented for the combined sex sample of the Cape Range population.

Parameter	Pilbara – females	Cape Range – females	ANOVA results	Cape Range – both sexes
Snout-vent Length	365.2 ± 65.02 (10) (254–443)	324.7 ± 76.20 (3) (237–375)	F = 0.839, df = 12, p = 0.379	301.6 ± 62.7 (8) (237–375)
Tail Length	61.0 ± 13.69 (10) (41–77)	66.7 ± 12.67 (3) (53–78)	F = 0.462, df = 12, p = 0.536	63.4 ± 10.6 (5) (53–78)
Total Length	426.2 ± 75.52 (10) (295–520)	414.3 ± 85.07 (4) (290–483)	F = 0.065, df = 13, p = 0.803	365.0 ± 72.0 (6) (290–444)
Tail Length as% of total length	14.2 ± 1.24% (10) (11.5–15.5%)	17.2 ± 1.45% (3) (15.5–18.3%)		17.5 ± 1.1% (5)
Ventral body scales	137.2 ± 2.30 (10) (133–141)	125.7 ± 2.31 (3) (123–127)	**F = 57.95, df = 12, p = 0.008**	126.2 ± 1.9 (5) (123–128)
Subcaudal scales	46.0 ± 2.75 (5) (43–50)	47.6 ± 4.51 (5) (41–52)	F = 0.460, df = 9, p = 0.516	48.0 ± 4.2 (6) (41–52)
Undivided subcaudal scales	22.5 ± 2.07 (10) (18–28)	21.4 ± 6.19 (5) (11–27)	F = 0.192, df = 14, p = 0.608	21.7 ± 5.6 (6) (11–27)
Divided subcaudal scales	22.5 ± 2.07 (10) (19–26)	26.2 ± 5.31 (5) (20–34)	F = 3.92, df = 14, p = 0.069	26.3 ± 4.8 (6) (20–34)
Total body scales	183.0 ± 3.08 (5) (180–188)	171.0 ± 2.65 (3) (168–173)	**F = 31.15, df = 7, p = 0.001**	172.8 ± 4.1 (4) (168–178)

western margin of the Hamersley Range (n=7; e.g., WAM R113114, WAM R125735); and from Yandicoogina near the northest margin of the Pilbara uplands (WAM R78136). Additional localities include Millstream in the Fortesque River valley (animal photographed by David Robinson) and 60 km NNW of Newman in the Ophthalmia Range (roadkill sighting; Brian Bush, pers. comm.).

The relative abundance of the melanistic form in any area is difficult to determine from voucher collections. Of the total sample of 13 specimens collected since 1991 from around Pannawonica, seven are melanistic individuals. However, this high percentage may well reflect collecting bias, as Ball (1993) reported a single melanistic individual out of 18 adders located during 6 hours of spotlighting along the Pannawonica Road on the night of 29 January 1993.

Acanthophis pyrrhus Boulenger, 1898

Acanthophis pyrrhus Boulenger, 1898: 75. (Type locality: Station Point, Northern Territory).

Acanthophis armstrongi Wells and Wellington, 1985: 43. *Nomen nudum.* (Type locality: 3 km E Giralia, Western Australia).

Revised diagnosis

An elongate, slender-bodied *Acanthophis*, predominantly reddish in colour. Most similar to *A. wellsi* in general appearance but differing from that species and all others in having prefrontal scales divided and strongly keeled, body scales with strong keeling extending down onto flanks and significantly higher ventral scale counts.

Further differs from *A. wellsi* in having higher modal midbody scale count (21 *vs* 19), higher subcaudal scale counts, less prominent spotting of lower labial and mental scales and in details of hemipenial morphology (see below).

Further differs from *A. praelongus* in lacking strong lateral flanges on the supraocular scales and in having lower modal midbody scale counts (21 vs 23).

Description

Summary mensural and meristic data are given in Table 6, together with results of statistical tests for sexual dimorphism.

SVL 160–622 (n=51). Mean SVL of adult males (404.0) and adult females (451.4) not significantly different. TailL 31–118 (n=51); or 15.6–39.1% of Total Length; mean TailL is not significantly different between males (89.6) and females (86.7).

Ventral scales 136–158 (n=52). Mean ventral scale counts of males (145.4) and females (144.1) not significantly different. Combined subcaudal count is 43–63 (n=44), mean subcaudal count significantly higher in males (59.0) than females (50.8). Undivided subcaudals 13–39 (n=53), mean USC significantly higher in males (32.0) than females (24.7). Divided subcaudals 15–37, mean DSC not differing between sexes. Caudal 'lure' dorso-ventrally expanded and compressed, and bearing more finely divided scales which project free of surface to impart a 'feathered' appearance. Tail tip most often dark (58%; n=33), but not uncommonly creamy white (27%) or banded (15.2%).

Body scales in 19–23 rows at midbody, modal 21 (81%; n=52). Upper six rows of body scales bear prominent keels; more lateral scale rows are weakly keeled or smooth.

Head oval-shaped, broadest posteriorly but not narrowing abruptly onto facial region (Figure 2a). Snout moderately depressed and elongate.

Head scales extremely rugose. Prefrontals invariably divided into lateral and medial scales. Supranasal, medial prefrontal, frontal and parietal scales with strong longitudinal ridging aligned in linear series. Lateral prefrontal scales with low ridge in alignment with keeled preocular. Single supraocular scale without lateral flange but with strong oblique ridge and other irregular sculpting. Preocular always single (n=50). Suboculars usually 2 (98%; n=50), rarely 3 (2%). Postoculars usually 2 (98%; n=50), rarely 3 (2%). Numerous temporal scales, usually arranged in 3+3+5, 3+4+5 pattern. Primary temporals always 3 (n=47). Secondary temporals 3 (66%; n=47) or 4 (34%). Tertiary temporals usually 5 (64%; n=47), less often 4 (33%), rarely 6 (3%). All but lowermost temporal scales bear distinct keels.

Rostral scale relatively low and broad. Upper labials always 6, fifth and sixth largest of series. 'Temporolabial' scale counted as part of secondary temporal series.

Main features of head and body pattern can be seen in Figures 1e and 2.

Body and tail are conspicuously banded in all specimens. Bands usually two scales in width (occasionally 1 or 3), colour alternating between pale brick-red/pale yellowish brown and darker reddish-brown/brown. Body usually with 43–47 dark bands, further 15 or so on tail. Conspicuous black spotting occurs across both anterior and posterior margins of dark bands along entire length of body and onto tail.

Crossbands become diffuse on lower flanks where they give way to two rows of black spots; these are most conspicuous on the neck and fade posteriorly onto the body. Ventral scales are immaculate.

The dorsum of the head is the same colour as the paler crossbands. Upper lip with extensive white zone extending onto lower temporal scales; posterior upper labials mottled with pale brick-red. Lower labials usually with poorly developed,

Table 6 Summary mensural and meristic data for *Acanthophis pyrrhus*, presented separately for male and female specimens and then for a 'pooled' sample which includes unsexed specimens including juveniles. The results of One-way ANOVA (F values and statistical significance) are shown for each parameter. Significant sexual dimorphism is observed in the total number of subcaudal scales, the number of undivided subcaudal scales and the total number of ventral scales.

Parameter	Sex	N	Mean ± SD (Range)	ANOVA results
Snout-Vent Length	M	10	398.5 ± 67.81 (302–498)	F = 3.60, df = 31, p = 0.067
	F	22	455.3 ± 82.63 (248–603)	
	all	51	399.7 ± 121.05 (160–622)	
Tail Length	M	10	87.9 ± 18.50(65–115)	F = 0.0247, df = 31, p = 0.876
	F	22	87.0 ± 11.97 (60–105)	
	all	51	80.6 ± 23.23 (31–118)	
Total Length	M	9	499.0 ± 79.69 (386–613)	F = 1.366, df = 23, p = 0.255
	F	15	545.1 ± 100.51 (345–708)	
	all	42	472.7 ± 151.42 (345–708)	
Tail Length as% of Total Length	M	9	17.9 ± 1.40	
	F	15	16.5 ± 5.29	
	all	42	20.5 ± 3.63 (15.6–39.1)	
Ventral body scales	M	12	145.2 ± 4.69 (137–152)	F = 0.011, df = 32, p = 0.918
	F	21	145.0 ± 4.36 (139–158)	
	all	52	145.2 ± 4.14 (136–158)	
Subcaudal scales	M	9	59.0 ± 1.87 (57–62)	**F = 41.33, df = 19, p = 0.000**
	F	11	50.2 ± 3.74 (43–57)	
	all	37	53.7 ± 5.03 (43–63)	
Undivided subcaudal scales	M	10	31.1 ± 3.81 (27–39)	**F = 11.41, df = 30, p = 0.002**
	F	21	24.0 ± 6.12 (13–38)	
	all	53	25.9 ± 6.07 (13–39)	
Divided subcaudal scales	M	9	27.4 ± 2.88 (23–31)	F = 0.031, df = 25, p = 0.861
	F	17	27.8 ± 6.05 (15–37)	
	all	44	27.6 ± 4.74 (15–37)	
Total ventral scales	M	9	204.3 ± 6.44 (194–213)	**F = 9.422, df = 19, p = 0.006**
	F	11	193.8 ± 8.45 (182–215)	
	all	33	199.5 ± 8.27 (182–215)	

centrally located 'spots' of same pale brick-red colour, but these are absent in some individuals. Mental scale and adjacent chinshields are usually immaculate but have an indistinct, inverted-V mark in some specimens.

No everted hemipenes of *A. pyrrhus* were available for study. Dissection of one individual (WAM R79008) revealed that the inverted organ divides at the level of subcaudal 8 and extends back to subcaudal 12. The spermatic sulcus divides at subcaudal 7, below the point of separation of the horns. The basal portion of the hemipenis is longitudinally ribbed and lacks spines. The spinose zone commences just below the hemipenial bifurcation and continues onto the separate horns. The spines are largest proximally and reduce in size towards the tips of the horns. The terminal part of both horns is smooth save for some weak longitudinal ribbing, i.e., it appears to lack the conspicuous terminal flounce (cupula) seen in *A. wellsi*.

Taxonomic remarks

The type specimen of *Acanthophis pyrrhus* (BMNH 1946.1.18.62) was not examined during this study. However, Boulenger's (1898) description mentions all of the key diagnostic features of the larger sample documented here. These include the rugose head-shields, divided prefontals, midbody scales in 21 rows, and a high number of ventral (146) and subcaudal (50) scales. A lack of spotting on the lower labials and throat can also be inferred from his description.

For sake of completeness, we have listed *Acanthophis armstrongi* Wells and Wellington, 1985 as a junior synonym of *A. pyrrhus*. However, as indicated earlier, this is a *nomen nudum* and thus has no nomenclatural standing. As will be dicussed at greater length below, this specimen is also quite possibly of hybrid origin.

Hoser (1998: 35) made inappropriate use of the unavailable name *armstrongi* Wells and Wellington to taxonomically distinguish populations of *A. pyrrhus* from "the Great Sandy Desert of WA and adjacent areas, including coastal parts of the Pilbara". He noted that specimens of *A. pyrrhus* from this area "appear to have more yellow colouring dorsally than those seen from Central

Australia", but qualified this observation by noting "whether this is a general trend difference between both forms is not yet known" (Hoser 1998: 36). As indicated below, the present analysis does not support subspecific distinction between northwestern and Central Australian populations of *A. pyrrhus*.

Distribution and geographic variation

Widely distributed throughout central and western Australia (Figure 3), from southwestern Queenland (Ingram and Raven 1991) through Central Australia north to Barrow Creek, south to the Everard Ranges and west to Balgo Mission and Gahnda Rockhole. In northwestern Australia it occurs in coastal plain habitats from the Port Hedland area along the Eighty Mile Beach to Broome and east to "Wynne Creek" on the northern margin of the Great Sandy Desert (Figure 4). In southern Australia it is known only from Ooldea on the northeastern margin of the Nullarbor Plain. In southwestern Australia it is recorded from scattered points between Kalgoorlie and Albion Downs Homestead in the eastern Goldfields, to Wurarga and Bunjil in the northern Wheatbelt and north to Middalya Homestead, close to the southern border of Exmouth Gulf.

Geographic variation within *A. pyrrhus* was investigated by dividing the total sample into three subpopulations, based on the major physiographic clustering of localities: 1) a northwestern group; 2) a central Australian group; and 3) a southwestern group. Mensural and meristic data for each of these subpopulations are compared in Table 7. The most striking contrast is between the northwestern and southwestern populations which show significant

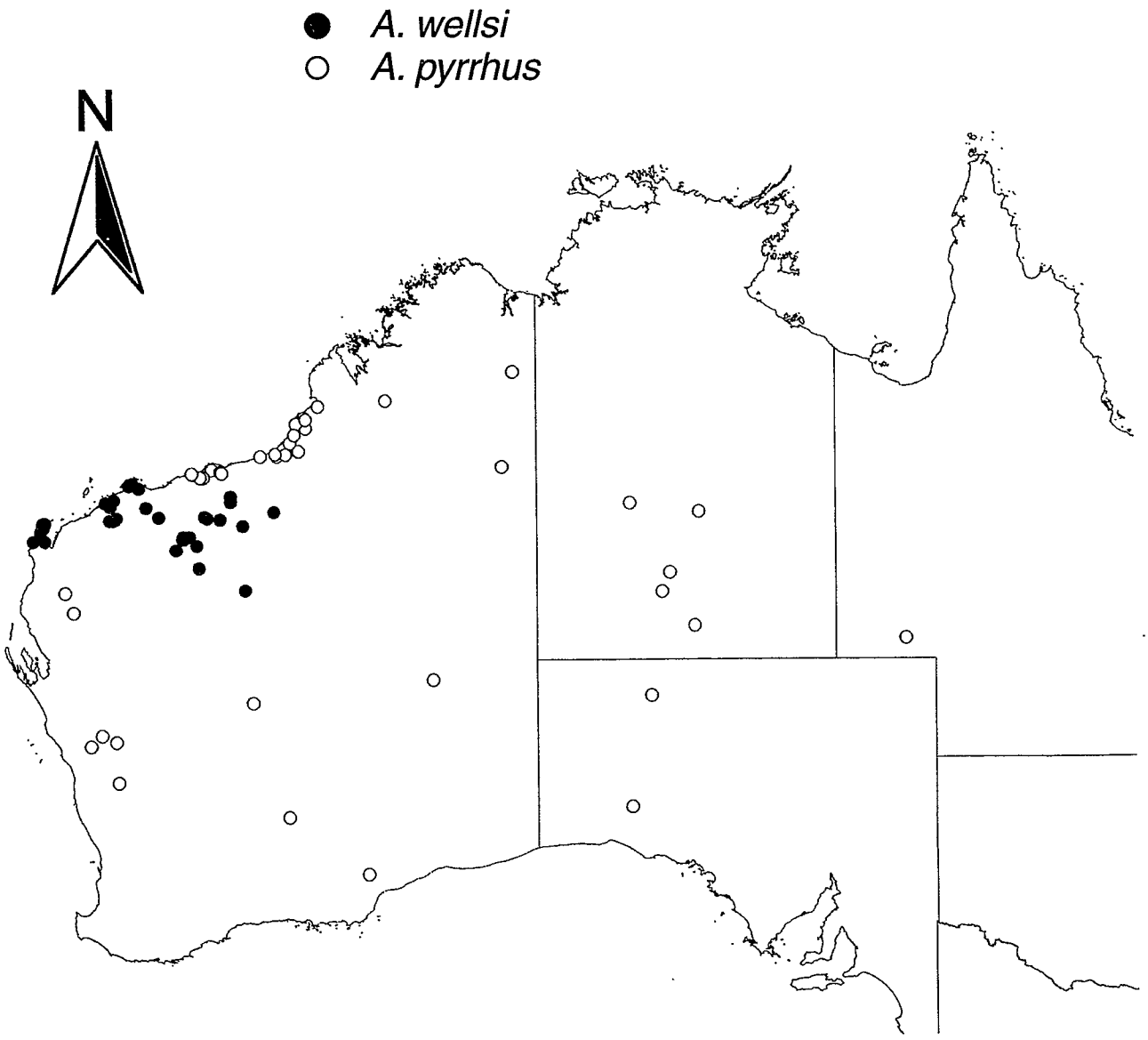

Figure 3 Map showing broad distribution of *A. wellsi* and *A. pyrrhus*, not including possible hybrids.

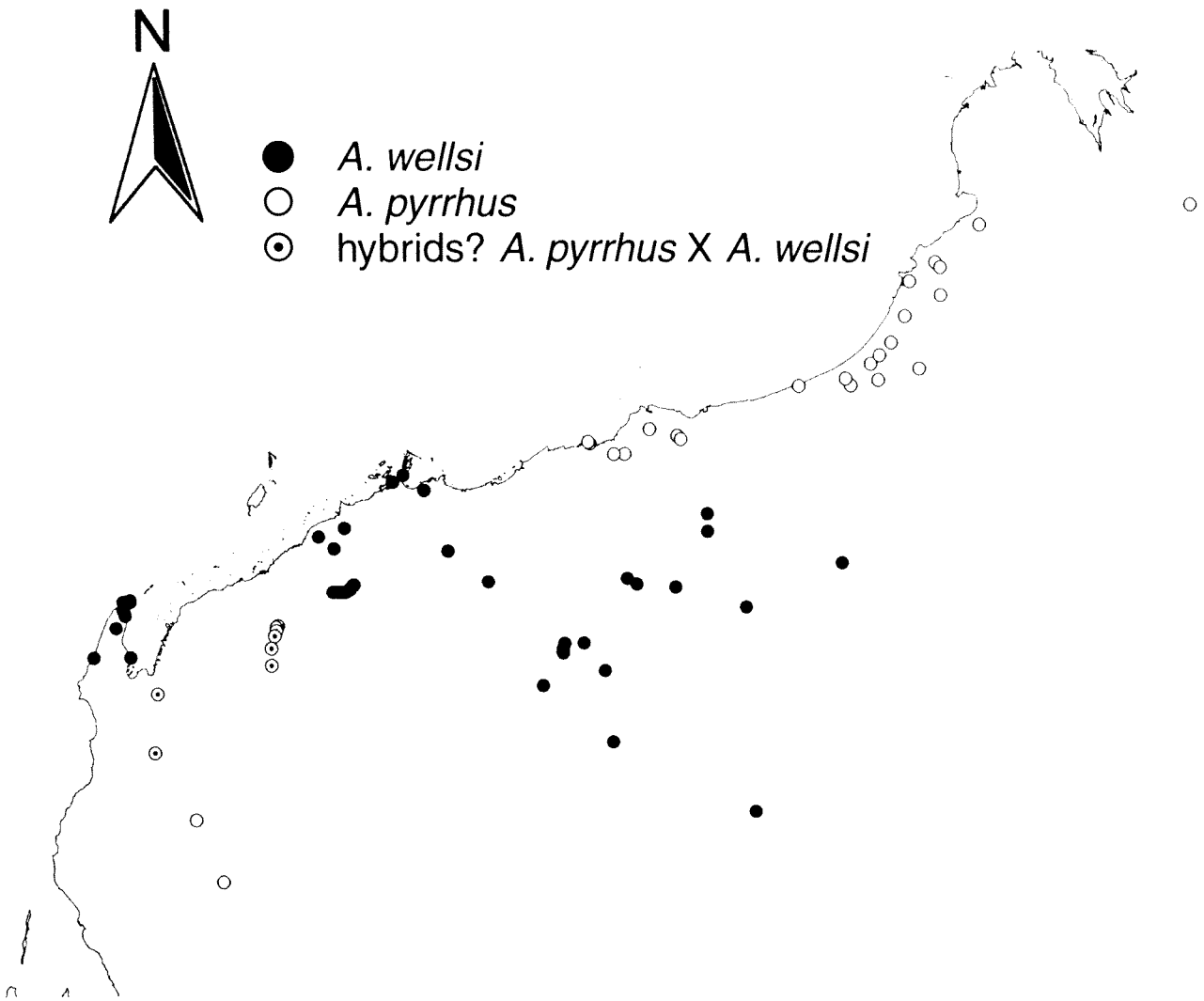

Figure 4 Map showing detailed distribution of *A. wellsi* and *A. pyrrhus* in northwestern Australia, including specimens of possible hybrid origin.

differences in both ventral and subcaudal counts (both higher in northwestern animals). However, values for the Central Australian population are intermediate between the two, suggesting the possibility of a cline from north to south via Central Australia. As might be expected on more general zoogeographic and physiographic grounds, SAM R1106 from Ooldea is consistent with the southwestern population of *A. pyrrhus* in its relatively low ventral and subcaudal counts (142 and 49, respectively).

Four adult female specimens from Durrie Station in southwestern Queensland have ventral counts of 127–143 which are relatively low in comparsion with the Central Australian female sample (139–144, n=6). However, these specimens are consistent in all other respects with typical *A. pyrrhus*.

Possible hybrid populations – *A. wellsi* X *A. pyrrhus*?

The most compelling evidence of hybridization between *A. wellsi* and *A. pyrrhus* comes from the country between the Pilbara region and the Cape Range Peninsula (Figure 4). This zone of lowlying, sandy habitats has produced a total of nine *Acanthophis* specimens, the majority coming from around Cane River Homestead (Table 8). One of the Cane River specimens (WAM R80442) appears to be indistinguishable in all respects from Pilbara region *A. wellsi*. In contrast, all of the remaining specimens show an admixture of *wellsi*-like and *pyrrhus*-like features, and several show abnormal features of varying degrees of severity. WAM R80430 is very close to typical *A. wellsi* but is unusual in having a partial division of the parietal

Table 7 Summary mensural and meristic data for each of three regional populations of *Acanthophis pyrrhus*. Data are presented for males only for most parameters, but additionally for a combined sample (both sexes + juveniles) for ventral scale count which does not exhibit sexual dimorphism. The results of One-way ANOVA (F values and statistical significance) are shown for each parameter. The northern population has significantly higher ventral scale counts than the southern population, with the central population intermediate between these. Regional samples are defined as follows: Northern = northern WA, north of the Pilbara ranges; Central = central Australia; Southern = southern WA, south of the Pilbara and central Australian ranges.

	Northern	Central	Southern	ANOVA results
MALES ONLY				
Snout-vent Length	439.0 ± 25.46 (2) (421–457)	437.5 ± 83.54 (13) (248–585)	491.5 ± 94.04 (6) (348–603)	F = 0.87, df = 20, p = 0.436
Tail Length	90.0 ± 22.21 (2) (75–105)	83.8 ± 12.24 (13) (60–97)	92.5 ± 12.03 (6) (75–105)	F = 1.10, df = 20, p = 0.351
Total Length	529.0 ± 46.67 (2) (496–562)	563.0 ± 110.28 (6) (345–676)	584.0 ± 105.98 (6) (423–708)	F = 0.915, df = 13, p = 0.429,
Tail Length as % of total length	17.0 ± 2.83% (2) (15–19%)	14.7 ± 1.12 (6) (13–16%)	16.2 ± 0.98% (15–18%)	
Ventral body scales	158 (1)	145.9 ± 2.82 (13) (142–151)	141.3 ± 2.07 (6) (139–144)	**F = 18.80, df = 19, p = 0.000**
Subcaudal scales	57 (1)	50.0 ± 2.65 (47–52)	49.2 ± 3.82 (6) (43–54)	F = 2.13, df = 9, p = 0.189
Undivided subcaudal scales	26 (1)	24.2 ± 6.67 (13) (13–38)	23.2 ± 6.68 (6) (15–31)	F = 0.967, df = 19, p = 0.908
Divided subcaudal scales	31 (1)	28.9 ± 4.73 (9) (23–37)	26.0 ± 8.53 (6) (15–37)	F = 0.459, df = 15, p = 0.629
Total body scales	215 (1)	193.7 ± 4.16 (3) 189–197)	190.5 ± 5.72 (6) (182–198)	**F = 9.09, df = 1, p = 0.011**
COMBINED SAMPLE				
Ventral body scales	147.1 ± 4.63 (22) (136–158)	144.8 ± 3.40(19) (137–151)	142.4 ± 2.12 (10) (139–145)	**F= 5.77, df = 50, p = 0.005**

scales on both sides (not observed in any other *A. wellsi* or *A. pyrrhus*). WAM R80431 has stronger dorsal keeling than is typical of *A. wellsi* and also has an atypical, obliquely keeled prefrontal scale on the left side only. WAM R80433 has a typical *A. wellsi* pattern and lacks obvious scale anomalies, yet its ventral count of 144 is higher than the maximum (141) recorded for the Pilbara population of *A. wellsi*. WAM R80432 has the parietal scales partially divided by an anomalous suture on both sides and also has a total of 6 prefrontal scales which are strongly asymmetric. WAM R80437 is consistent with *A. wellsi* in both body and facial patterning, but is more *pyrrhus*-like in having divided, keeled

Table 8 Measurements, meristics and morphological data for nine possible hybrid individuals (*A. wellsi* X *A. pyrrhus*) from the Cane River – Giralia region.

Specimen No. (all WAM)	R80430	R80431	R80432	R80433	R80437	R80442	R80443	R61357	R71228
Sex	F	M	M	F	F	M	F	F	F
Snout-Vent Length	198	347	355	418	175	263	324	634	364
Tail Length	31	60	57	52	30	43	50	91	66
Total Length	229	407	412	470	205	306	374	725	430
Tail as% of Total Length	13.5	14.7	13.8	11.1	14.6	14.1	13.4	12.6	15.4
Ventral body scales	140	131	132	144	138	138	140	143	143
Total subcaudal scales	49	49	47	–	53	49	48	–	50
Undivided subcaudals	24	26	30	25	37	25	25	29	32
Divided subcaudals	25	23	17	–	16	24	23	–	18
Total ventral scales	189	180	179	–	191	187	188	–	193
Mid-body scale rows	20	19	19	20	19	19	19	–	–
Number of prefrontals	2	2	6	2	4	2	2	3	2
Lateral scales keeled	–	–	–	–	–	–	–	+	+
Labial scales spotted	+	+	+	–	+	+	+	–	–

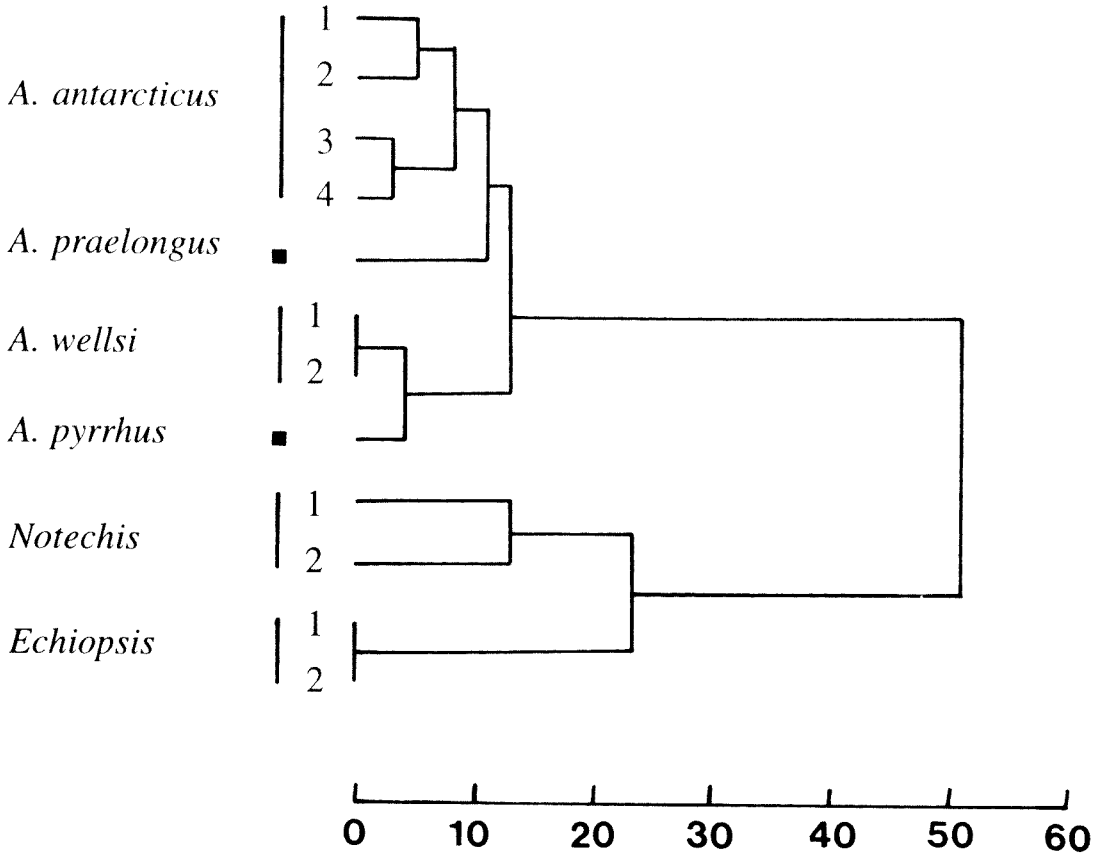

Figure 5 UPGMA dendrogram based on matrix of % genetic fixed differences between various populations and individuals of *Acanthophis* and the outgroup taxa *Echiopsis curta* and *Notechis* spp.

prefrontals and strong body keeling which extends well down the flanks. This specimen also shows several other abnormal features, namely a transversely divided frontal scale, a posteriorly fragmented parietal scale, loss of the right preocular scale and a bulging right eye.

WAM R61357 from 3 km E of Giralia was figured by Storr (1981) as a typical example of *A. pyrrhus*, and later designated by Wells and Wellington (1985) as the holotype of *Acanthophis armstrongi* (see earlier comments regarding the status of this taxon). This specimen shows a predominance of features normally associated with *A. pyrrhus*, including extensive keeling of body scales, 21 midbody scale rows, a high ventral count (143) and an oval-shaped head with a white upper lip. However, the presence of an undivided prefrontal on one side and the absence of black spotting across the rear of the dark cross-bands are suggestive of an influence, albeit a weak one, from *A. wellsi*. The geographic proximity to other populations showing anomalous scale developments and unusual, 'intermediate' morphologies, also gives cause for doubt concerning the status of this specimen. For the present, WAM R61357 is perhaps best treated with the Cane River series as a potential hybrid or backcross animal.

WAM R71228 from Mia Mia (east of Giralia) is also similar to *A. pyrrhus* in having strongly keeled body scales, 21 midbody scale rows, high ventral (143) and subcaudal (50) counts, an oval-shaped head with white upper lip and rugose frontonasal, prefrontal and frontal scales. However, its prefrontal scales are undivided, unlike any specimen of *A. pyrrhus* away from this zone of potential hybridization.

Another possible hybrid individual from this general area is currently held in captivity by Mr Brad Maryan of Perth (Figure 1f). This specimen, from 4.5 km NW of Cane River, has undivided, weakly keeled prefrontal scales like *A. wellsi*, but shows strong and laterally extensive keeling of the body scales as well as a *'pyrrhus'*-like body pattern with black spotting across both the anterior and posterior margins of the dark cross-bands.

The high incidence of abnormalities and morphological intermediates in the Giralia-Cane River area is consistent with the presence of a contemporary 'hybrid swarm' between *A. wellsi* and *A. pyrrhus*. Theoretically, the 'Giralia-Cane River' series might include both F1 hybrids and backcross individuals in varying combinations, and thus be of diverse genetic parentage. However, alternatives to the 'hybrid swarm' hypothesis are not difficult to find (e.g., phenotypic instability in marginal habitat), and it would be prudent to regard this as

no more than a working hypothesis until such time as it can be fully documented through analysis of appropriate biochemical markers.

Away from the Giralia-Cane River area, the morphology of both *A. wellsi* and *A. pyrrhus* is extremely conservative, with very low incidence of scale or pattern anomalies. As noted earlier, one exception is WAM R93212 from Vlaming Head, at the extreme northern end of the Cape Range peninsula, which has divided but unkeeled prefrontals. However, since *A. pyrrhus* is not known to occur anywhere on the peninsula, this anomaly must either be an expression of natural variation within *A. wellsi*, or else, an indicator of past interspecific interaction, perhaps in Pleistocene or early Holocene times when lowered sea levels might have created more extensive coastal plain habitats for *A. pyrrhus*.

A second example of prefrontal division within *A. wellsi* is provided by WAM R78136 from Yandicoogina, on the far eastern margin of the Pilbara uplands. This specimen shows unilateral division of the left prefrontal scale, but displays no other similarities to *A. pyrrhus*. The closest record of the later species is from "Mt Wynne" on the northern side of the Great Sandy Desert (WAM R2138). Nevertheless it is of interest to note that the Yandicoogina record also falls on the periphery of the range of *A. wellsi*, in an area where interaction with *A. pyrrhus* might be expected to occur.

Interspecific relationships

Successful analysis of interspecific relationships within any group generally hinges on the identification of meaningful 'outgroup' taxa which, for phenetic analyses, provide a sense of 'scale' for ingroup evolution, and for cladistic analyses, provide a basis for identification of character 'polarity' i.e., the direction that evolution has taken within the group. In the past, *Acanthophis* has generally been regarded as an isolated genus, without any especially close relatives. Recent genetic, immunological and morphological work on Australian elapids (Mengden 1985; Schwaner *et al.* 1985; Shine 1985) has indicated that its affinities probably lie among the dozen or so genera of terrestrial live-bearing elapids, most of which also possess an undivided anal scale and at least some undivided subcaudal scales. Among these taxa, the closest affinity may be with the monotypic genus *Echiopsis*, which shares an increased number of temporal scales with *Acanthophis* (Greer 1998: 188), along with a similar venom structure (Marshall and Hermann 1984; Marshall 1985). However, the results of the limited genetic analysis reported here suggest that *Echiopsis curta* and *Acanthophis* spp. are not especially close relatives, with the former being closer genetically to *Notechis* spp. For the present, it would thus seem unwise to employ any one particular elapid genus as an immediate outgroup to *Acanthophis*. Other potential sister taxa for *Acanthophis* include the species of *Denisonia* (*sensu* Cogger 1996; i.e., *devisi, maculata*) which are similar in various aspects of morphology (stocky body-form, broad headed, barred patterning of the upper lips, low number of ventral and subcaudal scales, cross-banding in *D. devisi*) and in behavioural characteristics (cryptozoic; nocturnal; flattened, rigid defensive posture).

Despite the methodological limitation imposed by uncertain outgroup relations, the genetic and morphological data provide some insights into the pattern of evolution within the genus *Acanthophis*. These data are discussed separately so as to clearly distinguish between the contribution of each kind of evidence. This contrasts with the 'total evidence' approach (e.g., Kluge 1989), which in the present case would undoubtedly provide a more fully resolved cladogram but one of doubtful validity.

Genetic characters

The limited genetic data have been analysed using both phenetic and cladistic methodologies [see Richardson *et al.* (1986) for discussion of analytical methods]. Although the results are based on very small numbers of individuals, they are nonetheless informative of general patterns and further serve to highlight areas in need of closer examination.

The broad pattern of intra- and inter-specific genetic comparisons was explored by an UPGMA based on the matrix of percent fixed allelic differences (i.e., proportion of loci at which two indidivuals fail to share any allele). The resultant dendrogram is shown in Figure 5. As anticipated, *A. wellsi* is phenetically closest to *A. pyrrhus*, while *A. antarcticus* and *A. praelongus* are approximately equidistant from each other and from the *A. wellsi* - *A. pyrrhus* couplet. The four populations of *A. antarcticus* form a discrete cluster on the dendrogram but show considerable intraspecific variation. Closer examination of this widespread southern and eastern Australian taxon is obviously warranted.

The various *Notechis* and *Echiopsis* individuals are genetically far more divergent from each of the *Acanthophis* species, with fixed allelic differences at around 50% of all loci. The two samples of *Notechis*, each representing different species, differ at five loci (*Ca, Gpt, Gsr-1, PepB* and *Pgm-1*) and thus show approximately the same level of divergence as *A. wellsi* and *A. antarcticus*. The *Notechis* species show fixed differences with *Echiopsis curta* at seven loci (*Aat-1, Acoh-1, Acoh-2, Ada, Gsr-1, Lgl* and *PepB*). The two specimens of *E. curta* share alleles at all loci, pointing to a low level of genetic differentiation between eastern and western populations of this species.

For the cladistic analysis, *Echiopsis curta* and the

two *Notechis* species were employed as outgroup taxa. Eleven loci contain variation of cladistic significance (including autapomorphies). Each of the species of *Acanthophis* has at least one uniquely derived allele. In contrast, evidence of interspecific relationships is ambigous, with one potential synapomorphy observed between *A. wellsi* and each of *A. pyrrhus* (*Est*^{b}) and *A. praelongus* (*Pgdh*^{b}). No derived alleles are shared between these latter two species or between *A. antarcticus* and any other taxon.

Among the outgroup taxa, one unique allele (*Acoh-1*^{c}) is shared by the *Notechis* species, while *Echiopsis curta* has a total of eight unique alleles. The species of *Echiopsis* and *Notechis* also share many alleles not detected in any *Acanthophis* species; however, under the outgroup method these alleles cannot be assigned any polarity.

Morphological characters

The various species of *Acanthophis* differ from each other in a combination of meristic 'shifts' and minor morphological features. Without delving into internal anatomy, the number of characters available for cladistic analysis is thus relatively small, negating the need for any quantitative analysis.

Table 9 lists the character states for each of eight characters which serve to distinguish among the various species of *Acanthophis*. The evolutionary polarity of certain of these characters has been discussed by Wallach (1985) on the basis of a comprehensive survey of Australian and a selection of non-Australian elapids. His observations will be tempered here with observations on the condition in the group of terrestrial live-bearing elapids with which *Acanthophis* is generally associated.

Character 1. Midbody scale rows: Wallach (1985) considers values between 19–21 to be plesiomorphic for elapids. Within *Acanthophis* the lowest values are found in *A. wellsi* (mode 19) and the highest in *A. praelongus* (mode 23). Values of 15–19 are common among terrestrial live-bearing elapids. We regard 19 midbody scales as the ancestral value and higher values as derived within *Acanthophis*.

Character 2. Ventral scale number: Wallach (1985) regards high ventral numbers (around 200) as the ancestral condition. Among terrestrial live-bearing elapids, most taxa have 150–200 ventral scales. Values below 150, such as are found in *Acanthophis* spp., are relatively uncommon, but are also observed in the genera *Echiopsis*, *Elapognathus*, *Denisonia* and *Drysdalia*, several of which have been nominated as possible sister taxa of *Acanthophis*. For this reason, we are undecided regarding the significance of high ventral counts in *A. pyrrhus*. Taken at face value, it would seem to be plesiomorphic within *Acanthophis*; however, we suspect that it may represent a case of secondary body elongation to achieve greater mobility (discussed further below).

Character 3. Subcaudal scale number: Values of around 50–70 are probably ancestral for elapids in general (Wallach 1985); subcaudal counts for *Acanthophis* fall at the bottom end of this range, while values for most other terrestrial live-bearers are somewhat lower again. The various *Acanthophis* species differ only slightly from one another in subcaudal counts; the mean value is highest in *A. pyrrhus* and lowest in *A. antarcticus* and *A. wellsi*. The high subcaudal count of *A. pyrrhus* is partly a consequence of its relatively longer tail (see Character 4), but also reflects the more finely scaled and elaborate nature of its caudal lure. In *A. wellsi* the caudal lure is less specialized in shape and aspects of scalation, but is more often set off from the remainder of the tail by its white or cream colouration. The caudal lure of *A. praelongus* is similar to that of *A. wellsi*, while that of *A. antarcticus* tends to be deeper and flattened, but without the 'feathered' scalation of *A. pyrrhus*.

Character 4. Relative tail length: Wallach (1985) cites a relative tail length of 15–20% as the likely

Table 9 Character states for eight morphological attributes that distinguish the various species of *Acanthophis*. Values provided for midbody scale rows are sample modes. Values for ventral and subcaudal scale counts and relative tail lengths are sample means. The sample of *A. antarcticus* is drawn from Western Australia and the meristic values may not apply to other regional populations of this variable taxon. The rational for establishing the ancestral state of each character is discussed in the text.

	A. wellsi	*A. antarcticus*	*A. praelongus*	*A.pyrrhus*	Ancestral state in genus
1. Midbody scale rows	19	21	23	21	19
2. No. ventral scales	134	119	129	145	130–145
3. No. subcaudal scales	47	46	51	53	45–50
4. Rel. tail length	15.8%	20.6%	22.2%	20.5%	15–20%
5. Lateral scale keeling	weak	weak	weak	strong	weak
6. Head scale rugosity	weak	weak	moderate	strong	weak
7. Prefrontal scales	entire	entire	entire	divided	entire
8. Lip pattern	barred	barred	barred	unbarred	barred?

ancestral condition. Values for *Acanthophis* species and for most other terrestrial live-bearers fall within this range. The tail is relatively shortest in *A. wellsi* and longest in *A. praelongus*. It is interesting to note that interspecific trends in tail lenth do not match those in subcaudal counts, indicating that the two variables are not strictly correlated.

Character 5. Body scale keeling: Keeling of body scales is an unquestionably derived feature (Wallach 1985). Although all *Acanthophis* species show scale keeling along the dorsum, this is strongly developed and also laterally extensive only in *A. pyrrhus*. Keeling of body scales is found among many arid-adapted squamates, but is also characteristic of various groups of water snakes; it is presumably of diverse functional and/or physiological significance.

Character 6. Condition of prefrontal scales: These are almost always entire among elapids. Within *Acanthophis*, the alternative condition of divided prefrontal scales is characteristic for *A. pyrrhus* and occurs as a not uncommon variant in *A. antarcticus* (Storr 1981). It is unquestionably a derived character state which may serve to link *A. pyrrhus* to *A. antarcticus*.

Character 7. Head scale rugosity: The head scales are smooth in the great majority of elapid snakes. Although some sculpting of the head scales is present in all *Acanthophis* species, this feature is taken to its extreme in *A. pyrrhus* in which many of the major head shields bear one or more major ridges. Subdivision of the prefrontal scale in this species might be related to this phenomenon, as the prefrontal scales bear especially strong longitudinal keels. On the other hand, occasional subdivision of the prefrontal scale is also observed in *A. antarcticus*, which lacks such pronounced keeling.

Character 8. Lip patterning: The upper lip and buccal floor are boldly marked in all *Acanthophis* species except *A. pyrrhus* in which these areas are faintly marked or immaculate. Similar marking is present in various other elapids including the potentially closely-related *Denisonia* spp. and we are therfore inclined to view the condition in *A. pyrrhus* as the more derived one.

Overall, *A. wellsi* emerges from this admittedly limited morphological analysis as potentially the most plesiomorphic living member of the genus. This is particularly evident in its low midbody count but also in its lack of apparent specialization in any of the considered features. *Acanthophis praelongus* differs from this ancestral form only in having an increased number of scale rows (MBS to a mode of 23) and a slight increase in the number of subcaudal scales.

Acanthophis antarcticus and *A. pyrrhus* are both signficantly more derived, although each has diverged in quite different evolutionary directions. In the case of *A. antarcticus*, the trend has been towards increased stoutness, with an increase in scale rows (MBS to mode of 21) and a reduction in ventral scale number. In *A. pyrrhus*, a similar increase in scale series (MBS to mode of 21) is combined with a marked increase in ventral scale number and a more slender body form. Observation of captive specimens of *A. pyrrhus* and *A. wellsi* indicates that both of these species are considerably more mobile and agile than the heavier-bodied, stockier *A. antarticus*. Whether *A. pyrrhus* in particular exhibits a greater degree of mobility or even arboreality is a question that can only be answered through further ecological and behavioural study of these poorly known species.

Additional to the changes in body proportion, *A. pyrrhus* has also become exceptionally rugose, with extensive body keeling and heavily sculpted head scalation. Subdivision of the prefrontal scales, a highly diagnostic feature of this species, may also be related to this increased irregularity of all scale surfaces. One final feature of note about *A. pyrrhus* is the apparently derived loss of bold patterning from the upper lip and buccal floor; the significance of this development is obscure.

DISCUSSION

The Pilbara Adder, *Acanthophis wellsi* is readily distinguished on morphological criteria from each of the other currently recognised species of *Acanthophis*. This is particularly so in the case of *A. pyrrhus*, the Desert Adder, with which *A. wellsi* was formerly confused. With its elongate body and excessively rugose head and body scales, *A. pyrrhus* is in many ways the most specialised member of the genus and it is clearly well-adapted to life in some of Australia's harshest environments - the sand and stony deserts of the major sedimentary basins. The fact that the Pilbara Adder lacks an eqivalent degree of morphological specialisation, despite the fact that it occurs in an equally harsh climatic zone, probably indicates a greater reliance on behavioural specialisations, especially the use of cooler microhabitats among and under rocks and in sheltered gullies.

Acanthophis wellsi is closest in overall morphology to *A. praelongus*. However, it is readily distinguishable from this species on combinations of meristic values (especially the elevated MBS of the latter) and aspects of colouration. Cladistic analysis of morphological variation within the genus suggests that the general similarity between these two species is most likely due to the common retention of ancestral features.

The presence of these two relatively plesiomorphic species in northern Australia suggests a possible place of origin for the genus in

that region. Interestingly enough, this would be away from the modern geographic centre of diveristy of the terrestrial live-bearers, the majority of which are found in southern and eastern Australia (Shine 1985). However, the presence of other members of this group (e.g., *Denisonia devisi, Parasuta* spp., *Suta* spp.) in both inland and northern Australia cautions against any simplistic interpretation of these distributional patterns.

To date, there has been no recorded instance of sympatry between two species of *Acanthophis* and it has thus not been possible to examine the extent of reproductive isolation between congeners (i.e., to apply the 'biological species' concept). Instead, recognition of the various morphological entities as species must rely on some other criterion, such as the 'phylogenetic species' concept with its emphasis on the historical individuality of taxa [see Baum (1992) for an introduction to this literature; and Frost and Hillis (1990) for some herptological examples].

The limited genetic data available indicate that each of the four *Acanthophis* species does indeed represent a discrete evolutionary lineage, albeit within a close knit evolutionary unit. Phenetic analysis of the data suggests that the two most arid-adapted species, *A. wellsi* and *A. pyrrhus*, are sibling-taxa within the genus. However, cladistic analysis of the data fails to provide unambiguous support for a *wellsi-pyrrhus* clade, but suggests alternative cladistic links between *A. wellsi* and each of *A. pyrrhus* and *A. praelongus*. The genetic evidence for interspecific afinities is thus inconclusive.

Storr (1981) suggested that the various forms of *Acanthophis* could be treated tentatively as 'allospecies' (i.e., weakly differentiated taxa which have originated through allopatric speciation, *sensu* Mayr 1959). The relatively small genetic distances observed between each of the four species of *Acanthophis* would appear to support Storr's view. However, in this context it is worth noting that the genetic data are seemingly in conflict with immunological data presented by Schwaner *et al.* (1985) based on Microcompliment Fixation of transferrin. These data show quite large molecular distances between antigens for each of *A. praelongus* and *A. pyrrhus* and an antiserum for *A. antarcticus* [23 and 14 units respectively; compared with 25–47 units (most values > 30) between *Acanthophis* and other genera of Australian elapids. The explanation for this discrepency presumably relates to variable rates of molecular *vs* genic evolution, but in this instance it is not clear which one is slow and which is fast.

Storr (1981) also remarked on the apparent lack of evidence for 'gene flow' between the various species of *Acanthophis*. From the more detailed analysis presented here, it appears likely that *A. wellsi* and *A. pyrrhus* do in fact hydridise where their geographic ranges abut. The strongest evidence for this comes from the area between Giralia and Onslow where a population of *A. pyrrhus* appears to intrude between the Pilbara and Cape Range populations of *A. wellsi*. Specimens from this area show an admixture of normally distinct species characteristics, together with a high incidence of scale and other abnormalities. This evidence is highly suggestive of hybridization; however, more detailed investigation including genetic analysis is required to determine the nature and extent of the interaction. A captive breeding program currently underway in collaboration with members of the Western Australian Society of Amateur Herpetologists will hopefully also shed light on the potential for hybridization between these and other species of *Acanthophis*.

The presence of partially melanistic individuals within some populations of *A. wellsi* is significant in view of the growing literature on colour and pattern polymorphism among snakes and other reptiles (Vinegar 1974; Bechtel 1978; Wolf and Werner 1994). Captive cross-breeding experiments currently underway may help determine to underlying genetic basis of this variation (cf., Zweifel 1981). However, field studies of *A. wellsi* will be necessary in order to understand the full significance of pattern polymorphism in the ecology and population dynamics of this inhabitant of a complex, arid-zone environment.

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Appendix: Lists of Material Examined

Material included in morphological analysis

Acanthophis wellsi

Burrup Peninsula (20°36'S, 116°48'E): WAM R 84284; 10 km S Cleaverville (20°45'S, 117°00'E): WAM R1142708; 14 km NE of Balmoral (21°06'S, 116°14'E): WAM R 75003; Marble Bar (21°10'S, 119°44'E): WAM R438, 12671, 14061 and 12672 (10 km N); Mardie Stn (21°11'S, 115°59'E): WAM R13873, WAM R26822; Mardie Road House (21°18'S, 116°08'E): WAM R81838; Mt Herbert (21°20'S, 117°13'E): WAM R20239; Carawine Gorge (21°29'S, 121°02'E): WAM R 99741; Woodstock Station (21°37'S, 118°57'E): WAM R13223 and 104188; Tambrey Stn (21°38'S, 117°36'E): WAM R4550; Pannawonica (21°39'S, 116°19'E): WAM R113432 and 125733; 2.9–4.7 km W Pannawonica (21°40'S, 116°18'E): WAM R 125731, 125734 and 127581; 6 km W Pannawonica (21°41'S, 116°17'E): WAM R125730; 7.5 km W Pannawonica (21°42'S, 116°16'E): WAM R125736; Yandicoogina (21°42'S, 119°25'E): WAM R78136; 6 km E Deepdale Camp, Robe River (21°43'S, 116°07'E): WAM R102201; 23 km W Pannawonica (21°43'S, 116°07'E): WAM R113114; 26 km W. of Pannawonica (21°43'S, 116°10'E): WAM R127585 and 127586; Deepdale HS, Robe River (21°43'S, 116°11'E): WAM R73731; 28.5 km W Pannawonica (21°43'S, 116°11'E): WAM R125735; 14 km SW of Pannawonica (21°43'S, 116°13'E): WAM R119366; 10.2 km W Of Pannawonica (21°43'S, 116°14'E): WAM R125732 and 125737; North West Cape (21°47'S, 114°10'E): WAM R8318; Vlaming Head Lighthouse (21°48'S, 114°10'E): WAM R2999, 19674, 93212; Ned's, Well, NW Cape (21°53'S, 114°06'E): WAM R28325; Nullagine (21°54'S, 120°06'E): WAM R9335; Exmouth (21°56'S, 114°07'E): WAM R26759; Shothole Canyon (22°03'S, 114°02'E): WAM R93215; Wittenoom (22°14'S, 118°20'E); WAM R18493; 11 km E of Wittenoom (22°14'S, 118°31'E): WAM R15100; on range, Wittenoom Gorge (22°17'S, 118°19'E): WAM R17121; Wittenoom Gorge (22°17'S, 118°19'E): WAM R21538; Wittenoom Gorge, Blue Asbestos Mine (22°19'30"S, 118°19'00"E): WAM R8886; mouth of Yardie Creek (22°20'S, 113°49'E): WAM R61495; Exmouth Gulf (22°20'S, 114°10'E): WAM R8658; Karratha (22°30'S, 118°43'E): WAM R 102060; Marandoo (22°38'S, 118°07'E): WAM R56097; 22.4 km SE Marillana Homestead (22°47'10"S, 119°15'47"E): WAM R73134; 31 km SE of Mt Meharry (23°11'05"S, 118°47'30"E): WAM R 67921; Mundiwindi (23°52'S, 120°10'E): WAM R12280.

Acanthophis pyrrhus

Forrest River Mission (14°35'S, 127°30'E): AM R128358; Mt Wynne (18°06'S, 124°27'E): WAM R2138; 16 km SW of Thangoo Homestead (18°16'S, 122°24'E): WAM R75012; La Grange Bay (18°37'S, 121°58'E): WAM R3437; Badur Hill, La Grange (18°40'S, 122°01'E): WAM R28097 and 70701; Frazier Downs (18°48'S, 121°43'E): WAM R28098 and 46079; 16 km S of La Grange (18°56'S, 122°01'E): WAM R28100–28107; 4.6 km S 'Nita Downs' Turnoff, Great Northern Highway (19°08'S, 121°40'E): AM R100900; 13 km SE of Anna Plains Homestead (19°23'S, 121°32'E): WAM R79006; Anna Plains (19°30'S, 121°25'E): WAM R28099; 37 km NE of Sandfire Roadhouse (19°35'S, 121°20'E): WAM R75010; 27 km NE of Sandfire Roadhouse (19°38'S, 121°48'E): WAM R79008; 6.6 km N Sandfire Roadhouse (19°43'S, 121°05'E): AM R101455; 55 km S of Anna Plains HS (19°44'S, 121°24'E): WAM R91671 and 91672; 4 km ENE Shootana Hill, Wallal Downs Station (19°47'S, 120°38'E): AM R117638; 6 km ENE of Sandfire Roadhouse-Anna Plains Station (19°47'S, 121°08'E): WAM R79030; Balgo Mission Area (20°08'S, 127°59'E): WAM R69975; Degrey (20°11'S, 119°11'E): WAM R2130; 12 km WNW Goldsworthy (20°15'S, 119°27'E): WAM R79138; 7 km NNW of Goldsworthy (20°17'S, 119°29'E): WAM R79139; Port Hedland area (20°18'S, 118°35'E): AM R47477 and 47478; Port Hedland (20°19'S, 118°36'E): WAM R81846, 85116 and 85117; 38 km N of Port Hedland Great Northern Highway Intersection (20°25'S, 118°50'E): WAM R124878; 30 km SE South Hedland (20°25'S, 118°56'E): WAM R104357; Yuendumu (21°15'S, 131°48'E): SAMA R2547a, 3547b and 8163; Barrow Creek (21°31'S, 133°53'E): SAMA R497, 498a, 498b and 498c; Milton Park (23°22'S, 133°00'E): SAMA R14211; 5 km SW Lyndon River Bridge NW Coastal Hwy (23°32'S, 114°16'E): WAM R71601; near Middalya (23°54'S, 114°46'E): WAM R49985; Hermannsburg (23°57'S, 132°46'E): SAMA R1152; 38.9 km E Binthalya Homestead (24°30' 04"S, 115°01' 03"E): WAM R123191; Finke River (24°59'S, 133°45'E): SAMA R496; Durrie Station, via Birdsville (25°23'S, 140°06'E): QM J22451, 31646, 39570, 455512; Gahnda Rockhole (26°36'S, 125°52'E): WAM R15101; Everard Ranges (27°06'S, 132°26'E): SAMA R494; Albion Downs (27°17'S, 120°23'E): WAM R30599; Tallering Station (28°13'S, 115°51'E): WAM R9996; Wurarga (28°25'S, 116°17'E): WAM R7868 and 10033; Bunjil (29°39'S, 116°21'E): WAM R1767; Ooldea (30°27'S, 131°50'E): SAMA R1106; Kalgoorlie (30°44'S, 121°28'E): WAM R70699; Mullewa (28°32'S, 115°31'E): WAM R70700; Balladonia (32°28'S, 123°52'E): AM R6192; "Central Australia": SAMA R 495a,b,c.

Possible hybrids: *Acanthophis wellsi* X *A. pyrrhus*

7 km NW of Cane River Homestead (22°02'S, 115°35'E): WAM R80430; 7 km NW of Cane River

Homestead (22°03'S, 115°34'E): WAM R 80431; 6 km W of Cane River Homestead (22°05'S, 115°34'E): WAM R80437; 8 km SW of Cane River Homestead (22°08'S, 115°33'E): WAM R80432 and 80442 (7 km); 21 km SW of Cane River Homestead (22°15'S, 115°31'E): WAM R80443; 15 km N of Nanutarra Roadhouse (22°25'S, 115°31'E): WAM R80433; 3 km E of Giralia (22°41'S, 114°25'E): WAM R61357; 16 km NNW Mia Mia Homestead (23°15'S, 114°23'E): WAM R71228.

Material examined electrophoretically

Acanthophis wellsi

Population WE1 (Pannawonica, Western Australia): WAM R113114, R113166, R113167, R113374, R113377, R113378.

Population WE2 (Cleaverville, Western Australia): WAM R114270.

Acanthophis pyrrhus

Population PY1 (Yuendumu, Northern Territory): EBU E25.

Acanthophis praelongus

Population PR1 (near Heathlands, Queensland): QM J54143.

Acanthophis antarcticus

Population AN1 (Karragullen, Western Australia): WAM R113180.

Population AN2 (Coffin Bay, South Australia): SAMA R24412, R28460.

Population AN3 (Reevesby Island, South Australia): SAMA R27242, R28364.

Population AN4 (Ardrossan, South Australia): SAMA R24221.

Echiopsis curta

Population E1 (Lort River, Western Australia): SAMA R22971.

Population E2 (Hambridge Conservation Park, South Australia): SAMA R27494.

Notechis ater

Population N1 (Little Dip Conservation Park, South Australia): SAMA R24776.

Notechis scutatus

Population N2 (Coomalbidgup, Western Australia): SAMA R22370.

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