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A new species of death adder (*Acanthophis*: Serpentes: Elapidae) from north-western Australia

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Abstract

Australian death adders (genus *Acanthophis*) are highly venomous snakes with conservative morphology and sit-and-wait predatory habits, with only moderate taxonomic diversity that nevertheless remains incompletely understood. Analyses of mitochondrial and nuclear gene sequences and morphological characteristics of death adders in northern Australia reveal the existence of a new species from the Kimberley region of Western Australia and the Northern Territory, which we describe as *Acanthophis cryptamydros* **sp. nov.** Although populations from the Kimberley were previously considered conspecific with Northern Territory death adders of the *A. rugosus* complex, our mtDNA analysis indicates that its closest relatives are desert death adders, *A. pyrrhus*. We found that *A. cryptamydros* **sp. nov.** is distinct in both mtDNA and nDNA analysis, and possesses multiple morphological characteristics that allow it to be distinguished from all other *Acanthophis* species. This study further supports the Kimberley region as an area with high endemic biodiversity.

Key words: Australian Monsoonal Tropics, mtDNA, nDNA, systematics, taxonomy, *Acanthophis cryptamydros* **sp. nov.**

Introduction

The Kimberley region in north-western Australia is an area of high endemism (Slatyer *et al.* 2007; Bowman *et al.* 2010; Powney *et al.* 2010; Palmer *et al*. 2013; Pepper & Keogh 2014). Ongoing collections of animal and plant groups in recent years has led to the identification of many new species (e.g., frogs: Anstis *et al.* 2010; Doughty 2011; lizards: Doughty *et al.* 2012; Oliver *et al.* 2012, 2014; Pepper *et al.* 2011; snails: Köhler 2010, 2011; flowering plants: Barrett *et al.* 2009; Carlson *et al.* 2011; Maslin *et al.* 2013). Snakes have received some attention in the Kimberley region of Western Australia and the Australian Monsoonal Tropics (e.g. *Pseudechis*: Kuch *et al.* 2005; *Demansia*: Shea & Scanlon 2007; *Anilios*: Marin *et al.* 2013), yet many genera have not been subject to extensive systematic revision recently.

The death adders, *Acanthophis* Daudin, 1803 are a widespread genus of elapid snakes distributed across Australia and New Guinea, and on several Indonesian islands to the west of New Guinea. Although the genus is highly distinctive due to its convergent viper-like morphology and ecology (Shine 1980; Greer 1997), species limits within the genus have remained poorly understood (Storr 1981; McDowell 1984; Aplin & Donnellan 1999; Wüster *et al.* 2005), partly due to extensive polymorphism within many species and even populations (e.g., Johnston 1996).

The systematics of the death adders from the Australian Monsoonal Tropics (northern Queensland, the Top End of the Northern Territory and the Kimberley region in northern Western Australia) have proven especially complex. While *A. pyrrhus* Boulenger, 1898 from the arid zone is highly distinctive, and *A. wellsi* Hoser, 1998 from the Pilbara region in Western Australia was discovered, defined and shown to be a clearly diagnosable, valid

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species by Aplin & Donnellan (1999), the affinities of the remaining populations remain poorly understood. Storr (1981) assigned all populations from the Kimberley to *A. praelongus* Ramsay, 1877, an arrangement retained by many subsequent authors (e.g., Cogger 2000; Storr *et al*. 2002; Wilson & Swan 2013). Storr, however, indicated there was considerable heterogeneity in morphology within *A. praelongus senso lato*. More recent studies on venom also found considerable variation in composition across the range of *A. praelongus* (Fry *et al.* 2002). A molecular genetic study found that populations from the Northern Territory and north-western Queensland fell in to two distinct clades with partly overlapping distribution, with each more closely related to *A. rugosus* Loveridge, 1948 from New Guinea than to other Australian taxa (Wüster *et al.* 2005). These recent studies, however, did not include representatives from the Kimberley region of Western Australia. The Kimberley forms have been explicitly or implicitly grouped with Top End *Acanthophis* in the *A. rugosus* complex (they were previously considered part of *A. praelongus*). Storr (1981) did not distinguish Kimberley *Acanthophis* from Top End populations based on his morphological data and thus it has been assumed that they are conspecific with the *A. rugosus* complex (e.g., Cogger 2014). No specific comparison between these populations was made by Storr (1981); however, as at the time of his revision he only had access to 16 northern specimens in the collection of the Western Australian Museum, of which 13 were from the Kimberley region and three from the Northern Territory.

As part of a reanalysis of the systematics of *Acanthophis*, here we compare the Kimberley death adders to other *Acanthophis* using multiple molecular loci and morphology. We found the Kimberley specimens to be genetically and morphologically distinct from other currently-recognized taxa, and therefore describe this species as new below.

Material and methods

Molecular phylogenetics. Appendix 1 shows the specimen data for individuals and samples that were used for molecular phylogenetic analysis. Genomic DNA (ventral scale clippings, liver, and blood samples) was extracted from *Acanthophis* specimens using a Qiagen DNeasy™ Tissue Kit. NADH dehydrogenase subunit 4 (*nd4*) and cytochrome *b* (*cytb*) sequences from the Wüster *et al*. (2005) study were obtained from GenBank. Sampling localities are shown in Fig. 1. Based on the relationships presented by Sanders *et al.* (2008), two species were used as outgroups: *Pseudechis papuanus* (the likely sister genus to *Acanthophis*) and *Oxyuranus scutellatus* (a more distant outgroup).

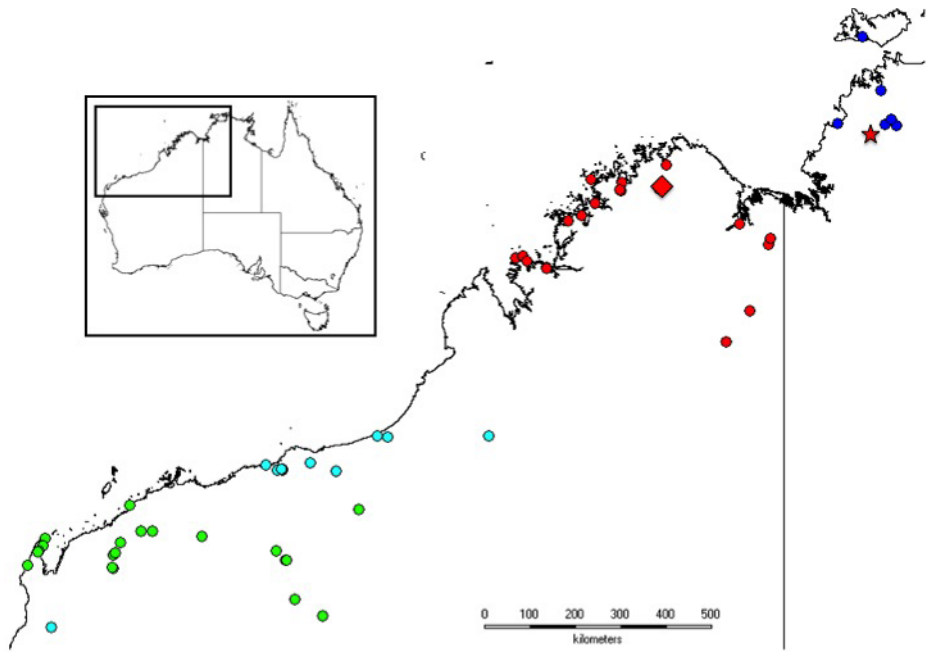

FIGURE 1. Distribution of *Acanthophis* sampled in northwest Australia. Only samples with accurate collection coordinates have been included, except specimen NTM R29109 (star; see text). Colored circles correspond to sampled specimens: red = *A. cryptamydros* **sp. nov.**; blue = *A. rugosus*; turquoise = *A. pyrrhus*; green = *A. wellsi*. The collection locality of the holotype of *A. cryptamydros* (WAM R174083) is displayed as a red diamond.

Three mitochondrial gene fragments (*nd4*, *cytb*, and *16s*) and two nuclear gene fragments (prolactin receptor (*prlr*) and ubinuclein 1 (*ubn1*)) were amplified using the polymerase chain reaction (PCR). Primer information is shown in Table 1. PCR reaction volume was 11 µl, which consisted of 9.6 µl of Abgene 1.1x ReddyMix™ (1.25 units Thermoprime Plus DNA polymerase; 75 mM Tris-HCl pH 8.8; 20mM $(NH_4)_2SO_4$; 1.5 mM $MgCl_2$; 0.01% (v/v) Tween®20; 0.2 mM of each dNTP; and a precipitant red dye for electrophoresis), 0.3 µl of required primer and ~10 ng/µl of template DNA per sample. Amplification conditions for reactions was denaturation at 94°C for 2 minutes (min); then 35 (*16s, ubn1* and *prlr*) or 40 (*nd4* and *cytb*) cycles of 94°C for 30 seconds (s); annealing at 43°C (*16s*), 48°C (*cytb*), 50°C (*ubn1* and *prlr*), or 54°C (*nd4*); 72°C amplification for 45 s; a concluding extension of 72°C for 5 min was used to finalize each reaction. Sequencing was carried out in the forward direction for mtDNA genes and in both directions for nDNA by Macrogen Inc., South Korea.

Sequences were proofread and aligned using CodonCode Aligner 3.7.1 using default settings and checked for pseudogenes, unexpected stop-codons or indels using Molecular Evolutionary Genetics Analysis 4.0.2 (MEGA) (Tamura *et al.* 2007) by translating the DNA sequences into amino acid sequences.

For phylogenetic analysis, Bayesian inference (BI) methods were applied to the mtDNA dataset and haplotype networks were applied to the two nuclear genes separately to infer phylogenetic relationships. BI analysis was implemented through MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). Coding genes were partitioned and the most suitable model of sequence evolution under the Akaike Information Criteria (AIC) for each gene and partition was identified using MrModeltest 2.3 (Nylander 2004), implemented in PAUP* 4.0b10 (Swofford 2002). MrBayes analyses ran for 10^7 generations, with two independent parallel runs with one cold and three heated chains each. Trees were sampled every 1000 generations and the first 10% of trees were discarded as burn-in. Effective sample size and burn-in for each parallel run were examined in Tracer v.1.5 (Rambaut & Drummond 2007). Analysis was run through the Bioportal (http://www.bioportal.uio.no/). Maximum likelihood (ML) analysis was also carried out on the partitioned mtDNA dataset using the program Randomized Axelerated Maximum Likelihood (RAxML) 7.2.2 (Pfeiffer & Stamatakis 2010) with 500 bootstrap replicates.

TABLE 1. Primers used during PCR. [a]Arévalo *et al.* (1994); [b]Wüster *et al.*(2008); [c]newly developed primers; [d]Townsend *et al.* (2008); [e]Axel Barlow (pers. comm.).

Primer Name	Primer (5' – 3')
nd4	
ND4[a]	CACCTATGACTACCAAAAGCTCATGTAGAAGC
H12763V[b]	TTCTATCACTTGGATTTGCACCA
cytb	
AcanF2[c]	CTACTATCCTCCAACCT
AcanR1[c]	CAGTTTGTTTGGGATTGATCG
16s	
16sL[a]	CGCCTGTTTATCAAAAACAT
16sR[a]	CCGGTCTGAACTCAGATCACGT
prlr	
PRLR_F1[d]	GACARYGARGACCAGCAACTRATGCC
PRLR_R3[d]	GACYTTGTGRACTTCYACRTAATCCAT
ubn1	
BaUBN_F[e]	CCTCTGGTTACTCAGCAGCA
BaUBN_R[e]	ATTGGCCACTCCTTGTGTTC

seqPHASE (Flot 2010) was used prior to the implementation of PHASE 2.1.1 (Stephens *et al.* 2001; Stephens & Scheet 2005) to infer nuclear haplotypes when heterozygous positions were present in the dataset. Heterozygous positions were considered to be true if they received a probability of >0.7. Resulting sequences were checked for indels or stop codons in MEGA prior to producing haplotype networks in Network 4.6.0.0 using maximum parsimony criteria.

In order to assess patterns of genetic variation across all three loci together (the two mtDNA genes were combined and treated as a single locus), we used the program POFAD 1.03 (Joly & Bruneau 2006) to generate standardized multilocus distances between specimens. POFAD allows the incorporation of allelic variation, and is thus very useful when assessing genetic distances between specimens in nuclear loci. Moreover, it allows equal weighting of all loci, rather than allowing the more variable loci to dominate the analysis. Only individuals that had all loci successfully amplified were used in the analysis and MEGA was used to produce the data matrices of *p*-distances for each gene, which were generated using pairwise deletion of missing data. Due to its nature, the *ubn1* dataset contains indels spanning two separate codons. MEGA treats such data as missing and thus the *p*-distance would be 0. To overcome this problem, a single nucleobase for each indel was inserted into the end of each sequence with those containing the indel having a different nucleobase coded for them compared to those without. The resulting standardized between-specimen multilocus distance matrix was visualised with a principal coordinates analysis (PCO) using the MVSP program (www.kovcomp.com).

Morphological analysis. Appendix 1 shows specimen data for all specimens, including type material, examined for morphological comparisons from the collections of the Western Australian Museum (WAM) and Museum and Art Gallery of the Northern Territory (NTM). We used 14 genotyped specimens from the phylogenetic analysis and a further 86 non-genotyped specimens to identify consistent morphological characteristics between the new species and other Australian *Acanthophis* species, including those within the *A. rugosus* group.

Table 2 presents the morphological variables measured. Characters examined for the morphological analysis included body measurements, scale counts, and the size, shape, and positioning of head scales of each specimen. Measurements, scale counts, and morphological nomenclature follow that of Storr *et al*. (2002) and Cogger (2014). There were missing scores for some specimens due to poor condition, such as road mortalities and very old or poorly preserved specimens.

TABLE 2. Meristic and morphological characters measured in this study.

Character	Description
ToL	Total body length, from snout to tail tip, excluding terminal spine
SVL	Snout-vent length, from anteriormost point of snout to posterior edge of anal scale
TailL	Tail length, from anterior edge of first subcaudal scale to tail tip, excluding terminal spine
HeadL	Head length, from tip of snout to posterior margin of the of the quadrate
HeadW	Head width, at widest point, posterior to eyes
VS	Ventral scales, counted from anteriormost ventral to but not including anal scale
MBSR	Midbody scale rows, at middle of SVL
AntSR	Anterior scale rows, posterior to head
PostSR	Posterior scale rows, anterior to vent
ScST	Subcaudal scales total, from the first subcaudal posterior to vent to posterior most scale on tail tip, including single and paired scales, excluding terminal spine
ScSS	Subcaudal scales single, as for ScST, excluding paired ScS
ScSP	Subcaudal scales paired, as for ScST, excluding single ScS
FrL	Frontal length, from anteriormost edge to posterior most edge
FrW	Frontal width, at widest point
SupOcL	Supraocular length, from anteriormost edge to posterior most edge
SupOcW	Supraocular width, at widest point
SupLab	Supralabial scales
InfLab	Infra labial scales

SVL and TailL were measured with a ruler to the nearest 1.0 mm. TailL is presented as length (mm) and as a percentage of SVL. All other meristic variables including HeadL and HeadW, FrL and FrW, and SupOcL and SupOcW were measured with digital calipers to the nearest 0.1 mm. Head and selected scale meristics are presented as length and width (mm) and width as a percentage of length. MBSR counts were taken at approximately 50% of the SVL. Due to variation in the number of scale rows along the length of the body, often reducing anteriorly and posteriorly, multiple counts were taken to determine the minimum number of scale rows. Scale row counts were also taken from posterior to the head (AntSR), and anterior to the vent (PostSR). VS were counted from the anteriormost ventral to, but not including, the anal scale following the Dowling (1951) method. Subcaudal scale counts were taken from the first subcaudal posterior to the vent to the terminal scale on the tail tip, excluding spine. Where possible, the sex of specimens was determined from everted hemipenes, presence of follicles or eggs, or by direct examination of reproductive organs via ventral incision.

Color in life was based on recently collected specimens and photographs of specimens in life. In addition to the dorsal color and pattern, the coloration and extent of pigmentation on the ventral surface of specimens was also examined.

Results

Molecular genetics. A total of 2,874 bp were used in phylogenetic analysis: 684 for *nd4* (169 were variable and 153 were parsimony informative); 752 for *cytb* (179 were variable and 161 were parsimony informative); 473 for *16s* (53 were variable and 26 were parsimony informative); 508 for *prlr* (19 were variable and 13 were parsimony informative); and 457 for *ubn1* (19 were variable and 9 were parsimony informative).

The consensus Bayesian inference (BI) tree is shown in Fig. 2 with maximum likelihood (ML) scores mapped on. The Kimberley *Acanthophis* clade is closest genetically to *A. pyrrhus* in the mitochondrial phylogeny, with a mean *p*-distance of 7.4%. The rest of the phylogenetic relationships are consistent with those presented by Wüster *et al.* (2005), and are summarized as follows. Sister to these two lineages is the Pilbara endemic *A. wellsi*. These three lineages form a well-supported sister group to the remaining Australian populations (i.e., *A. antarcticus*, *A. praelongus*, and an '*A. rugosus* group' comprised of multiple more weakly-diverged lineages). *Acanthophis laevis* from New Guinea forms the sister taxon to all other species.

The nDNA data further support the Kimberley population as an independently evolving lineage (Figs. 3 and 4), with only a small amount of haplotype sharing occurring in both *prlr* and *ubn1* (Fig. 3). In *prlr* there are two haplotypes shared between *A. rugosus* and Kimberley specimens. In both *prlr* and *ubn1* one haplotype is shared between *A. wellsi* and specimens from the Kimberley. Specimens from Kimberley, however, also contain multiple unique haplotypes; six in *prlr* and five in *ubn1*. The principal coordinate analysis of standardized multilocus distances supports the distinction of the Kimberley population compared to other closely related species (Fig. 4).

Morphology. Table 3 summarizes the meristic differences among the forms examined. In terms of overall body length and proportions, the Kimberley specimens were relatively homogeneous, and broadly overlapped with specimens from the *A. rugosus* group and other Australian *Acanthophis* species. More apparent, however, were differences in quantitative characters, scalation, and pattern that corresponded with lineages identified from the molecular analyses revealing diagnosable groups. Populations of *Acanthophis* from the Kimberley region of Western Australia and western Northern Territory differ from lineages with the *A. rugosus* group by possessing the following characteristics (see below for comparisons with other species): 22 or 23 MBSR; 125–139 VS; undivided prefrontal scales; posterior edge of frontal scale not extending beyond posterior edge of supraoculars; laterally flared supraoculars; area of lower secondary temporal scale equal to or smaller than sixth supralabial; anterior dorsal scales with prominent keels and unpigmented ventrum except for 1–3 rows of spots on ventrolateral edge.

Systematics

Our mtDNA results generally conform to the topology presented by Wüster *et al.* (2005). Contrary to the traditional grouping of the Kimberley populations with the '*Acanthophis rugosus'* group, however, the Kimberley population (Fig. 2) is the sister of *A. pyrrhus*, with *A. wellsi* as the sister taxon to this group. Moreover, each taxon

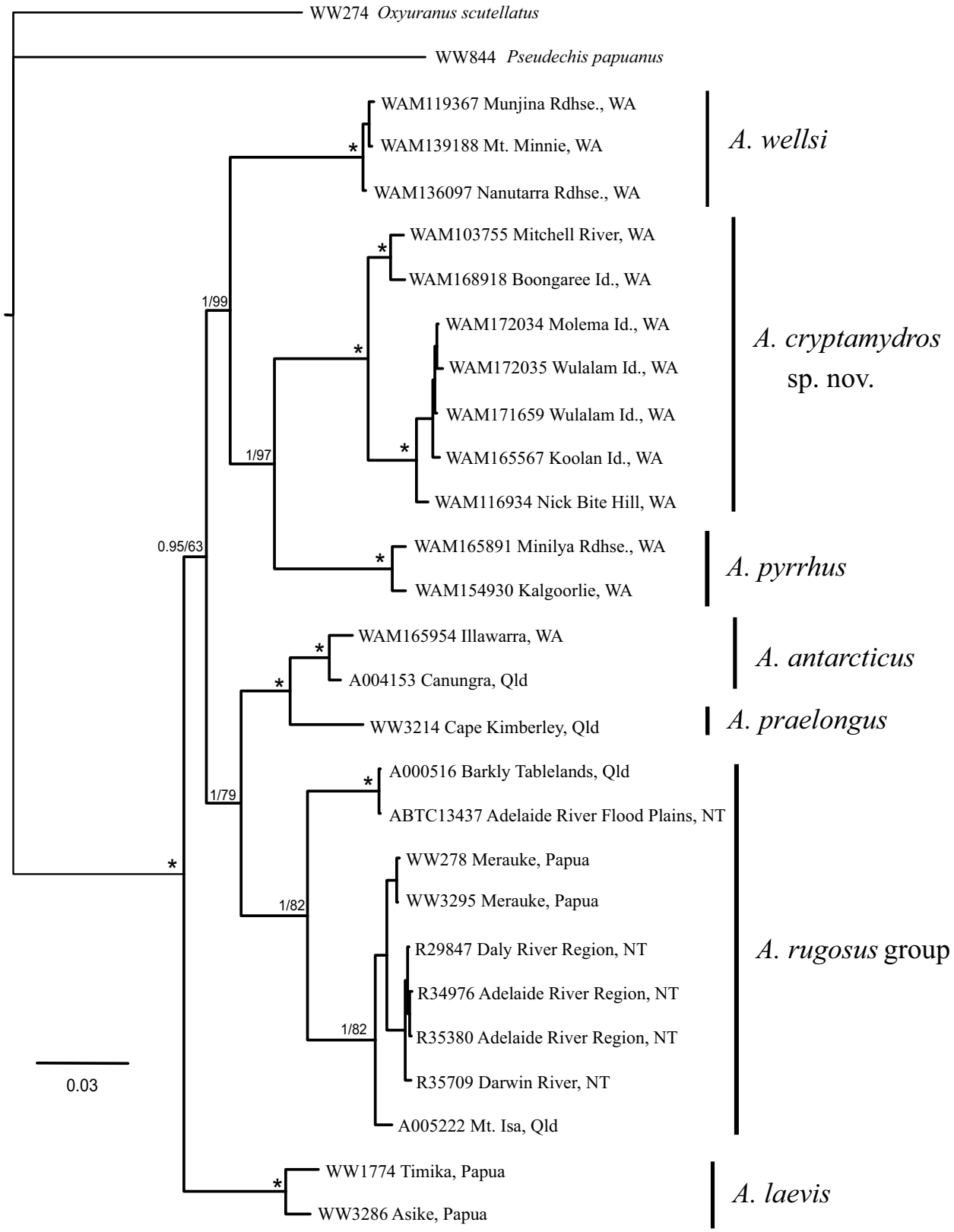

FIGURE 2. Mitochondrial phylogeny of *Acanthophis* inferred from Bayesian inference. Numbers at nodes indicate Bayesian posterior probability and maximum likelihood bootstrap supports, respectively. *s on nodes indicate maximum support for BI and ML.

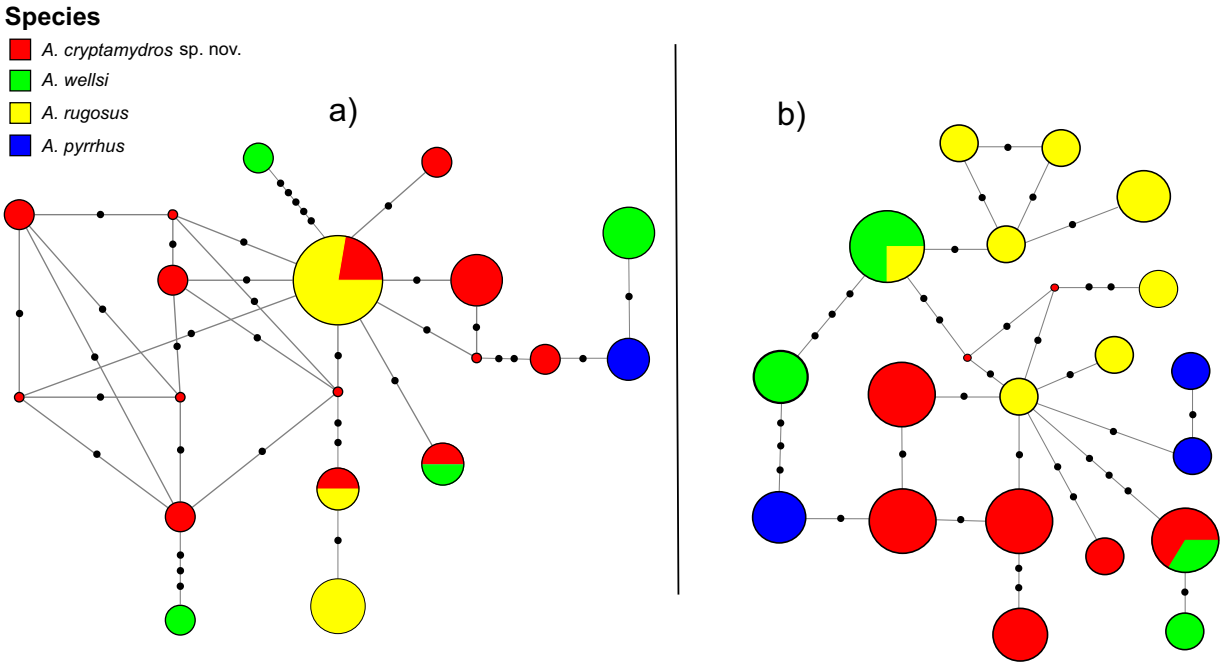

FIGURE 3. Haplotype networks showing relationships between *A. cryptamydros* **sp. nov.**, *A. wellsi, A. rugosus*, and *A. pyrrhus* for the two nuclear genes: a) *prlr*; and b) *ubn1*. Black circles indicate median vectors. Size of haplotypes is proportional to the number of specimens containing that haplotype.

(except *A. pyrrhus* and *A. wellsi* in *ubn1*) is distinguished by possessing one or several unique haplotypes not shared with other taxa. In particular, the Kimberley specimens show distinctive haplotype assemblages (Fig. 3), with multiple unique haplotypes not shared with other species, in both nuclear genes sampled. This is also reflected in patterns of overall genetic differentiation across all three loci, in which the Kimberley population forms a distinct but cohesive cluster (Fig. 4).

Morphological analysis found several characteristics that consistently diagnose the Kimberley population from all other Australian *Acanthophis* species (see above). Although characters in *Acanthophis* can vary widely and do show overlap with values in other species, the Kimberley taxon is reliably diagnosed in most cases by using a combination of scale characteristics and color pattern.

The consistent differences between the Kimberley death adders and all other *Acanthophis* across three independent genetic loci, morphology, and color pattern lead us to conclude that these populations represent a separate species from all other Australian *Acanthophis*. Since the only existing name applicable to this taxon, *Acanthophis lancasteri* Wells & Wellington, 1985, is a *nomen nudum* (Aplin & Donnellan 1999), we describe it as a new species below, diagnosing it from its congeners and all other currently recognized Australian *Acanthophis* species.

Elapidae

Acanthophis Daudin, 1803

Type species. *Boa antartica* (= *Acanthophis antarcticus*) Shaw & Nodder, 1802, by monotypy.

Diagnosis. Species assigned to the genus *Acanthophis* are moderately large, stout terrestrial elapid species most similar to vipers (Viperidae) from other continents. Species within the genus have distinctive wide and stout heads anterior to a defined narrowing forebody that rapidly broadens to the widest point towards midbody. Tail slender, distal portion laterally compressed terminating in a tail spine.

Etymology. From the Greek words *acanthi* meaning ‘spine’ and *ophis* meaning ‘snake’, in reference to the terminal tail spine present on species within the genus.

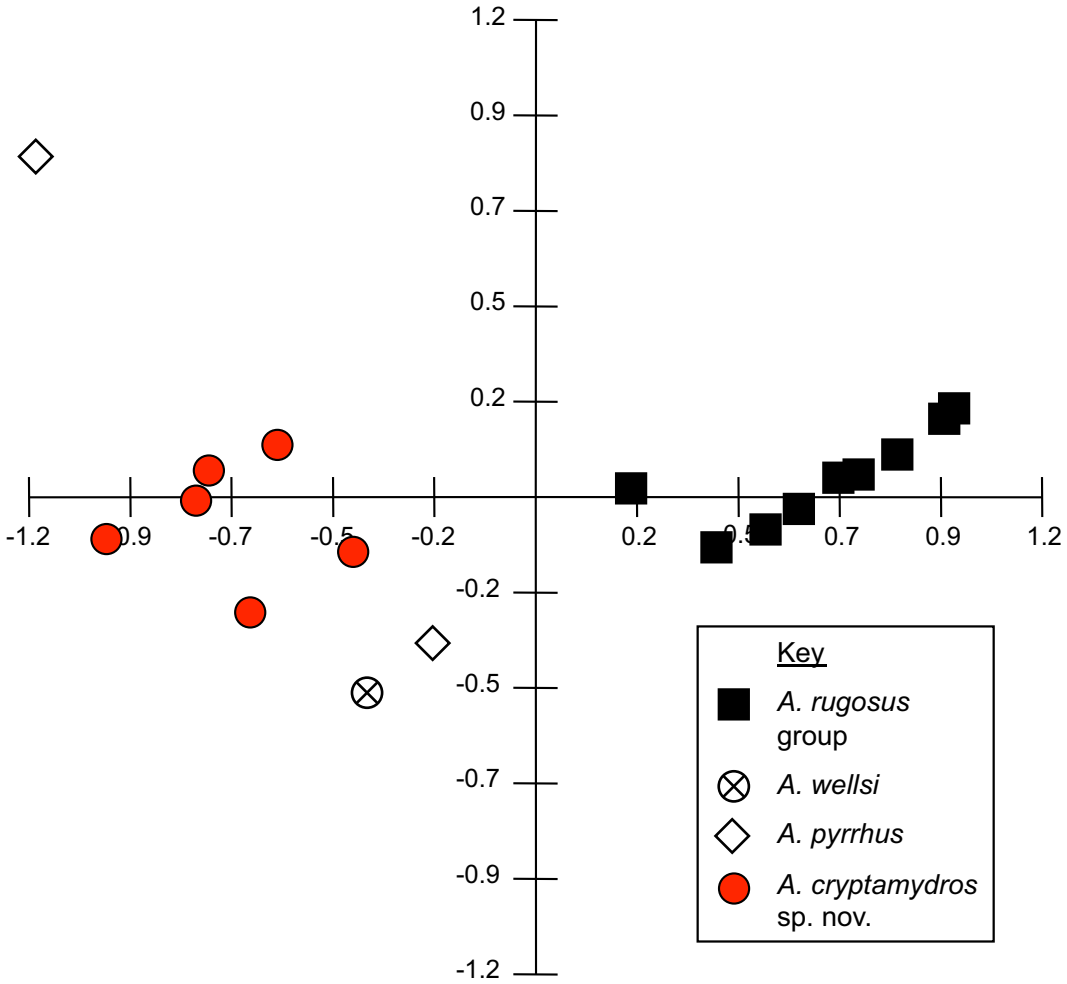

FIGURE 4. Principal coordinates analysis of *Acanthophis* taxa considered here, based on mean *p*-distance of all three loci used herein, with equal weighting.

***Acanthophis cryptamydros* sp. nov.**
Kimberley death adders
Figs. 5–8

Holotype. WAM R174083, medium-sized male collected 1 km north-west of Theda Station homestead, Western Australia (14°46'59.10"S, 126°29'22.02"E), on 8 March 2014 by R. Ellis, G. Bourke, and R. Barrett. Fixed in 10% formalin, stored in 70% ethanol at WAM. Liver samples stored in 100% ethanol at WAM and SAM.

Paratypes. WAM R70690, sub-adult male, 45 km north-northeast Halls Creek, WA (17°51'00"S, 127°50'00"E); WAM R81245, adult male, Packsaddle Springs, near Kununurra, WA (15°54'00"S, 128°41'00"E); WAM R103755, adult male, Surveyors Pool, Mitchell River National Park, WA (14°39'46"S, 125°44'34"E); WAM R165567, adult male, Koolan Island, WA (16°08'04"S, 123°45'05"E); WAM R168918, adult female, Boongaree Island, WA (15°4'39.36"S, 125°11'13.56"E); WAM R172034, adult female, north-west Molema Island, WA (16°14'17"S, 123°49'49"E).

Diagnosis. A moderately stout *Acanthophis* to 645 mm total length. Distinguished from all other Australian *Acanthophis* by a combination of midbody scales in 22 or 23 rows, 125–139 ventrals, undivided prefrontal scales, posterior edge of frontal scale not extending beyond posterior edge of supraoculars, laterally flared supraoculars, area of lower secondary temporal scale equal to or smaller than sixth supralabial, anterior dorsal scales with prominent keels, and ventrum unpigmented except for 1–3 rows of spots on ventrolateral edge.

FIGURE 5. *Acanthophis cryptamydros* **sp. nov.** holotype (WAM R174083) in life (photograph—R.J. Ellis).

Description of holotype (WAM R174083). A medium-sized male *Acanthophis,* measurements and counts: ToL 482 mm; SVL 394 mm; TailL 88 mm (22% of SVL); HeadL 24.9 mm; HeadW 17.4 mm; MBSR 23; AntSR 20; PostSR 17; VS 129; ScST 54; SupLab 6; InfLab 7.

From above, head pear-shaped and distinct from neck, widest at interparietal scale angling forward to rostral and back to posterior jaw edge, narrowing to body; tip of snout blunt, broadly rounded; head in profile deepest at interparietal scale, snout convex; top of snout slightly concave where rostral and internasals converge; head scales rugose; rostral scale twice as wide as high, apex rounded, distal edges with low straight sides, ventral edge concave above lingual fossa; nasal scales narrowly separated by two internasals, approximately twice as wide as tall, rugose; nostril centered on nasal scale, opening dorsally and posteriorly, a shallow divot posterior to nostril; internasals as wide as long, in broad contact with each other, narrow contact with rostral, broad contact with nasals and prefrontals; prefrontals 1.5 times long as wide, narrowing laterally, 0.75 times area of frontal, 1.5 times area of internasals; frontal scale roughly rectangular, anterior edge slightly wider than posterior edge, approximately 1.5 times as long as wide (FrL 4.7 mm, FrW 3.0 mm), apex of posterior edge not extending beyond posterior edge of supraoculars; two parietals, as wide as long, anterior edge in contact with posterior angles of frontal, anterior edge of parietal sharing border with posterior edge of frontal, anterolateral edge in broad contact with supraocular, narrow contact with upper postocular, posterior border irregularly scalloped; preocular single, supraocular single, postoculars two, suboculars two; preocular in contact with prefrontal, nasal, third supralabial and anterior subocular scales; supraocular much longer than wide (SupOcL 5.03 mm, SupOcW 2.90 mm), thicker and rugose in appearance to other head scales, angled upwards at 30º; primary temporal scales two, lower primary temporal 2.5 times larger than upper, upper primary temporal feebly keeled; secondary temporal scales four, gradually increasing in size from dorsalmost to ventralmost, first and second with moderate keels, third and fourth smooth, fourth secondary temporal larger than prior three, located in the notch formed by fifth and sixth supralabials, two times smaller than sixth supralabial; supralabials six, sixth largest, fifth slightly smaller; first supralabial in contact with rostral and nasal, second in contact with nasal; third in contact with nasal, preocular, primary subocular, secondary subocular; fourth in contact with secondary subocular and lower postocular; fifth in contact with lower

subocular, second primary temporal, fourth secondary temporal and sixth supralabial; mental triangular; infralabials seven, fourth infralabial largest, first in contact with postmental scale; anterior chin shields in contact with infralabials one to four; posterior chin shields in contact with fourth infralabial only, anterior and posterior chin shields forming a butterfly-like shape; six rows of intergulars between chin shields and anteriormost ventral.

Body width widest at midbody tapering gradually forward to base of head and posteriorly to cloaca; scale rows 23 at midbody (i.e., at 64th ventral scale from anterior), decreasing to 20 behind the head, 17 anterior to vent; 129 ventral scales; anal scale single; 54 subcaudal scales, first subcaudal paired, anteriormost 29 single, followed by 29 paired; scales on side of body diamond-shaped, scales in vertebral zone more narrow; dorsal keeling strongest on anterior quarter of body, 10–12 longitudinal scale rows wide; keeling weak along remainder of length; dorsolateral and lateral scales weakly keeled to smooth, ventral scales smooth (Figs. 5–7).

Tail elongate, TailL 88 mm (22% of SVL), tapering from cloaca to laterally compressed caudal lure; ScST 54 (ScSS 30, ScSP 24). Caudal lure much higher than wide ending with terminal tail spine.

Eyes small with vertically elliptic pupil, iris mottled in appearance, similar in coloration to surrounding ocular scales.

Coloration. In life, ground color of dorsal and lateral surfaces pale orange-brown; 33 darker cross-bands (Fig. 5); cross-bands two to four midbody scales wide with dark brown border; dorsal scales edged with black anteriorly; tail coloration same as dorsum with 12 bands; tail tip and terminal spine black with white to cream flecks; first midbody scale dark in center, distal edge pale; ventral scales cream-white and lacking pigmentation other than lateralmost edges; ventral coloration of tail similar in appearance to ventrum with patches of dark pigment in center of posteriormost subcaudal scales prior to black tail tip and terminal spine; supralabials stippled with black, stronger stippling on posterior labials, ventral edge pale white; infralabials pale white with dark oblong vertical blotch in center of scale, on posterior scales the ventral edge of the blotch is angled posteriorly.

In preservative, dorsal ground color dull orange brown; overall pattern is subdued with less contrast between light and dark cross-bands (Fig. 6).

FIGURE 6. *Acanthophis cryptamydros* **sp. nov.** holotype (WAM R174083) showing dorsal and ventral coloration and pattern.

FIGURE 7. Head scalation and patterning of *Acanthophis cryptamydros* **sp. nov.** holotype (WAM R174083).

FIGURE 8. Variation in *Acanthophis cryptamydros* **sp. nov.** WAM R174083 (holotype), NTM R29109 and WAM R172034 (paratype).

Variation. SVL up to 555 mm; TailL 15–24% of SVL, mean 20% (N = 22). FrW 47–73% of FrL, mean 59% (N = 26). Apex of posterior edge terminates equal to (N = 13) or prior to (N = 13) posterior supraocular edge, never post. Fourth secondary temporal equal to (N = 13) or smaller than (N = 13) sixth supralabial. MBSR 22–23 (N = 24), mostly 23 (N = 21), occasionally 22 (N = 3). AntSR 16–23, mean 19 (N = 24), PostSR 16–19, mean 18 (N = 24). Ventral scales 125–139, mean 130 (N = 23). First anterior subcaudal scale usually divided, not separated (N = 9), occasionally undivided (N = 5), divided and separated by two (N = 4), three (N = 3) or one (N = 1) by a small rounded scale. ScST 46–56, mean 50, ScSP 20–40, mean 30 and ScSS 14–32, mean 21 (N = 22).

Ground color of dorsal and lateral surfaces variable from dull red-orange, tan-brown or gray in coloration with darker cross bands (Fig 6). Dorsal cross bands 44–61, mean 50 (N = 23); SVL 35–46, mean 39, Tail 9–15, mean 11 (N = 23). Tail tip black with white ventral surface, occasional small white lateral flecks (80%, N = 16), less often white (15%, N = 3) or banded (5%, N = 1). Ventral scales cream-white and lacking pigmentation other than lateral-most edges of ventral scale. Supralabials pale white, mottled in appearance fusing to darker markings on adjacent scales, lower edge of supralabials pale. Infralabials white-edged with dark pigment, both solid and mottled in appearance in center of scale extending to upper edge of scale.

Sexual dimorphism is not obvious, although female TailL % of SVL is shorter than males: female TailL 15–19% of SVL, mean 18 (N = 10); male TailL 21–24% SVL, mean 22% (N = 10). The tail tapers much more abruptly posterior to the vent in females, whereas in males the tail tapers gradually. The number of ventral and subcaudal scales is similar in both sexes (Table 3).

Distribution. *Acanthophis cryptamydros* **sp. nov.** is known from the Kimberley region of Western Australia. The species' range in Western Australia is known to extend from Wotjulum (WAM R11241) in the west, 45 km north-north-east of Halls Creek in the south (WAM R70690), and Kununurra in the east (WAM R137470). *Acanthophis cryptamydros* **sp. nov.** is also known to occur on some offshore islands including Koolan, Bigge, Boongaree, Wulalam, and an unnamed island in Talbot Bay (Palmer *et al.* 2013).

A single specimen (NTM R29109) with incomplete data (no collection date or precise latitude and longitude) is reported as occurring from Adelaide River in the Northern Territory (Fig. 1); however, this locality may be in error. Further collecting from the area may resolve the issue.

Habitat and ecology. The holotype (WAM R174083) was collected early morning towards the end of the 'wet season' (early March) from among basalt boulders in savannah woodland at the edge of a low plateau near a small sandstone outcrop. Vegetation among the basalt boulder habitat was dominated by *Eucalyptus tectifica* and *Corymbia greeniana* amongst mixed shrubs over mixed groundcovers and annual/perennial grasses (Fig. 9). Shrub cover was dominated by *Grevillea mimosoides*, *Grewia retusifolia*, *Indigofera* sp. and *Olearia arguta* (Fig. 9). The specimen was observed retreating to grass tussocks after being disturbed. The specimen was tightly coiled within the grass tussock before attempting to move to another tussock when disturbed. WAM R145216 was collected from thick grasses on a creek bank subjected to minor sheet flooding at Little Mertens Falls. Collection notes and accession data of other specimens describe individuals collected from among grasses or leaf litter in sandstone habitats. One specimen was collected from under a rock in a vine thicket near a beach on an unnamed island in Talbot Bay (WAM R172034), and another from leaf litter in *Acacia* woodland on Wulalam Island (WAM R172035). Two specimens were collected from roads or tracks (WAM R70690, WAM R165567).

Examination of the stomach contents of two specimens revealed a mixture of frogs, lizards, and mammals. A juvenile specimen (WAM R1251B) had an adult *Heteronotia* species (aff. *H. binoei*). In the gut of an adult specimen (WAM R141552), a subadult *Lophognathus* species (*L. gilberti*), an adult *Litoria* species (aff. *L. nasuta* or *L. watjulumensis*), and hair belonging to a native murid species, *Pseudomys* sp. (aff. *P. johnstoni* or *P. delicatulus*) were found. Two small reptilian eggs were also collected from the adult, possibly from the *Lophognathus* ingested. Accession data for WAM R116934 identified a *Ctenotus pantherinus* (WAM R117001) from examination of its stomach contents. An ecological study of Australian and Papuan death adders by Shine *et al*. (2014) included five specimens of *A. cryptamydros*; however, examination of stomach contents revealed no prey items, only a small quantity of dirt. Examination of the gut contents of other northern *Acanthophis* species indicated a diet consisting of a wide range of vertebrate species, especially lizards but also including frogs, mammals, and some birds (Shine *et al.* 2014).

Examination of reproductive organs of an adult female specimen (WAM R106033) revealed 13 well-developed follicles approximately 10 x 14 mm in size (month of collection unknown).

Comparison with other species. Distinguished from *A. pyrrhus* by higher average MBSR (23 vs. 21), fewer ventral scales (125–139 vs. 136–158), pigment on lateral periphery of ventral scales (vs. no pigment on ventral scales), presence of pigment patches on infralabials (infralabials unpigmented in *A. pyrrhus*), less prominent dorsal keeling (strongly keeled in *A. pyrrhus*, tapering to a sharp point on posterior edge), head scales less rugose, posterior edge of frontal scale not extending beyond posterior edge of supraoculars (equal to or beyond in *A. pyrrhus*), and undivided pair of prefrontal scales (divided in *A. pyrrhus*).

TABLE 3. Summaries of characters and ratios measured for *A. cryptamydros* **sp. nov.** and *A. 'rugosus* group'. All measurements in mm. Mean±S.D. (range). See Table 2 for abbreviations. Sample size listed in column headings, unless noted for individual characters below. Damaged specimens where accurate counts or measurements could be obtained or those less than 300 mm SVL were excluded from measurements and ratios but included in scale counts.

	A. cryptamydros **sp. nov.**		*A. 'rugosus* group'	
Character	N = 23		N = 14	
	(9♂, 7♀)		(9♂, 5♀)	
SVL	428±57 (322–555) N = 20		486±97 (375–690)	
	♂♂ N = 9	♀♀ N = 7	♂♂ N = 9	♀♀ N = 5
	412±41	468±54	434±57	581±82
	(374–496)	(392–555)	(375–530)	(482–690)
TailL	86±9 (72–110) N = 20		94±11 (80–110)	
	♂♂ N = 9	♀♀ N = 7	♂♂ N = 9	♀♀ N = 5
	90.6±9	81.4±5	92±11	98±9
	(79–110)	(76–89)	(79–110)	(85–108)
TailL/SVL	0.20±0.03 (0.15–0.24) N = 20		0.20±0.03 (0.15–0.23)	
	♂♂ N = 9	♀♀ N = 7	♂♂ N = 9	♀♀ N = 5
	0.22±0.01	0.18±0.01	0.21±0.01	0.17±0.03
	(0.21–0.24)	(0.15–0.19)	(0.20–0.23)	(0.15–0.22)
HeadL	26.1±2.4 (22.7–32.0) N = 20		31.1±5.5 (25.5–42.3)	
HeadW	16.4±2.2 (13.8–20.2) N = 20		19.4±4.6 (13.1–27.1)	
HeadW/HeadL	0.63±0.05 (0.54–0.71) N = 20		0.60±0.04 (0.51–0.66)	
VS	130±4 (125–139) N = 20		127±4 (123–136)	
ScST	50±3 (46–56) N = 20		46±6.14 (29–55)	
	♂♂ N = 9	♀♀ N = 7	♂♂ N = 9	♀♀ N = 5
	53±2	49±2	47±7	45±3
	(51–56)	(46–51)	(29–55)	(42–49)
MBSR	22.9±0.3 (22–23)		22.0 ±0.9 (21–23)	
AntSR	19.2±1.3 (16–23)		20.3±0.6 (19–21)	
PostSR	17.8±0.9 (16–19)		18.0±0.7 (17–19)	
PreOc	1.0±0 (1)		1.1±0.3 (1–2)	
SupOc	1.0±0 (1)		1.1±0.3 (1–2)	
PostOc	2.0±0.2 (2–3)		2.1±0.3 (2–3)	
SubOc	2.2±0.4 (2–3)		2.7±0.5 (2–3)	
Ptemp	2±0 (2)		2.0±0 (2)	
Stemp	4.4±0.5 (4–5)		4.0±0.4 (3–5)	
SupLab	6.0±0 (6)		6.0±0 (6)	
InfLab	7.0±0 (7)		7.1±0.3 (7–8)	
FrL	5.6±0.5 (4.7–6.7) N = 20		7.2±0.9 (6.0–9.0)	
FrW	3.3±0.3 (2.6–4.1) N = 20		3.4±0.5 (2.8–4.4)	
FrW/FrL	0.59±0.06 (0.47–0.73) N = 20		0.48±0.02 (0.45–0.52)	
SupOcL	5.5±0.5 (4.8–6.4) N = 20		6.4±0.7 (5.2–7.4)	
SupOcW	3.1±0.3 (2.8–3.7) N = 20		3.7±0.5 (3.0–4.6)	

FIGURE 9. Type locality habitat of *Acanthophis cryptamydros* **sp. nov.** in Theda Station, Kimberley region, Western Australia (photograph—R.J. Ellis).

Differs from *A. wellsi* by higher midbody scale rows (22–23 vs. 19–21), less prominent dorsal keeling, posterior edge of frontal scale not extending beyond posterior edge of supraoculars (equal to or beyond in *A. wellsi*), and more laterally flared supraocular (absent or less prominent in *A. wellsi*). Differs from melanistic forms of *A. wellsi* by the absence of prominent black coloration on head and black dorsal bands.

Distinguished from *A. antarcticus* by higher average MBSR (23 vs. 21), more ventral scales (125+ vs. 124-), and more prominent anterior dorsal keeling (vs. smooth or very weakly keeled in *A. antarcticus*).

Most similar to *A. rugosus* group in appearance, but differs through higher average ventral scale counts (130 vs. 127), despite considerable overlap in range, lacking dark pigment on the ventrum other than lateral edge (vs. distinct blotching of dark pigment), posterior edge of frontal scale not extending beyond posterior edge of supraoculars (beyond in 13 of 14 specimens, equal in one specimen) and size of lower secondary temporal not larger than sixth supralabial in area (*A. cryptamydros* equal in 13 specimens, smaller in 13 vs. *A. rugosus* equal in 10, larger in 4). See Table 3 for further details.

Comparisons of *A. cryptamydros* **sp nov.** to the *A. rugosus* group are complicated by the likely existence of a number of undescribed species within the latter, which greatly increases variation within this complex. We comment on morphological characters that are useful in distinguishing these two taxa.

Etymology. The specific epithet is modified from the Greek words *kryptos* (cryptic, hidden) and *amydros* (indistinct, dim) in reference to the cryptic nature of the species and its indistinct appearance relative to its surroundings making its presence unknown to predators and prey. Used as a noun in apposition.

Remarks. The *A. rugosus* group is likely to contain a number of undescribed species. Taxonomic resolution of this group will further define differences between individual species within the group and *A. cryptamydros* **sp. nov.** The discovery of *A. cryptamydros* **sp. nov.** as a previously undescribed major lineage within *Acanthophis* highlights the incompleteness of our understanding of phylogenetic structure and species limits within the genus. At the same time, it also highlights the importance of the Kimberley region of Western Australia as a center of endemism (Doughty 2011; Oliver *et al.* 2012; Pepper & Keogh 2014).

Lethal ingestion of the cane toad (*Rhinella marina*) has been documented in previous studies on *Acanthophis* specimens from the Kimberley region and Northern Territory (Phillips & Shine 2007; Hagman *et al.* 2009; Phillips *et al.* 2010; Pearson *et al.* 2014) indicating the species is likely to be at risk of significant decline as cane toads continue to move west across the Kimberley region. A detailed assessment on potential threats to the species including cane toads will identify the need for listing as a species requiring protection under state or federal legislation.

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References

Anstis, M., Tyler, M.J., Roberts, J.D., Price, L.C. & Doughty, P. (2010) A new species of *Litoria* (Anura: Hylidae) with a highly distinctive tadpole from the north-western Kimberley region of Western Australia. *Zootaxa*, 2550, 39–57.

Aplin, K.P. & Donnellan, S.C. (1999) 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. *Records of the Western Australian Museum*, 19, 277–298.

Arévalo, E., Davis, S.K. & Sites, J.W. Jr. (1994) Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosoms races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. *Systematic Biology*, 43, 387–418.
http://dx.doi.org/10.1093/sysbio/43.3.387

Barrett, M.D., Craven, L.A. & Barrett, R.L. (2009) *Calytrix gomphrenoides* (Myrtaceae), a new species from the Kimberley Region of Western Australia. *Nuytsia,* 19, 1–8.

Boulenger, G.A. (1898) Description of a new death adder (*Acanthophis*) from central Australia. *Annals and Magazine of Natural History*, Series 7, 2, 75.
http://dx.doi.org/10.1080/00222939808678016

Bowman, D.M.J.S., Brown, G.K., Braby, M.F., Brown, J.R., Cook, L.G., Crisp, M.D., Ford, F., Haberle, S., Hughes, J., Isagi, Y., Joseph, L., McBride, J., Nelson, G. & Ladiges, P.Y. (2010) Biogeography of the Australian monsoon tropics. *Journal of Biogeography*, 37, 201–216.
http://dx.doi.org/10.1111/j.1365-2699.2009.02210.x

Carlson, K.M., Mansfield, D.H. & Smith, J.F. (2011) A new species in the *Lomatium foeniculaceum* (Apiaceae) clade revealed through combined morphometric and phylogenetic analyses. *Systematic Botany*, 36, 495–507.
http://dx.doi.org/10.1600/036364411X569688

Cogger, H.G. (2000) *Reptiles and Amphibians of Australia*. 6th Edition. Reed New Holland, Sydney, N.S.W., 808 pp.

Cogger, H.G. (2014) *Reptiles and Amphibians of Australia. 7th Edition*. CSIRO Publishing, Collingwood, Victoria, 1032 pp.

Daudin, F.M. (1803) *Histoire Naturelle, générale et particulière des Reptiles*. *Vol. 5*. Dufart, Paris, 365 pp.

Doughty, P. (2011) An emerging frog diversity hotspot in the northwest Kimberley of Western Australia: another new frog species from the high rainfall zone. *Records of the Western Australian Museum*, 26, 209–216.

Doughty, P., Palmer, R., Sistrom, M.J., Bauer, A.M. & Donnellan, S.C. (2012) Two new species of *Gehyra* (Squamata: Gekkonidae) geckos from the north-west Kimberley region of Western Australia. *Records of the Western Australian Museum*, 27, 117–134.

Dowling, H.G. (1951) A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology*, 1, 97–99.

Flot, J.-F. (2010) SEQPHASE: a web tool for interconverting PHASE input/output files and FASTA sequence alignments. *Molecular Ecology Resources*, 10, 162–166.
http://dx.doi.org/10.1111/j.1755-0998.2009.02732.x

Fry, B.G., Wickramaratna, J.C., Hodgson, W.C., Alewood, P.F., Kini, R.M., Ho, H. & Wüster, W. (2002) Electrospray liquid chromatography/mass spectrometry fingerprinting of *Acanthophis* (death adder) venoms: taxonomic and toxinological implications. *Rapid Communications in Mass Spectrometry*, 16, 600–608.
http://dx.doi.org/10.1002/rcm.613

Greer, A. (1997) *The Biology and Evolution of Australian Snakes*. Surrey Beatty & Sons, Chipping Norton, NSW, 358 pp.
Hagman, M., Phillips, B.L. & Shine, R. (2009) Fatal attraction: Adaptations to prey on native frogs imperil snakes after invasion of toxic toads. *Proceedings of the Royal Society B*, 276, 2813–2818.
http://dx.doi.org/10.1098/rspb.2009.0192
Hoser, R.T. (1998) Death adders (genus *Acanthophis*): an overview, including descriptions of five new species and one subspecies. *Monitor, Journal of the Victorian Herpetological Society*, 9, 20–30, 33–41.
Joly, S. & Bruneau, A. (2006) Incorporating allelic variation for reconstructing the evolutionary history of organisms from multiple genes: An example from Rosa in North America. *Systematic Biology*, 55, 623–636.
http://dx.doi.org/10.1080/10635150600863109
Johnston, G. (1996) Genetic and seasonal variation in body colour of the Australian death adder, *Acanthophis antarcticus* (Squamata: Elapidae). *Journal of Zoology*, 239, 187–196.
http://dx.doi.org/10.1111/j.1469-7998.1996.tb05446.x
Köhler, F. (2010) Uncovering local endemism in the Kimberley, Western Australia: Description of new species of the genus *Amplirhugada* Iredale, 1933 (Pulmonata: Camaenidae). *Records of the Australian Museum*, 62, 217–284.
http://dx.doi.org/10.3853/j.0067-1975.62.2010.1554
Köhler, F. (2011) Descriptions of new species of the diverse and endemic land snails *Amplirhagada* Iredale, 1933 from rainforest patches across the Kimberley, Western Australia (Pulmonata: Camaenidae). *Records of the Australian Museum*, 63, 167–202.
http://dx.doi.org/10.3853/j.0067-1975.63.2011.1581
Kuch, U., Keogh, J.S., Weigel, J., Smith, L.A. & Mebs, D. (2005) Phylogeography of Australia's King Brown snake (*Pseudechis australis*) reveals Pliocene divergence and Pleistocene dispersal of a top predator. *Naturwissenschaften*, 92, 121–127.
http://dx.doi.org/10.1007/s00114-004-0602-0
Loveridge, A. (1948) New Guinean reptiles and amphibians in the Museum of Comparative Zoology and United States Museum. *Bulletin of the Museum of Comparative Zoology*, 101, 303–430.
Marin, J., Donnellan, S.C., Hedges, B., Puillandre, N., Aplin, K.P., Doughty, P., Hutchinson, M.N., Couloux, A. & Vidal, N. (2013) Hidden species diversity of Australian burrowing snakes (*Ramphotyphlops*). *Biological Journal of the Linnean Society*, 110, 427–441.
http://dx.doi.org/10.1111/bij.12132
Maslin, B.R., Barrett, M.D. & Barrett, R.L. (2013) A baker's dozen of new wattles highlights significant *Acacia* (Fabaceae: Mimosoideae) diversity and endemism in the north-west Kimberley region of Western Australia. *Nuytsia,* 23, 543–587.
McDowell, S.B. (1984) Results of the Archbold Expeditions. No. 112. The snakes of the Huon Peninsula, Papua New Guinea. *American Museum Novitates*, 2775, 1–28.
Nylander, J.A.A. (2004) *MrModeltest 2.3*. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.
Oliver, P.M., Doughty, P. & Palmer, R. (2012) Hidden biodiversity in rare northern Australian vertebrates: the case of the clawless gecko (*Crenadactylus,* Diplodactylidae) of the Kimberley. *Wildlife Research*, 39, 429–435.
http://dx.doi.org/10.1071/WR12024
Oliver, P.M., Laver, R.J., Melville, J. & Doughty, P. (2014) A new species of velvet gecko (*Oedura*: Diplodactylidae) from the limestone ranges of the southern Kimberley, Western Australia. *Zootaxa*, 3873 (1), 49–61.
http://dx.doi.org/10.11646/zootaxa.3873.1.4
Palmer, R., Pearson, D.J., Cowan, M.A. & Doughty, P. (2013) Islands and scales: a biogeographic survey of reptiles on Kimberley islands, Western Australia. *Records of the Western Australian Museum,* 81 (Supplement), 183–204.
http://dx.doi.org/10.18195/issn.0313-122x.81.2013.183-204
Pearson, D.J., Webb, J.K., Greenlees, M.J., Phillips, B.L., Bedford, G.S., Brown, G.P., Thomas, J. & Shine, R. (2014) Behavioural responses of reptile predators to invasive cane toads in tropical Australia. *Austral Ecology*, 39, 448–454.
http://dx.doi.org/10.1111/aec.12102
Pepper, M., Doughty, P., Hutchinson, M.N. & Keogh, J.S. (2011) Ancient drainages divide cryptic species in Australia's arid zone: Morphological and multi-gene evidence for four new species of Beaked Geckos (*Rhynchoedura*). *Molecular Phylogenetics and Evolution*, 61, 810–822.
http://dx.doi.org/10.1016/j.ympev.2011.08.012
Pepper, M. & Keogh, J.S. (2014) Biogeography of the Kimberley, Western Australia: a review of landscape evolution and biotic response in an ancient refugium. *Journal of Biogeography*, 41, 1443–1455.
http://dx.doi.org/10.1111/jbi.12324
Pfeiffer, W. & Stamatakis, A. (2010) Hybrid MPI/Pthreads Parallelization of the RAxML Phylogenetics Code. *In:* Ninth IEEE International Workshop on High Performance Computational Biology (HiCOMB), Atlanta, pp. 1–8.
Phillips, B. & Shine, R. (2007) When dinner is dangerous: Toxic frogs elicit species-specific responses from a generalist snake predator. *The American Naturalist*, 170, 936–942.
http://dx.doi.org/10.1086/522845
Phillips, B.L., Greenlees, M.J., Brown, G.P. & Shine, R. (2010) Predator behaviour and morphology mediates the impact of an invasive species: cane toads and death adders in Australia. *Animal Conservation*, 13, 53–59.
http://dx.doi.org/10.1111/j.1469-1795.2009.00295.x
Powney, G.D., Grenyer, R., Orme, C.D.L., Owens, I.P.F. & Meiri, S. (2010) Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. *Global Ecology and Biogeography*, 19, 386–396.

http://dx.doi.org/10.1111/j.1466-8238.2009.00521.x
Rambaut, A. & Drummond, A.J. (2007) Tracer v1.4. Available from: http://beast.bio.ed.ac.uk/Tracer (accessed 29 July 2015)
Ramsay, E.P. (1877) Description of a supposed new species of Acanthophis from North Australia. *Proceedings of the Linnean Society of New South Wales*, 2, 72–74.
Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
http://dx.doi.org/10.1093/bioinformatics/btg180
Sanders, K.L., Lee, M.S.Y., Foster, R. & Keogh, J.S. (2008) Molecular phylogeny and divergence dates for Australian elapids and sea snakes (Hydrophiinae): evidence from seven genes for rapid evolutionary radiations. *Journal of Evolutionary Biology*, 21, 682–695.
http://dx.doi.org/10.1111/j.1420-9101.2008.01525.x
Shaw, G. & Nodder, F.P. (1802) Boa antarctica. *Naturalist's Miscellany*, 13, 535.
Shea, G.M. & Scanlon, J.D. (2007) Revision of the small tropical whipsnakes previously referred to *Demansia olivacea* (Gray, 1842) and *Demansia torquata* (Gunther, 1862) (Squamata: Elapidae). *Records of the Australian Museum*, 59, 117–142.
http://dx.doi.org/10.3853/j.0067-1975.59.2007.1488
Shine, R. (1980) Ecology of the Australian death adder, *Acanthophis antarcticus* (Elapidae): evidence for convergence with the Viperidae. *Herpetologica*, 36, 281–289.
Shine, R., Spencer, C.L. & Keogh, J.S. (2014) Morphology, reproduction and diet in Australian and Papuan death adders (*Acanthophis,* Elapidae). *PLoS ONE*, 9, e94216.
http://dx.doi.org/10.1371/journal.pone.0094216
Slatyer, C., Rosauer, D. & Lemckert, F. (2007) An assessment of endemism and species richness patterns in the Australian anura. *Journal of Biogeography*, 34, 583–596.
http://dx.doi.org/10.1111/j.1365-2699.2006.01647.x
Stephens, M. & Scheet, P. (2005) Accounting for decay of linkage disequilibrium in haplotype inference and missing-data imputation. *American Journal of Human Genetics*, 76, 449–462.
http://dx.doi.org/10.1086/428594
Stephens, M., Smith, N.J. & Donnelly, P. (2001) A new statistical method for haplotype reconstruction from population data. *American Journal of Human Genetics*, 68, 978–989.
http://dx.doi.org/10.1086/319501
Storr, G.M. (1981) The genus *Acanthophis* (Serpentes: Elapidae) in Western Australia. *Records of the Western Australian Museum*, 9, 203–210.
Storr, G.M., Smith, L.A. & Johnstone, R.E. (2002) *Snakes of Western Australia*. Western Australian Museum, Perth, 309 pp.
Swofford, D.L. (2002) *PAUP* 4.0 - Phylogenetic Analysis Uing Parsimony (*and other methods)*. Sinauer Associates, Sunderland, MA, U.S.A.
Tamura, K., Dudley, J., Nei, M. & Kumar, S. (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) Software Version 4.0. *Molecular Biology and Evolution*, 24, 1596–1599.
http://dx.doi.org/10.1093/molbev/msm092
Townsend, T.M., Alegre, R.E., Kelley, S.T., Wiens, J.J. & Reeder, T.W. (2008) Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: An example from squamate reptiles. *Molecular Phylogenetics and Evolution*, 47, 129–142.
http://dx.doi.org/10.1016/j.ympev.2008.01.008
Wells, R.W. & Wellington, C.R. (1985) A classification of the Amphibia and Reptilia of Australia. *Australian Journal of Herpetology*, Supplementary Series, 1, 1–61.
http://dx.doi.org/10.1071/AJZS113
Wilson, S. & Swan, G. (2013) *A Complete Guide to Reptiles of Australia*. New Holland Publishers, Sydney, 592 pp.
Wüster, W., Dumbrell, A.J., Hay, C., Pook, C.E., Williams, D.J. & Fry, B.G. (2005) Snakes across the Strait: trans-Torresian phylogeographic relationships in three genera of Australian snakes (Serpentes: Elapidae: *Acanthophis, Oxyuranus,* and *Pseudechis*). *Molecular Phylogenetics and Evolution*, 34, 1–14.
http://dx.doi.org/10.1016/j.ympev.2004.08.018
Wüster, W., Peppin, L., Pook, C.E. & Walker, D.E. (2008) A nesting of vipers: Phylogeny and historical biogeography of the Viperidae (Squamata: Serpentes). *Molecular Phylogenetics and Evolution*, 49, 445–459.
http://dx.doi.org/10.1016/j.ympev.2008.08.019

APPENDIX 1. Specimens used in this study including GenBank accession numbers. Genus abbreviations are as follows: *A.= Acanthophis*, *O.= Oxyuranus*, *P.= Pseudechis*. Under the species column a *(H)* indicates the holotype and a *(P)* indicates the paratypes for *A. cryptamydros* **sp. nov.** Reg. no. indicates museum registration number and abbreviations are as follows: specimens from the Western Australian Museum distinguished by 'WAM'; specimens from the Museum and Art Gallery of the Northern Territory distinguished by 'NTM'; specimens from Queensland Museum by 'QM'; specimens from South Australia Museum by 'SAM'; specimens from W. Wüster's personal tissue archive by 'WW'. Collection coordinates are given in columns Lat. (S) which indicates latitude, and Long. (E) which indicates longitude. Column Mor. Indicates the specimens examined for morphology with a ● and when ●● is present specimens were also used in morphological analysis

Species	Reg. no.	Sex	Locality	State	Lat. (S)	Long. (E)	*nd4*	*cytb*	*16s*	*prlr*	*ubn1*	Mor.
A. antarcticus	QM 4153		Canungra	QLD	28°07'45"	153°06'19"	KT183462	KT026541	KT026514			
A. antarcticus	WAM 2160		Eucla	WA	31°43'	128°54'						●
A. antarcticus	WAM 26689		Araluen	WA	32°08'	116°07'						●
A. antarcticus	WAM 26803		Canning Dam	WA	32°09'	116°08'						●
A. antarcticus	WAM 28096		Esperance 40 km W	WA	33°52'	121°53'						●
A. antarcticus	WAM 37720		Madura	WA	32°00'	126°35'						●
A. antarcticus	WAM 40197		Caiguna	WA	32°16'	125°29'						●
A. antarcticus	WAM 54251		Canning Dam	WA	32°09'	116°07'						●
A. antarcticus	WAM 58779		Pickering brook	WA	32°02'	116°06'						●
A. antarcticus	WAM 64698		Canning Dam	WA	32°09'	116°08'						●
A. antarcticus	WAM 105964	M	10 km SE Mount Dale	WA	32°13'	116°20'						●

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APPENDIX 1. (continued)

Species	Reg. no.	Sex	Locality	State	Lat. (S)	Long. (E)	*nd4*	*cytb*	*16s*	*prlr*	*ubn1*	Mor.
A. antarcticus	WAM 108193	F	Howick Hill 4 km W	WA	33°44’	122°45’						●
A. antarcticus	WAM 113756		Mundaring Weir	WA	31°58’	116°07’						●
A. antarcticus	WAM 165696	F	Illawarra	WA	32°06'57”	116°08'48”						●
A. antarcticus	WAM 165697	F	Karragullen	WA	32°07'05”	116°09'08”						●
A. antarcticus	WAM 165698	F	Illawarra	WA	32°09’	116°11'33”						●
A. antarcticus	WAM 165954	F	Illawarra	WA	32°10'50”	116°14'35”	KT183456	KT026535	KT026508			●
A. cryptamydros	WAM 5709		Kunmunya Mission	WA	15°26’	124°40’						●●
A. cryptamydros	WAM 10628		Wyndham	WA	15°29’	128°07’						●
A. cryptamydros	WAM 11241	U	Wotjulum	WA	16°11’	123°37’						●●
A. cryptamydros	WAM 13517A		Yirrkala	WA	12°15’	136°53’						●
A. cryptamydros	WAM 13517B		Yirrkala	WA	12°15’	136°53’						●
A. cryptamydros	WAM 21519		Ranken River	WA	20°04’	137°01’						●
A. cryptamydros	WAM 29141		Koolan Island	WA	16°09’	123°45’						●
A. cryptamydros	WAM 34078		Kalumburu	WA	14°18’	126°38’						●

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APPENDIX 1. (continued)

Species	Reg. no.	Sex	Locality	State	Lat. (S)	Long. (E)	*nd4*	*cytb*	*16s*	*prlr*	*ubn1*	Mor.
A. cryptamydros	WAM 34079		Kalumburu	WA	14°18’	126°38’						●
A. cryptamydros	WAM 37761	M	Koolan Island	WA	16°09’	123°45’						●●
A. cryptamydros	WAM 37762		Koolan Island	WA	16°09’	123°45’						●●
A. cryptamydros	WAM 37763	M	Koolan Island	WA	16°09’	123°45’						●●
A. cryptamydros	WAM 37764	U	Koolan Island	WA	16°09’	123°45’						●●
A. cryptamydros	WAM 41457		Bigge Island	WA	14°36’	125°07’						●
A. cryptamydros	WAM 46836	F	Prince Regent River Nat Res	WA	15°20’	124°56’						●●
A. cryptamydros **(P)**	WAM 70690	M	45 km NNE Halls Creek	WA	17°51’	127°50’						●●
A. cryptamydros	WAM 70698		Gibson Point, Parry Harbour	WA	14°00’	128°59’						●
A. cryptamydros **(P)**	WAM 81245	M	Packsaddle Springs, nr. Kununurra	WA	15°54’	128°41’						●●
A. cryptamydros **(P)**	WAM 103755	M	Surveyors Pool	WA	14°39'46”	125°44'34”	KT183455	KT026534	KT026507	KT026579	KT026562	●●
A. cryptamydros	WAM 106033	F	Koolan Island	WA	16°09’	123°45’						●●
A. cryptamydros	WAM 116934	F	Bungle Bungle Nat. Park	WA	17°14’	128°19’	KT183459	KT026538	KT026510	KT026581	KT026565	●●
A. cryptamydros	WAM 137470		Kununurra	WA	15°47’	128°44’						●●

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APPENDIX 1. (continued)

Species	Reg. no.	Sex	Locality	State	Lat. (S)	Long. (E)	*nd4*	*cytb*	*16s*	*prlr*	*ubn1*	Mor.
	WAM											
A. cryptamydros	141552	U	Mertens Falls	WA	14°50’	125°44’						●●
	WAM		Little Mertens									
A. cryptamydros	145216	M	Falls	WA	14°49’	125°42’						●●
	WAM											
A. cryptamydros	164794	F	unknown	WA								●●
A. cryptamydros	WAM											
(P)	165567	M	Koolan Island	WA	16°08'04”	123°45'05”	KT183460	KT026540	KT026512	KT026582	KT026566	●●
A. cryptamydros	WAM		Boongaree									
(P)	168918	F	Island	WA	15°05’	125°12’	KT183457	KT026536		KT026578	KT026561	●●
	WAM		Wulalam									
A. cryptamydros	171659	F	Island	WA	16°22'13”	124°13'37”		KT026539	KT026511	KT026580	KT026563	●●
A. cryptamydros	WAM		NW Molema									
(P)	172034	F	Island	WA	16°14'17”	123°49'49”	KT183458	KT026537	KT026509		KT026564	●●
	WAM		Wulalam									
A. cryptamydros	172035	F	Island	WA	16°22'21”	124°13'49”	KT183461	KT026560	KT026513	KT026583	KT026567	●●
A. cryptamydros	WAM											
(H)	174083	M	SE Theda HS	WA	14°46'59”	126°29'22”						●●
	NTM		Dorat Rd,									
A. cryptamydros	29109		Adelaide River	NT								●●
	WW		Kuala Kencana									
A. laevis	1774		(nr Timika)	IND			KT183476	KT026544	KT026517			
	WW		Asike		06°39'11”	140°26'50”						
A. laevis	3286			IND			KT183465	KT026545	KT026518			
	WW		Cape									
A. praelongus	3214		Kimberley	QLD	16°16'38”	145°29'6”	KT183477	KT026546	KT026519			
	WAM		7 km NNW									
A. pyrrhus	79139		Goldsworthy	WA	20°17’	119°29’						●

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APPENDIX 1. (continued)

Species	Reg. no.	Sex	Locality	State	Lat. (S)	Long. (E)	*nd4*	*cytb*	*16s*	*prlr*	*ubn1*	Mor.
A. pyrrhus	WAM 85117		Port Hedland	WA	20°19’	118°36’						●
A. pyrrhus	WAM 91671		55 km S Anna Plains HS	WA	19°44’	121°24’						●
A. pyrrhus	WAM 91672		55 km S Anna Plains HS	WA	19°44’	121°24’						●
A. pyrrhus	WAM 104357		30 km SE South Hedland	WA	20°25’	118°56’						●
A. pyrrhus	WAM 123191		Kennedy Range National Park	WA	24°30'03”	115°01'03”						●
A. pyrrhus	WAM 124838		38 km N Port Heldand	WA	20°25’	118°50’						●
A. pyrrhus	WAM 124878		38 km N Port Heldand	WA	20°25’	118°50’						●
A. pyrrhus	WAM 129434		Port Hedland	WA	20°19’	118°36’						●
A. pyrrhus	WAM 129435		Port Hedland	WA	20°19’	118°36’						●
A. pyrrhus	WAM 135628		3 km W Sandfire Roadhouse	WA	19°46’	121°03’						●
A. pyrrhus	WAM 137991		143 km S Roebuck Plains Roadhouse	WA	19°45’	123°05’						●
A. pyrrhus	WAM 141275	F	37 km E South Hedland	WA	20°24’	118°56’						●
A. pyrrhus	WAM 141276	F	35 km E South Hedland	WA	20°24’	118°55’						●

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APPENDIX 1. (continued)

Species	Reg. no.	Sex	Locality	State	Lat. (S)	Long. (E)	*nd4*	*cytb*	*16s*	*prlr*	*ubn1*	Mor.
A. pyrrhus	WAM 146966	F	Carouse Dam, 110 km NE Kalgoorlie	WA	30°09'13"	122°21'22"						●
A. pyrrhus	WAM 154930	M	Carouse Dam, 110 km NE Kalgoorlie	WA	30°12'	122°24'	KT183467	KT026548	KT026521		KT026570	●
A. pyrrhus	WAM 156223	M	Shay Gap area	WA	20°26'38"	120°00'14"						●
A. pyrrhus	WAM 156224	F	Shay Gap area	WA	20°26'38"	120°00'14"						●
A. pyrrhus	WAM 162978		Mandora Station	WA	19°44'	120°50'						●
A. pyrrhus	WAM 165891	F	39 km NE Minilya Roadhouse	WA	23°34'	114°17'	KT183466	KT026547	KT026520	KT026585	KT026569	●
A. 'rugosus group'	NTM 9724	F	South Alligator River Floodplain	NT	12°40'59"	132°31'						●●
A. 'rugosus group'	NTM 17879	F	South Alligator River Floodplain	NT	12°40'59"	132°31'						●●
A. 'rugosus group'	NTM 17880	F	South Alligator River Floodplain	NT	12°40'59"	132°31'						●●
A. 'rugosus group'	NTM 17881	F	nr. Nguiu, Bathurst Is.	NT	11°43'54"	130°34'17"						●●
A. 'rugosus group'	NTM 29847	M	Daly River Rd., Daly River Region	NT	13°29'34"	131°02'24"	KT183471	KT026551	KT026525	KT026588	KT026573	●●

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APPENDIX 1. (continued)

Species	Reg. no.	Sex	Locality	State	Lat. (S)	Long. (E)	*nd4*	*cytb*	*16s*	*prlr*	*ubn1*	Mor.
A. 'rugosus group'	NTM 29918	M	Dorat Rd., Adelaide River Region	NT	13°24'04"	131°09'34"						●●
A. 'rugosus group'	NTM 31212	M	Anthonys Lagoon	NT	18°00'	135°04'						●●
A. 'rugosus group'	NTM 34976	M	Dorat Rd., Adelaide River Region	NT	13°31'36"	131°15'51"	KT183472	KT026552	KT026526	KT026589	KT026574	●●
A. 'rugosus group'	NTM 34980	M	Dorat Rd., Adelaide River Region	NT	13°23'37"	131°09'15"						●●
A. 'rugosus group'	NTM 35303	M	Dorat Rd., Adelaide River Region	NT	13°23'28"	131°09'01"						●●
A. 'rugosus group'	NTM 35380	M	Daly River Rd., Daly River Region	NT	13°29'13"	130°05'05"		KT026553	KT026527	KT026590	KT026575	●●
A. 'rugosus group'	NTM 35641	M	Daly River Rd., Daly River Region	NT	13°24'06"	131°09'37"						●●
A. 'rugosus group'	NTM 35709	F	Old Bynoe Road, Darwin River	NT	12°49' 20°40'09"	130°56'60" 139°30'48"	KT183473	KT026554	KT026528	KT026591	KT026576	●●
A. 'rugosus group'	QM 5222		Lake Moondarra, Mt Isa	QLD			KT183470	KT026550	KT026524			
A. 'rugosus group'	WW 278		Merauke	IND			KT183468	KT026558	KT026522			

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APPENDIX 1. (continued)

Species	Reg. no.	Sex	Locality	State	Lat. (S)	Long. (E)	*nd4*	*cytb*	*16s*	*prlr*	*ubn1*	Mor.
A. 'rugosus group'	WW 3295		Merauke	IND			KT183469	KT026549	KT026523			
A. 'rugosus group'	QM 516		Barkly Tablelands	QLD	19°16'0"	138°5'0"	KT183463	KT026542	KT026515			●
A. 'rugosus group'	SAM 13437		Adelaide River flood plains	NT			KT183464	KT026543	KT026516	KT026592	KT026577	●
A. wellsi	WAM 19674		Vlaming Head Lighthouse	WA	21°48'	114°10'						●
A. wellsi	WAM 26759		Exmouth	WA	21°56'	114°07'						●
A. wellsi	WAM 61495		Yardie Creek Mouth	WA	22°20'	113°49'						●
A. wellsi	WAM 93215		Shothole Canyon	WA	22°03'	114°02'						●
A. wellsi	WAM 113377	M	Pannawonica area	WA	21°39'	116°19'						●
A. wellsi	WAM 113378	F	Pannawonica area	WA	21°39'	116°19'						●
A. wellsi	WAM 119367		Munjina Roadhouse	WA	22°03'	118°48'	KT183454	KT026533	KT026506	KT026584	KT026568	
A. wellsi	WAM 129559		Newman area	WA	23°21'	119°44'						●
A. wellsi	WAM 136097		Nanutarra Roadhouse	WA	22°23'47"	115°31'20"	KT183475	KT026556	KT026530	KT026587	KT026572	
A. wellsi	WAM 139188		Mount Minnie	WA	22°07'11"	115°31'31"	KT183474	KT026555	KT026529	KT026586	KT026571	
A. wellsi	139366	M	Meentheena	WA	21°13'04"	120°27'20"						●

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APPENDIX 1. (continued)

Species	Reg. no.	Sex	Locality	State	Lat. (S)	Long. (E)	*nd4*	*cytb*	*16s*	*prlr*	*ubn1*	Mor.
A. wellsi	WAM 142608	M	2km NE Shothole Canyon	WA	22°02’	114°02’						●
A. wellsi	WAM 146967	F	19 km N Nanutarra Roadhouse	WA	22°22’	115°30’						●
A. wellsi	WAM 151150	F	3 km NE Mound Minnie	WA	22°05’	115°34’						●
A. wellsi	WAM 151282		100 km NW Wittenoom	WA	21°44'34”	117°19'09”						●
A. wellsi	WAM 154974	F	Shothole Canyon	WA	22°03'13”	114°01'11”						●
A. wellsi	WAM 156324	M	Chichester Range	WA	22°13'49”	118°58'53”						●
A. wellsi	WAM 156325	M	Chichester Range	WA	22°13'46”	119°00'05”						●
A. wellsi	WAM 157563	M	Robe River	WA	21°07'57”	115°52'10”						●
A. wellsi	WAM 163236		Jinayri Mine	WA	23°01'01”	119°10'23”						●
A. wellsi	WAM 165176		Mt Stewart-Wyloo area	WA								●
A. wellsi	WAM 170589		7 km SE Peedamulla	WA	21°52'15”	115°40'47”						●
A. wellsi	WAM 170708		Yandagee Gorge	WA	21°38'36”	116°05'48”						●
O. scutellatus	WW 274		Merauke	IND			AY340787	KT026557	KT026532			
P. papuanus	WW 844		Bamustu, Western Province	PNG			AY340144	KT026559	KT026531			