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Resolving taxonomic uncertainty in Australian sea snakes (Elapidae: Hydrophiinae): Evidence from museum specimens reassigns Australian *Hydrophis caerulescens* records to *Hydrophis donaldi*

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Abstract

An unverified component of Australia's rich sea snake fauna is *H. caerulescens*, which is known from nine specimens collected in the Gulf of Carpentaria and provisionally identified by McDowell in 1972 based on their diagnostically high number of maxillary teeth. Micro-CT images of two paratypes of *H. donaldi*, which was thought to be endemic to Australia's Gulf of Carpentaria, unexpectedly revealed a similarly high maxillary tooth count, prompting a re-assessment of both species. We examined 51 museum specimens and collated published morphological data for a further 55 individuals. Using counts of maxillary teeth, scale rows around the neck and body, temporal scale arrangement, and colour pattern, we identified all nine Australian records previously referred to *H. caerulescens*, and a single juvenile from southern New Guinea, were confidently identified as *H. donaldi*. This expands the known range of *H. donaldi* from a single locality in the Gulf of Carpentaria to include much of the fringe of the Gulf of Carpentaria, the Top End of the Northern Territory, and southern New Guinea. *Hydrophis donaldi* and *H. caerulescens* are not closest relatives; instead, their striking morphological similarity appears to represent yet another example of convergence in the taxonomically challenging *Hydrophis*. We present external morphological characters that distinguish *H. donaldi* from co-occurring congeners to support field identification of this poorly known species. Our study reduces the number of confirmed Australian sea snake species from 30 to 29 and underscores the need for targeted investigations of museum specimens to resolve remaining taxonomic uncertainties.

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Introduction

Australia supports a diverse assemblage of sea snakes (Elapidae; Hydrophiinae), with 29 species confirmed in the latest checklist (Rasmussen et al., 2013). The description of *Emydocephalus orarius* brought the currently accepted number to 30 species occurring in Australia (Nankivell et al., 2020). The most speciose and ecologically diverse group belongs to the genus *Hydrophis* (Sanders et al., 2013a; Sherratt et al., 2018), which includes 17 species known from Australia and a further two species listed as possibly occurring (Rasmussen et al., 2014). The genus *Hydrophis* is notorious for being difficult to correctly identify owing to substantial intraspecific variation and the use of difficult characters such as number of teeth on the maxillary behind the fang (Cogger, 2014; Smith, 1926).

One *Hydrophis* species defined by the number of teeth behind the maxillary fang is *H. caerulescens* (Shaw, 1802), which is the only sea snake to possess more than 14 such teeth. This is a small *Hydrophis* species, often called the Dwarf Sea Snake, and lives in shallow coastal and estuarine habitats where it feeds predominantly on gobies, particularly worm gobies (Voris and Voris, 1983). *H. caerulescens* was first described by Shaw in 1802 from the Indian Ocean, and its holotype remains extant at the Natural History Museum in London. While various 19th-century authors described numerous *Hydrophis* species which possessed more than 14 maxillary teeth behind the fang, in 1926 Smith placed all of them into synonymy with *H. caerulescens*. McDowell (1972) in his monograph of sea snake morphology and evolution noted two specimens that he identified as *H. caerulescens* on the basis of their distinctive number of maxillary teeth. These specimens were caught in the Gulf of Carpentaria as prawn trawl bycatch. While they possessed unusually low scale counts for *H. caerulescens* their high maxillary tooth count led McDowell to assign them to that species.

Using a combination of morphological and molecular characters, Ukuwela et al. (2012) described a distinctive new taxon from Australia, *Hydrophis donaldi* Ukuwela, Sanders and Fry 2012. This species was distinguished from *H. caerulescens* by possessing only 6–7 maxillary teeth and from all other *Hydrophis* by a combination of scale counts, head size and colour pattern. Additionally, mitochondrial and nuclear DNA confirmed its distinctiveness as a valid species separate from all sampled *Hydrophis,* including *H. caerulescens*. All known specimens of *H. donaldi* come from a single location at the mouth of the Mission River in Weipa, Queensland, where it is among the most scarcely encountered sea snake species at this location. Given its apparent scarcity, the industrial activity at its only confirmed location, and its absence from the well-sampled trawl grounds in the Gulf of Carpentaria, there is cause for alarm as to the conservation status of *H. donaldi*; however, the species is currently listed as Data Deficient on the IUCN Red List (Sanders et al., 2021).

This paper was prompted by our finding, while examining micro-computed tomography (micro-CT) scans, that two paratypes of *H. donaldi* have at least 14 maxillary teeth behind the fang (Figure 1). We therefore examined further *H. donaldi* specimens as well as *H. caerulescens* specimens from Australia to determine their taxonomic identities. We found that all specimens of *H. caerulescens* previously reported from Australia, as well as a single juvenile specimen from southern New Guinea, can be confidently assigned to *H. donaldi*. This substantial range extension has important implications for the conservation status of *H. donaldi*, suggesting it is less at risk than previously thought. This work also excludes *H. caerulescens* from Australian waters, leaving 29 sea snake species as confirmed to be found in Australian waters. We present a short species redescription below incorporating morphological data from an additional seven *H. donaldi* specimens from across the species' known distribution.

Methods

We examined 34 *H. caerulescens* from Asia and 17 *H. donaldi* specimens housed at the Australian Museum Sydney (AMS), Field Museum of Natural History (FMNH), Museum of Comparative Zoology Harvard (MCZ), Natural History Museum UK (NHMUK), Queensland Museum (QM) and Western Australian Museum (WAM). In addition, we used existing data from Smith (1926) for a further 55 *H. caerulescens* specimens that we could not examine in person. Neck (SR-neck) and midbody scale rows (SR-body) were counted as per Smith (1926), with three counts taken of each and the minimum value taken for the neck and maximum value for the midbody. Snout to vent length (SVL), tail length, forebody circumference and hindbody circumference were measured with a string and ruler. Linear measurements on the head as well as tail height were taken with a set of digital callipers. The number of teeth on the maxilla behind the venom fangs was counted by using a pin to manipulate soft tissue under a stereo microscope.

In addition to morphological data, we used genomic single nucleotide polymorphism (SNP) data to assess the distinctiveness of *H. donaldi* from its congeners. We used a subset of samples from a larger study of *Hydrophis* phylogenetics including putatively close relatives to *H. donaldi* as well as sympatric species from Australia (Table 2). Briefly, genomic DNA was extracted using a Gentra Puregene tissue kit (Qiagen, 2011) following the manufacturer's protocol and then quantified with a Quantus fluorometer to ensure 500 ng of DNA at a concentration of 50 ng/µl. Sequencing was outsourced to Diversity Arrays Technology Pty Ltd (DArTseq) who use a proprietary pipeline using two restriction enzymes (PstI and HpaII) to genotype Single Nucleotide Polymorphisms (SNPs). We obtained raw demultiplexed FASTA files from DArTseq then filtered adaptors and quality trimmed using default parameters in BBDuk (Bushnell, 2014) before removing common contaminants using kraken2 (Wood et al., 2019). We subsequently called SNPs using iPYRAD v.0.9.85 (Eaton and Overcast, 2020) using *de novo* assembly of reads with a cluster threshold of 0.85, mindepth of 5 and maxdepth of 100. Minimum genotyped samples per locus was set to 0.9. Variant call format files were generated and filtered on minor allele frequency (maf = 0.05) using vcftools (Danecek et al., 2011). One SNP per locus was randomly selected for phylogenetic tree reconstruction. These SNPs were concatenated into a single alignment. Phylogenetic tree reconstruction was implemented in IQ-TREE v3.0.1 (Wong et al., 2025) using a GTR+ASC model to account for ascertainment bias associated with using SNP datasets with no invariant sites. The trees were rooted using *Hydrelaps darwiniensis*, which is well supported as sister to the *Hydrophis* group in previous morphological and molecular studies (Sanders et al., 2013b; Ukuwela et al., 2016); node support was assessed using 1000 ultrafast bootstraps. Trees were visualised using FigTree v.1.4.4 (Rambaut, 2009).

Results

Examination of the holotype of *H. donaldi* revealed that this specimen had 14 teeth behind the maxillary fang and conformed to the morphology of all specimens previously labelled as *H. caerulescens* in the Australian region. These findings, combined with existing mitochondrial and nuclear genetic evidence (Ukuwela et al., 2012), show that all *H. caerulescens* from the Australian region, including a single specimen from Papua New Guinea, should be assigned to *H. donaldi*. After measuring specimens we found a number of morphological traits that reliably differed between the two species.

Hydrophis donaldi specimens had fewer neck and midbody scale rows than *H. caerulescens* as well as a smaller difference between these values. Although scale counts overlapped between the species, this was a rare occurrence with only a single *H. caerulescens* examined falling into the range of *H. donaldi* (Figure 2). There was a corresponding difference in scale rows anterior to the vent and midtail scale rows with *H. donaldi* having lower values in both cases. *Hydrophis donaldi* had significantly fewer but broadly overlapping ventral scale counts. While *Hydrophis* sea snakes frequently have some degree of fragmentation in the head shields which makes these somewhat unreliable characters, in almost all cases *H. donaldi* had a distinctly shaped upper temporal scale compared with *H. caerulescens*. The upper temporal in *H. donaldi* is substantially larger than the lower (even when fused with adjacent supralabial) and is narrow and rectangular anteriorly before widening posteriorly with convex hind edge, whereas *H. caerulescens* generally possesses a small and ovoid upper temporal (Figure 7).

There were subtle differences in colour pattern, with *H. donaldi* typically having a greater number of body and tail bands. The bands behind the neck on the dorsum of *H. donaldi* are typically roughly equal in size (Figure 5), while in *H. caerulescens* the dark bands are typically wider than the pale interspaces on the dorsum (Figure 6). Preserved juvenile *H. donaldi* have a bright blue ground colour, although it is unclear if this is the case in life, which fades to dark brown in adulthood, while *H. caerulescens* is typically black and white fading to greyish as the animal ages. While relative morphometric values were largely not significant between species, *H. donaldi* appears to reach a greater mean (726 mm versus 627

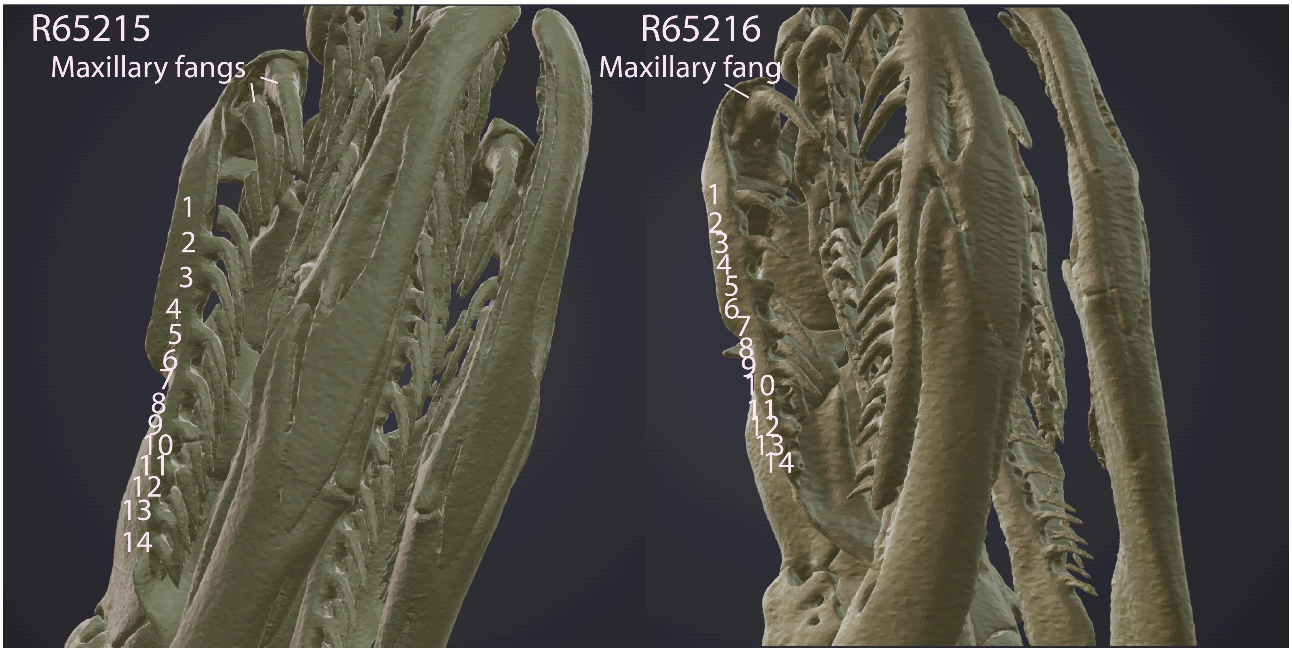


Figure 1 – CT scans of two *Hydrophis donaldi* paratypes, SAMA R65215 and SAMA R65216, with teeth behind the maxillary fang highlighted. CT scans were downloaded from MorphoSource, originally scanned for Sherratt et al. (2019).

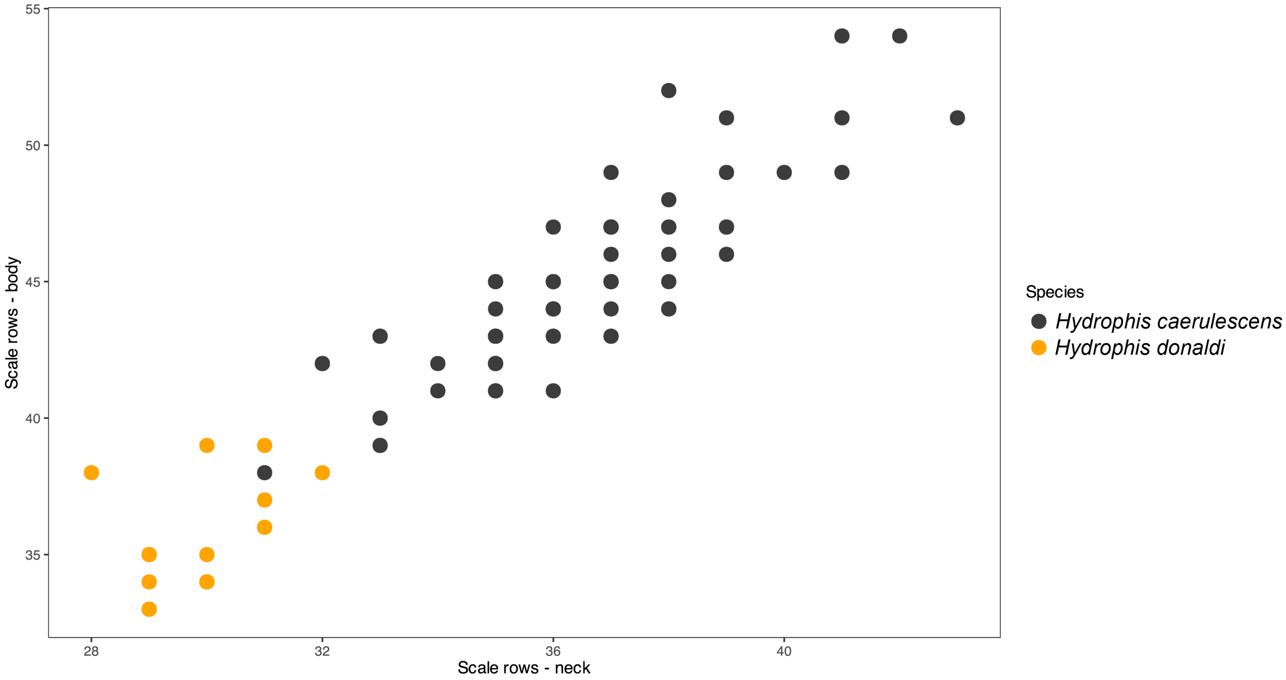


Figure 2 – Scatterplot of minimum scale rows around the neck (x axis) and maximum scale rows around the body (y axis) for *Hydrophis caerulescens* (black) and *Hydrophis donaldi* (orange).

Table 1 – Key meristic and morphological characters for *Hydrophis caerulescens* and *Hydrophis donaldi*, including Australian specimens of *H. caerulescens* which we reassign to *H. donaldi* herein. Absolute mean and standard deviation values are given except for Head Length and Head Width which are given as a proportion of SVL.

	Hydrophis caerulescens	***Hydrophis donaldi (prior ID H. caerulescens)***	***Hydrophis donaldi***
SVL	627 ± 125 (N = 34)	744 ± 203 (N = 9)	705 ± 133 (N = 8)
Tail Length	68 ± 17.1 (N = 34)	81.5 ± 27.9 (N = 9)	89.3 ± 22.9 (N = 8)
SR-neck	36 ± 2.3 (N = 89)	30 ± 1.45 (N = 9)	29 ± 0.52 (N = 8)
SR-body	44 ± 3.18 (N = 89)	37 ± 1.48 (N = 9)	34 ± 1.19 (N = 8)
Body bands	43 ± 4.94 (N = 34)	47 ± 4.85 (N = 9)	45 ± 1.17 (N = 8)
Ventrals	293 ± 17.1 (N = 84)	282 ± 14.5 (N = 9)	275 ± 15.6 (N = 8)
Head Length	0.0206 ± 0.0035 (N = 34)	0.0243 ± 0.0051 (N = 8)	0.0209 ± 0.0027 (N = 8)
Head Width	0.0128 ± 0.0017 (N = 34)	0.0130 ± 0.0025 (N = 8)	0.0109 ± 0.0016 (N = 7)
Forebody	29.9 ± 5.23 (N = 89)	34.0 ± 10.5 (N = 9)	31.1 ± 6.04 (N = 8)
Hindbody	57.9 ± 11.6 (N = 89)	61.1 ± 20.6 (N = 9)	59.1 ± 13.4 (N = 8)

mm in *H.* caerulescens) and maximum SVL (975 mm versus 790 mm in *H. caerulescens*).

The SNP dataset contained 8809 SNPs with 24.75% missing data. Consistent with previous attempts at reconstructing a phylogeny of *Hydrophis* (Sanders et al., 2013b; Ukuwela et al., 2016), there were well-supported clades along an often poorly supported backbone (Figure 3). The position of *H. donaldi* was somewhat uncertain, with it putatively grouping with well-supported sister species *H. caerulescens* and *H. atriceps* but with a bootstrap support value of only 82. Other well-supported clades included *H. elegans* and *H. pacificus* (BS = 98), as well as a clade consisting of *H. macdowelli* + *H. ocellatus* (BS = 100) and *H. stokesii* + (*H. major* + *H. zweifeli*) (BS = 94). Finally, support for the placement of *H. curtus* was poor, which came out as sister to *H. elegans* and *H. pacificus* (BS = 43).

Discussion

This study expands the known range of *H. donaldi* from a single locality to include much of the fringe of the Gulf of Carpentaria, the Top End of the Northern Territo-

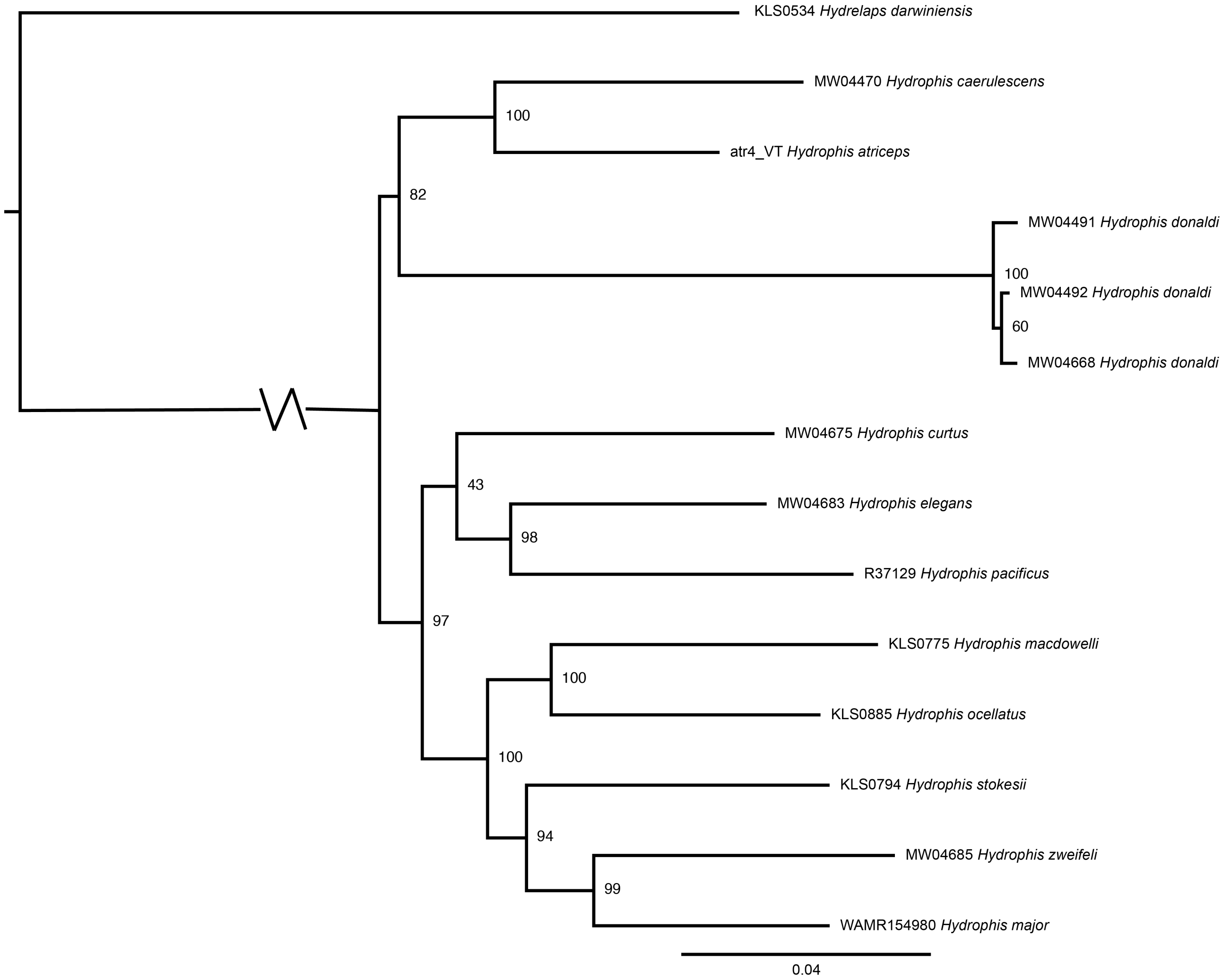


Figure 3 – Concatenated SNP tree of a subset of *Hydrophis* sea snakes reconstructed using 8809 SNPs in IQTree. Rooted using *Hydrelaps darwinensis*, the long branch separating the genus is not to scale to improve readability. Scale bar is substitutions per variant site.

ry, and southern New Guinea. Given its broader known range and occurrence in relatively pristine habitats, we recommend that *H. donaldi* be reassessed under IUCN Red List criteria to reflect its more positive conservation outlook. Assessments of *H. caerulescens* should also be updated to exclude its occurrence in Australian waters. As a result, the number of sea snake species confirmed to be found in Australia is reduced to 29.

We show that *H. donaldi* can be distinguished from other *Hydrophis* except *H. caerulescens* by possessing more than 14 maxillary teeth, and from *H. caerulescens* in almost all cases by possessing 29–32 scale rows around the neck and 33–39 scale rows around the body, in addition to differences in the temporal scale arrangement, colour pattern and morphometric characters. This also highlights the difficulty in using some informative taxonomic characters and reiterates the importance of specialist taxonomic training as well as technology such as micro-CT scanning. Molecular phylogenies show that *H. donaldi* and *H. caerulescens* are not allopatric sister species, making their striking morphological similarity another notable example of convergence (Ukuwela et al., 2013; Sherratt et al. 2018) in this species-rich genus.

Taxonomy

Hydrophis donaldi Ukuwela, Sanders and Fry, 2012

Hydrophis caerulescens [in part] (McDowell 1972)

Hydrophis donaldi (Ukuwela, Sanders and Fry 2012)

Hydrophis donaldi (Cogger 2014)

Hydrophis donaldi (Jolly et al. 2023)

Holotype: QM J90700, male, Weipa, Gulf of Carpentaria, Queensland (12°35′10.88″S, 141°57′47.21″E). Collected by B.G. Fry on 15th October 2000.

Paratypes: SAMA R65215, juvenile; SAMA R65216, male; SAMA R66274, male. All Weipa, Gulf of Carpentaria, Queensland (12°35′10.88″S, 141°57′47.21″E). Collected by B.G Fry on 15th October 2000. QM J63802, adult; QM J63803, adult; QM J63809, adult; QM J63810, adult; All Weipa, Gulf of Carpen-

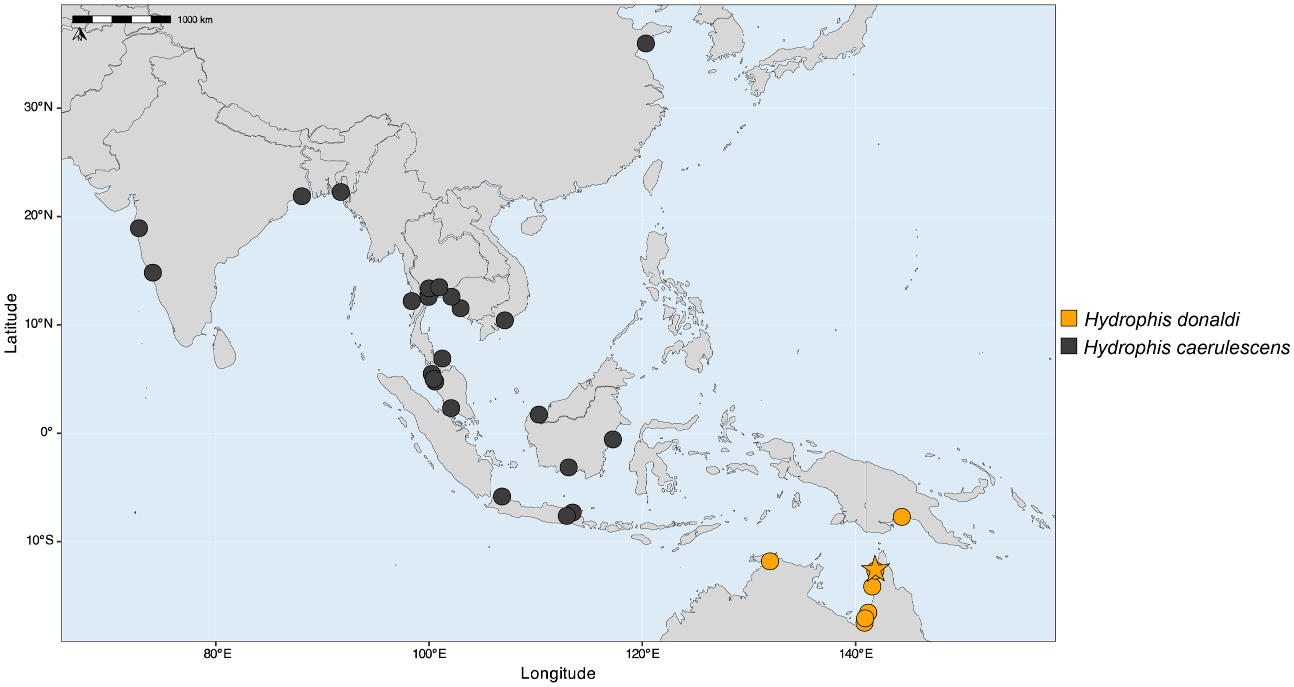


Figure 4 – Distribution map of *Hydrophis caerulescens* (black) and *Hydrophis donaldi* (orange) specimens used in this study. The star denotes the type locality of *H. donaldi*, the exact type locality of *H. caerulescens* is unknown.

Table 2. List of samples used for phylogenetic analysis.

Sample ID	Genus	Species	Location	Country
KLS0534	*Hydrelaps*	*darwiniensis*	Broome, Western Australia	Australia
atr4_VT	*Hydrophis*	*atriceps*	Vung Tau	Vietnam
MW04470	*Hydrophis*	*caerulescens*	Anganna, East Kalimantan	Indonesia
MW04675	*Hydrophis*	*curtus*	Weipa, Queensland	Australia
MW04491	*Hydrophis*	*donaldi*	Weipa, Queensland	Australia
MW04492	*Hydrophis*	*donaldi*	Weipa, Queensland	Australia
MW04668	*Hydrophis*	*donaldi*	Weipa, Queensland	Australia
MW04683	*Hydrophis*	*elegans*	Weipa, Queensland	Australia
KLS0775	*Hydrophis*	*macdowelli*	Broome, Western Australia	Australia
WAM R154980	*Hydrophis*	*major*	Shark Bay, Western Australia	Australia
KLS0885	*Hydrophis*	*ocellatus*	Exmouth Gulf, Western Australia	Australia
MAGNT R37129	*Hydrophis*	*pacificus*	Gulf of Carpentaria	Australia
KLS0795	*Hydrophis*	*stokesii*	Exmouth Gulf, Western Australia	Australia
MW04685	*Hydrophis*	*zweifeli*	Weipa, Queensland	Australia

taria, Queensland (12°45′4.03″S, 141°53′58.10″E). Collected by B.G. Fry on 1st March 1997.

Additional material: AMS R44516, female, Karumba, Gulf of Carpentaria, Queensland (17°28′58.8″S, 140°49′58.80″E). Collected by H. Heatwole 18th January 1971. AMS R44614, juvenile, details unknown. AMS R95057, adult, Gulf of Carpentaria, Queensland (16°33′57.60″S, 141°10′58.80″E). Collected on 5th February 1978. AMS R95063, adult, Gulf of Carpentaria, Queensland (17°4′58.80″S, 140°54′0″E). Collected on 6th February 1978. AMS R95132, adult, Gulf of Carpentaria, Queensland (14°9′0″S, 141°33′57.6″E). Collected 29th July 1978. AMS R177703, juvenile, Van Diemen's Gulf, Northern Territory (11°48′57.6″S, 131°57′57.6″E). Collected by J. Lombardo, February 1968. MCZ 134880, Juvenile, Babai, Mouth of Nakari River, Gulf Province, Papua New Guinea (7°42′38.754″S, 144°20′15.903″E). Collected by F.S.Parker on 15th September 1979.

Figure 5 – *Hydrophis donaldi* specimens formerly identified as *H. caerulescens*. Clockwise from top left: MCZ 134880; AMS R177703; AMS R44614; AMS R44516; AMS R95132 (head); AMS R95132.

Diagnosis

Hydrophis donaldi can be distinguished from all congeners by the following characters: 14 or more teeth on maxillary behind the fang, 29–32 scale rows on the neck, 33–39 scale rows around the midbody, bands on the nape approximately the same size as pale interspaces, upper temporal scale large and widens posteriorly with convex rear edge.

Morphology

A small and relatively slender *Hydrophis* (max SVL 97 cm), forebody circumference moderate compared with hindbody (mean ratio 1.83), head is distinct from the

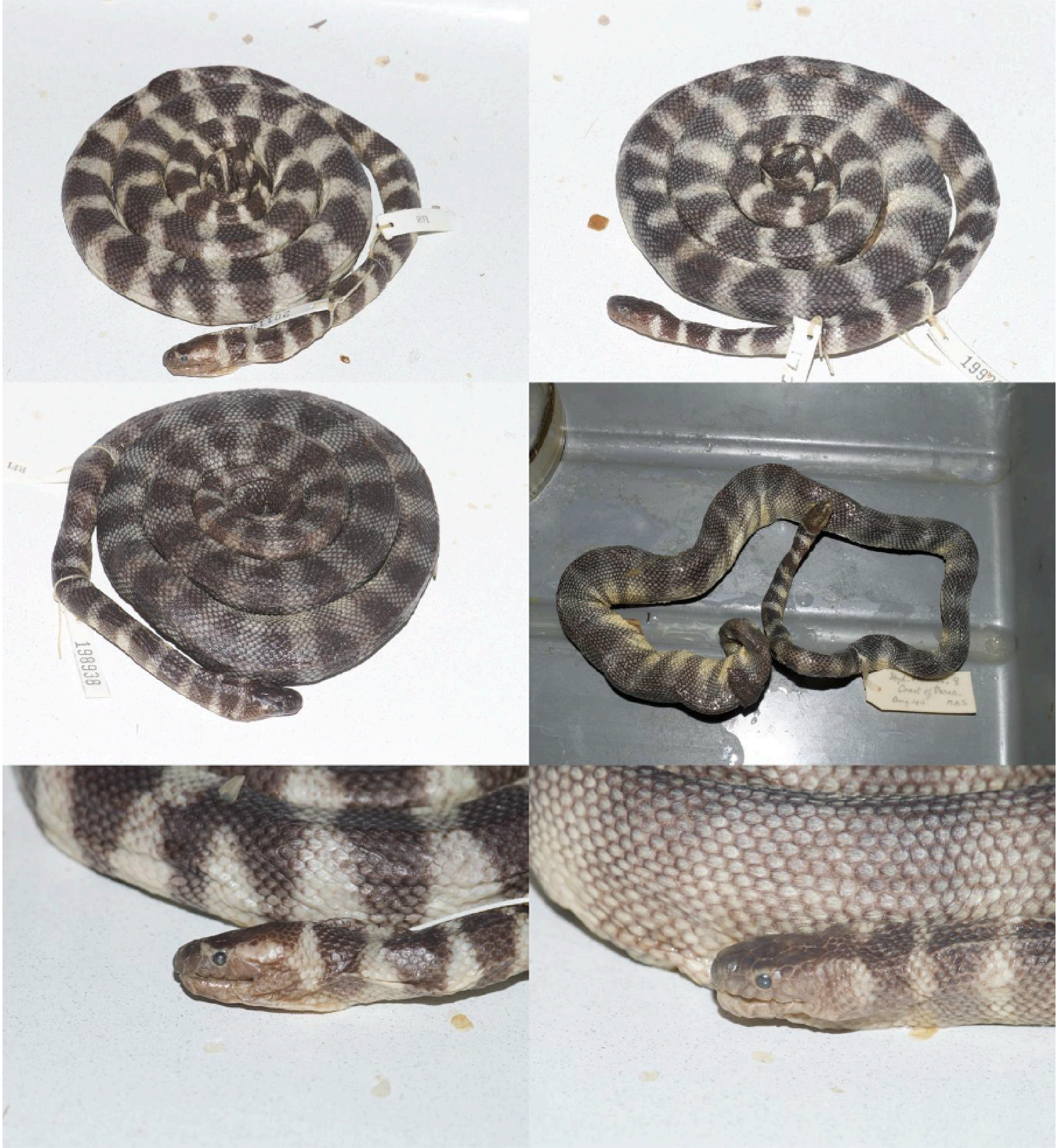
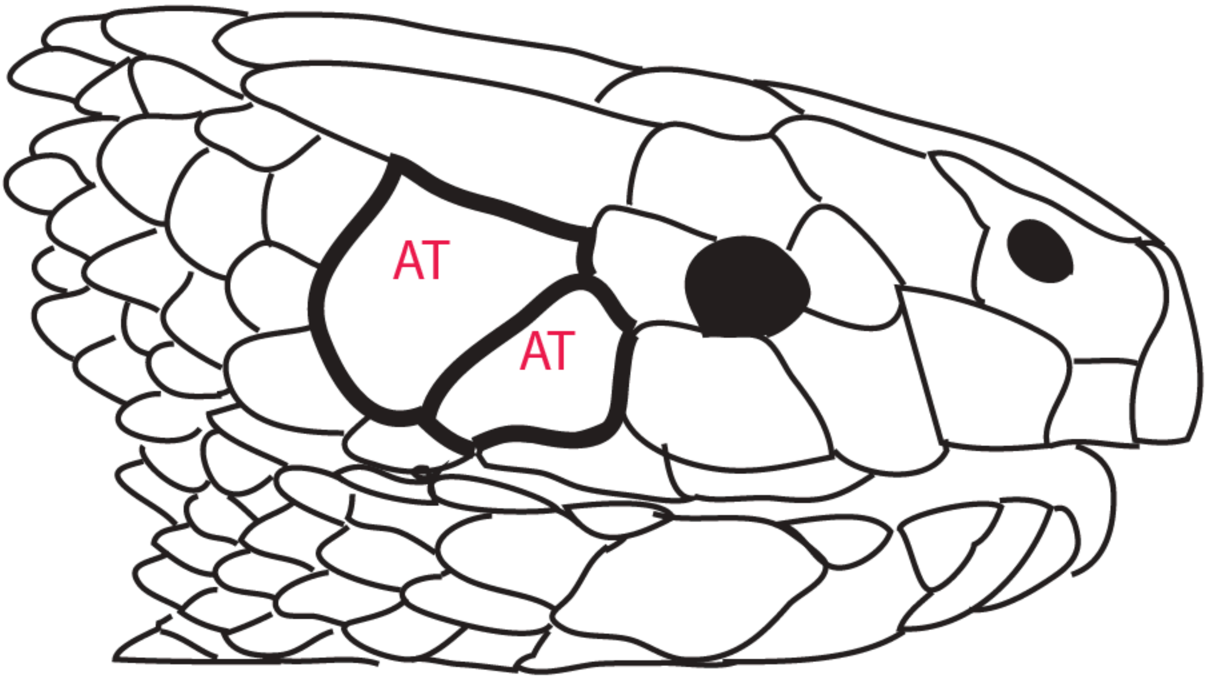


Figure 6 – *Hydrophis caerulescens* specimens examined in this study. Clockwise from top left: FMNH 201153; FMNH 199258; NHMUK 1917.2.7.1; FMNH 199253 (head); FMNH 201153 (head); FMNH 198938.

forebody. Body largely cylindrical with only slight lateral compression posteriorly, tail ranges between 8.9% and 14.9% of the SVL in length (mean = 11.6%), relatively narrow and thickened ventrally towards anterior. Head long and narrow, rostral scale has two grooves on the ventral surface and three points contacting each supralabial and between the nasal scales. Nasal scales large and symmetrical with valvular nostrils placed posteriorly. Prefrontals small but complete, frontal scale variable but typically small and roughly circular in shape, supraocular scales and parietal scales usually complete and symmetrical. One preocular and one postocular. Usually 7 supralabials, but occasionally 8 due to fragmentation. Between seven and 10 infralabials depending on degree of fragmentation. Number of anterior temporals is one or two, if two present the upper is large and shaped like an axehead, while the lower appears to be formed from the fragmentation of the supralabial below. Supralabials one and two contact the nasal, two and three contact the preocular and three and four contact the eye.

Scale rows around neck 28–32, scale rows around midbody 33–39, the difference between them is 4–10, 32–34



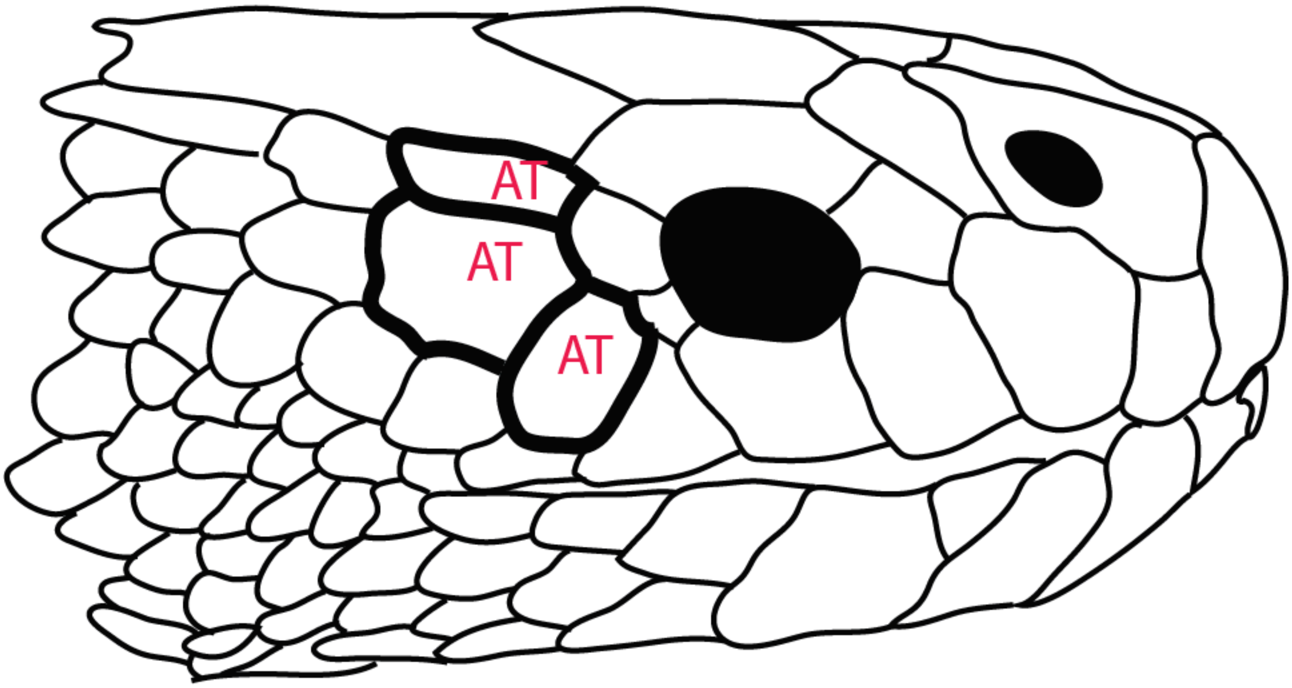


Figure 7 – Representative diagrams of head scalation in *Hydrophis donaldi* (top) and *Hydrophis caerulescens*. Attention is focussed on the shape and number of anterior temporals (AT).

scale rows anterior to vent and 20–29 scale rows around midtail. Scales slightly imbricate, with hind edge just overlapping posterior scale, scales diamond shaped on the neck to hexagonal on the hindbody. Juveniles have smooth body scales, but in adults keels start on the neck and run down middle of scales parallel to long axis. In larger adults keels enlarged, particularly posteriorly, to form sharp spines in centre of each scale. Each spine has straight anterior edge and curved posterior edge. Spines continue onto tail and present around body including on ventral scales. Ventral scales distinct throughout body, usually twice the size of adjacent body scales anteriorly, decreasing in size to the same as body scales posteriorly, ventral scale range 261–304. In adults two spines present on each ventral scale. Subcaudal scales range 43–51. Teeth behind the maxillary fang range 14–16. 23–27 teeth on pterygoid, 8 on palatine and 23 on dentary.

Colour Pattern

Colour pattern typically consists of variable pale dorsal colour alternating with 41–59 black bands, interspaces and bands are typically of similar width. Black bands widest on dorsum and taper slightly on flanks before disappearing entirely on ventral surface. Nape bands and interspaces usually of similar width, although first two bands often connected by thin dark projection. Dorsal colour either white or light blue in younger animals, which typically fades to bluish grey in adults where contrast between bands and interspaces is faint. Ventral colour paler than dorsum and usually brownish white. Head typically black with faint paler markings, most prominent around temporals. Colour pattern similar in life, but contrast usually greater and pale interspaces often more with a prominent brown tone.

Comparison with congeners

In possessing at least 14 teeth behind maxillary fang and in general appearance, *H. donaldi* is most similar to *H. caerulescens*, although they do not occur in sympatry. *Hydrophis donaldi* can be distinguished from *H. caerulescens* by possessing 29–32 scale rows on neck (versus 31–43), 33–39 scale rows on midbody (versus 38–54), bands on the nape approximately the same width as pale interspaces (versus dark bands approximately twice as wide as pale interspaces), upper temporal scale large and widens posteriorly to a convex rear edge (versus small and ovoid).

Number of teeth behind maxillary fang distinguishes *H. donaldi* from all sympatric species and all *Hydrophis* except for *H. caerulescens*; however, this character is difficult and dangerous to examine in live specimens, so we provide further details for field identification from sympatric species below.

Hydrophis elegans, H. kingii, *H. macdowelli*, *H. major*, *H. ocellatus*, *H. peronii* and *H. platura* possess complex patterns with spots or bars between bands, or countershading (versus simple banded pattern). *Hydrophis curtus* possesses distinctive enlarged, juxtaposed and squarish (block-like) scales on lower flanks with highly reduced ventral scales (versus flank scales similar size to other body scales and imbricate, ventral scales small but clearly distinctive along the length of the body). *Hydrophis pacificus* usually has three supralabial scales in contact with eye, a central keel running down each scale in adults and much greater adult body length of up to two metres (versus usually two supralabials in contact with eye, each scale possesses a sharp tubercle that often forms a spine in adults, and maximum body length of approximately one metre).

Distribution & habitat. Hydrophis donaldi is distributed on the eastern side of the Gulf of Carpentaria, from Karumba north to Weipa, with additional records from the Northern Territory and the Gulf region of Papua New Guinea (Figure 4). Apparently similar habitat occurs widely in northern Australia and southern New Guinea, but these regions are scarcely populated and rarely sampled for estuarine sea snakes.

Very little is known about the natural history of *H. donaldi*. All records come from river estuaries or nearby shallow coast where they have been collected by spotlighting at night and occasionally as bycatch in trawl nets. Specialist use of shallow, inshore habitats is indicated by the rarity of this species in the bycatch of the trawl fisheries operating in deeper offshore habitats in the Gulf of Carpentaria. No diet records are known.

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Supplementary Data

Detailed morphology and raw sequence data available at: https://doi.org/10.25909/31403427

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