



Phylogeny and morphology of the Australian snake genus *Neelaps* Günther, 1863 (Squamata: Elapidae), with resurrection of *Narophis* Worrell, 1961

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Abstract

Recent phylogenetic studies have shown that the affinities of the two currently recognised species of *Neelaps* Günther, 1863, *Neelaps bimaculatus* (Duméril, Bibron & Duméril, 1854) and *Neelaps calonotos* (Duméril, Bibron & Duméril, 1854), are unresolved. Here we provide an expanded molecular phylogeny and new morphology data to clarify generic boundaries. We did not find support for monophyly of *Neelaps*, confirming previous evidence. As a consequence, we allocate *bimaculatus* to the available synonym *Narophis* Worrell, 1961 and restrict *calonotos* to *Neelaps*, forming two monotypic genera. We redescribe both species under this revised classification. *Neelaps calonotos* adds to the list of endemic monotypic vertebrates in southwestern Western Australia, recognised globally as a biodiversity hotspot, and we comment on the name spelling, type specimens and conservation status of this distinctive species.

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Introduction

The genus *Neelaps* Günther, 1863 in its present concept comprises two small, slender, fossorial, oviparous snakes with glossy body scales mostly confined to the drier sandy regions of southern Western Australia and southwestern South Australia (Greer 1997; Storr *et al.*

2002; Cogger 2014; Wilson & Swan 2021). Generic allocation has been problematic for several small Australian elapids (e.g. Keogh *et al.* 2000; Maryan *et al.* 2020), and this also is the case for *Neelaps*. *Neelaps* species have been at various times placed in *Melwardia* Worrell, 1960, *Narophis* Worrell, 1961, *Neelaps*, *Simoselaps* Jan, 1859, and *Vermicella* Günther, 1858 (e.g. Worrell 1960, 1961;

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Storr *et al.* 1986; Hutchinson 1990), while other works have treated *Neelaps* as a subgenus (e.g. Storr 1985; Ehmann 1992). The only major alpha-taxonomic studies on the genus *Neelaps* were published over thirty-five years ago (Storr 1968, as *Vermicella*; Scanlon 1985), the latter including cranial and dentition morphology. These systematic morphological studies have improved our understanding of these small Australian elapids, but the affinities of *Neelaps* remain problematic (e.g. Storr *et al.* 2002).

Molecular phylogenetic studies on Australian elapids have demonstrated that while the other fossorial snake genera *Antaioserpens* Wells & Wellington, 1985, *Brachyuropis* Günther, 1863, *Simoselaps*, and *Vermicella* formed well-defined monophyletic clades, this was not the case with the genus *Neelaps*. Instead, phylogenetic analyses consistently show a non-monophyletic genus where *N. bimaculatus* is more closely related to *Antaioserpens/Brachyuropis/Simoselaps* while *N. calonotos* is more closely related to *Vermicella* (e.g. Keogh *et al.* 1998; Sanders *et al.* 2008; Lee *et al.* 2016; Zaher *et al.* 2019). This evidence has encouraged some authors to classify these species as either '*Simoselaps* *bimaculatus*' and '*Vermicella* *calonotos*' (Wallach *et al.* 2014; Chapple *et al.* 2019; Zaher *et al.* 2019), but these have not been widely accepted. We consider these classifications to be unconvincing due to the gross morphological and ecological differences between the '*Neelaps*' species and their closest relatives.

Our principal aim in this study is to provide an updated molecular phylogeny for *Neelaps*, and all pertinent genera and species, to resolve the relationships between the two species and their allies. We included a broad representation of samples from *Brachyuropis*, *Simoselaps*, and *Vermicella*. Our molecular results, supported by a revised set of morphological characters, clearly show that *N. bimaculatus* and *N. calonotos* comprise non-monophyletic clades, thus necessitating a revised classification of forming two monotypic genera *Narophis* and *Neelaps*.

Methods

Phylogeny. Sequence data were obtained from 53 liver, muscle, and heart tissue subsamples across the Australian fossorial elapid genera: *Antaioserpens*, *Brachyuropis*, *Neelaps*, *Simoselaps*, and *Vermicella*. In order to sample intraspecific variation, the *Neelaps* tissues were sampled from specimens with geographic coordinates across their range. Tissues were obtained from collections of the Australian Biological Tissue Collection, South Australian Museum, Adelaide (ABTC) and Western Australian Museum, Perth (WAM). Details for all specimens and other records used in this paper are presented in the Appendix.

To make use of existing data, we selected loci used in other published phylogenetic studies of Australian elapids (Sanders *et al.* 2008). For all individuals, we

sequenced data for the mitochondrial loci ND4 (~685bp) and 16S rRNA (~470bp), and included oxyuranine elapids *Cacophis squamulosus* (Duméril, Bibron & Duméril, 1854), *Furina diadema* (Schlegel, 1837) from Sanders *et al.* (2008). We also generated additional data for a subset of the '*Neelaps*' individuals representing major clades and incorporated these into the existing Sanders *et al.* (2008) mitochondrial and nuclear phylogeny. The additional mitochondrial loci were 12S rRNA (~940bp), Cyt-b (~1100bp), and the nuclear loci c-mos (~640bp), RAG-1 (~1068bp), and myHC-2 (~520bp). Genbank accessions for all fossorial elapids used are in the Appendix, for the remaining elapids see Sanders *et al.* (2008) Appendix I. For both phylogenetic analyses, *Laticauda colubrina* (Schneider, 1799) and *Naja naja* (Linnaeus, 1758) were used as outgroups (Sanders *et al.* 2008). We ran Maximum Likelihood estimation of the mitochondrial and nuclear dataset using IQ-TREE v 2.0 (Minh *et al.* 2020), using the partitioning and substitution models that best fit the data estimated by ModelFinder within IQ-TREE (Chernomor *et al.* 2016; Kalyaanamoorthy *et al.* 2017). Branch support was calculated by Ultrafast Bootstrap (UFboot) (Minh *et al.* 2013; Hoang *et al.* 2018), as well as the Shimodaira Hasegawa aLRT test (Guindon *et al.* 2010), both using 1000 replicates. These values provide strong support when in agreement with confidence thresholds at SH-aLRT \geq 80% and UFboot \geq 95% (Schmidt & Trifinopoulos 2020). Recent phylogenomic work has revealed that the fossorial elapids are monophyletic within the oxyuranine elapids (I. Brennan & J.S. Keogh, unpublished), therefore our analyses were run with a constraint tree to reflect this previously uncertain relationship (Sanders *et al.* 2008).

Morphology. We examined specimens held in collections at the Australian Museum, Sydney (AM), South Australian Museum, Adelaide (SAMA), and Western Australian Museum, Perth (WAM). We were unable to have the type specimens from the Muséum National d'Histoire Naturelle in Paris, France (MNHN) examined in detail due to closure of the collections, however online photos allowed us to illustrate and provide descriptions of them. Our selection of specimens examined for our morphological analysis was usually guided by preservation condition and maturity (e.g. juveniles largely excluded), whether or not a tissue sample had been genotyped and for geographic coverage. Specimens measured and counted are listed and denoted as such in the Appendix.

Figure 1 and Table 1 show the morphological characters measured and counted in this study. There are some missing values due to damage such as broken tails and the condition of very old or poorly preserved specimens. Measurements and scale counts follow the studies by Storr (1968), Scanlon (1985) and Maryan *et al.* (2020), with three additional measurements of rostral height (RH), temporal length (TempL) and temporal width (TempW), and morphological definitions follow those

used by Storr *et al.* (2002) and Cogger (2014). For the purpose of this study, ToL, SVL and TailL were measured with a metal ruler to the nearest 1.0 mm. TailL is presented as length (mm) and as a percentage of SVL. Specimens preserved in a circular or twisted position were straightened on a flat surface when measured for ToL, SVL, and TailL, or if not possible measured using a length of string. All other meristic characters of HeadL, HeadW, HeadD, SnL, BW, BD, RL, RW, RH, ISL, PSL, FrL, FrAW, FrPW, ParL, SupOcL, SupOcW, TempL, TempW, and EyeW were measured with digital calipers to the nearest 0.1 mm under a microscope, with bilateral scales and EyeW recorded on the right side only. VS counts were taken from the anterior most first broad ventral to, but not including the anal scale following the Dowling (1951) method. The following binary scale features were recorded: acute or obtuse angle of suture between internasals and rostral, preocular–frontal contact, preocular–nasal contact and preocular–second labial contact. Where possible, sex was determined from everted hemipenes, presence of follicles or eggs, or by internal examination of gonads.

We recorded colour pattern characters in the represented taxa as follows: presence or absence of the dark tip

of snout in *N. bimaculatus*; extent of the dark vertebral stripe and width (e.g. 1–3 scales wide) from complete, reduced or absent in *N. calonotos*; and extent of the dark head band behind parietals, number of scales in straight line between dark head and nape bands and number of scales in straight line enclosed by dark nape band in each species. Colour in life is based on illustrated figures and field observations of live individuals. The Appendix also denotes reliable photo or field observation to update the species map distributions.

An index of body robustness (IBR in Table 2) was calculated by dividing the SVL by the average of body width (BW) and body depth (BD), as follows: $IBR = (SVL / ((BW + BD) / 2))$. For the represented taxa, we used T-tests (alpha 0.05) to test for sexual dimorphism in each body size measure (ToL, SVL, TailL, TailL % SVL and IBR) and meristic scale count; these were calculated without prior assumption of equal variances. In addition to reporting the raw measurements of all mensural characters, we calculated body size scaled mensural characters by taking the residuals from a linear model between the log10 (character) against log10 (SVL). We used these body size scaled measures to perform T-tests between sexes and species as described previously. Statistical operations

Table 1. Morphological characters measured and counted in this study (see Fig. 1).

Character	Description
ToL	Total body length, measured from tip of rostral to tip of terminal scale.
SVL	Snout-vent length, measured from tip of rostral to posterior edge of anal scale.
TailL	Tail length, measured from posterior edge of anal scale to tip of terminal scale.
HeadL	Head length, measured from tip of rostral to posterior contact of parietals on nape.
HeadW	Head width, measured immediately behind eyes.
HeadD	Head depth, measured immediately behind eyes.
SnL	Snout length, measured from tip of rostral to anterior edge of frontal.
BW	Body width, measured at middle of SVL.
BD	Body depth, measured at middle of SVL.
RL	Rostral length, measured from anterior tip to posterior point.
RW	Rostral width, measured from lateral edges at or near border of mouth.
RH	Rostral height, measured from posterior point to first supralabial.
ISL	Internasal suture length, measured along midline.
PSL	Prefrontal suture length, measured along midline.
FrL	Frontal length, measured from anterior to posterior edges.
FrAW	Frontal anterior width, measured at anterior junction point with supraoculars.
FrPW	Frontal posterior width, measured at posterior junction point with supraoculars.
ParL	Parietal length, measured from anterior to posterior edges.
SupOcL	Supraocular length, measured from anterior to posterior edges.
SupOcW	Supraocular width, measured at middle above eye.
TempL	Temporal length, measured from anterior to posterior edges.
TempW	Temporal width, measured at middle.
EyeW	Eye width, measured at middle from anterior to posterior edges.
VS	Ventral scales, counted from first broad ventral to but not including anal scale.
VertSc	Vertebral scales, counted from first scale posterior to parietals on nape to above vent.
ScS	Subcaudal scales, counted from first divided scale posterior to vent but not including terminal scale.
MBSR	Midbody scale rows, counted diagonally at middle of SVL.
AntSR	Anterior scale rows, counted diagonally from first broad ventral posterior to head.
PostSR	Posterior scale rows, counted diagonally from last broad ventral anterior to vent.
SupLab	Supralabials.
InfLab	Infralabials.

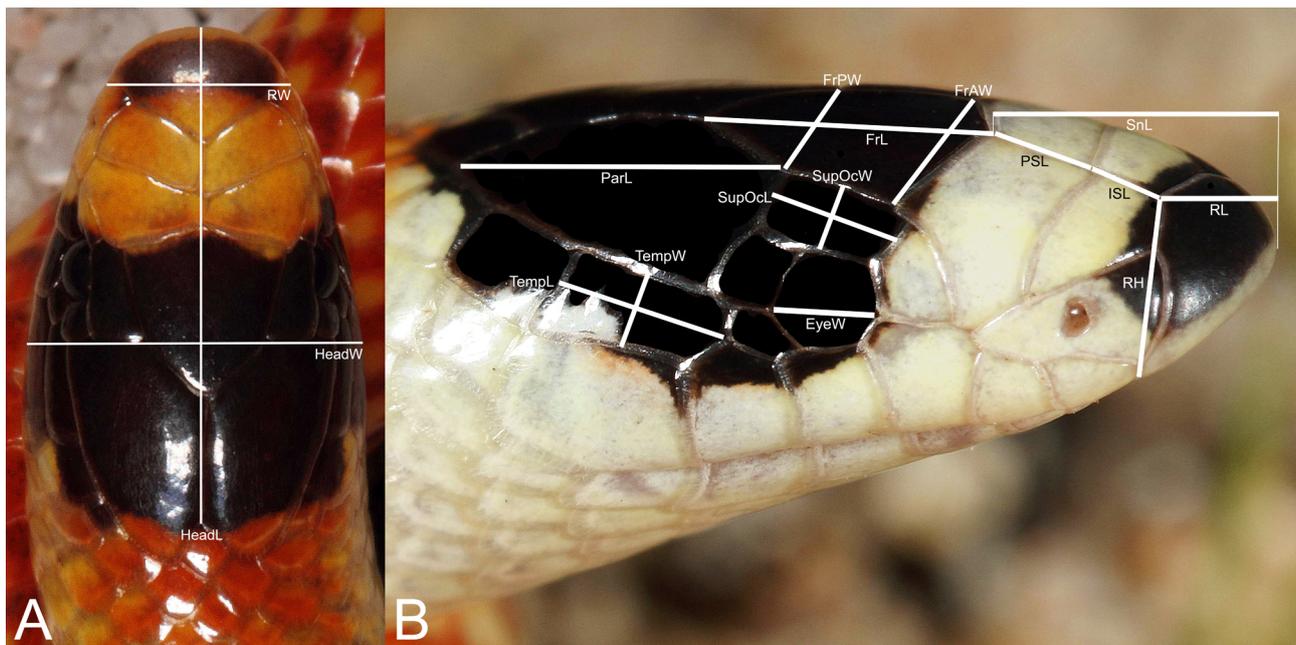


Figure 1. Dorsal head view of (A) *Narophis bimaculatus* and lateral head view of (B) *Neelaps calonotos*. HeadD, BW and BD are excluded, see Table 1 for more details of measurements (photos–B. Maryan).

were implemented in The R Project for Statistical Computing version 4.2.1.

Results

Phylogeny. The mitochondrial tree (Fig. 2) and combined nuclear and mitochondrial tree (Fig. S1) both provided strong support for non-monophyly of *Neelaps*. *Neelaps bimaculatus* is sister to the other fossorial elapids *Antaioserpens*, *Brachyuropis* and *Simoselaps*, while *N. calonotos* is sister to *Vermicella*. This key result remains without a monophyly constraint on all fossorial elapid genera (results not shown). Within *N. bimaculatus* (Fig. 2) there was support for a weakly differentiated clade (1.1% divergence), representing four northern coastal individuals (Fig. 6). In contrast, there was no appreciable intraspecific genetic structuring within *N. calonotos*, it simply comprises a shallow clade with no internal branch support. Our results confirm a previously reported result of non-monophyly of taxa within *Vermicella* (Derez *et al.* 2018), but taxonomic revision of these taxa is outside the scope of this paper.

Morphology. Table 2 shows the summarised mensural and meristic data for the represented taxa. Data are presented separately for each sex given that several small Australian elapids are sexually dimorphic in both metric and meristic attributes (e.g. Storr 1968; Shine 1984; Clarke & How 1995; How & Shine 1999). Total length was not sexually dimorphic in either species, but female *N. calonotos* had significantly longer SVL than males (Table 2, Fig. S2B). TailL % SVL was significantly dimorphic, with males showing longer tails relative to body size (Table 2, Fig. S2D). After scaling for body size, few characters were sexually dimorphic (Table 2, Fig. S3), except that female *N. bimaculatus* have deeper bod-

ies (BD, Fig. S3B) but do not differ in IBR (Fig. 2E), broader posterior width of frontal (FrPW, Fig. S3Q), and longer parietals (ParL, Fig. S3R), while *N. calonotos* males have wider anterior frontal (FrAW, Fig. S3P) and longer supraoculars (SupOcL, Fig. S3D). In terms of ratios of among key character measures, male *N. bimaculatus* have wider than deep rostral (RW & RH, Fig. S4C) and females had longer parietals relative to head length (ParL/HL, Fig. S4K), but *N. calonotos* did not show sexual dimorphism in key scale ratios.

Notably, almost all meristic and mensural features were significantly different between species (Table 2, Figs. S2, S3), except rostral height (RH). Apart from SVL, the most significantly different characters between species were all gross head dimensions, body widths, prefrontal suture length (PSL, Fig. S3N), parietal length (ParL, Fig. S3R) and temporal dimensions (TempL & TempW, Figs. S3S–T). The strong morphological differences among species were consistent when calculating the ratios of character dimensions (Fig. S4).

Taxonomic conclusions. The molecular data clearly demonstrates the genus *Neelaps* is non-monophyletic. Based on our combined evidence of molecular divergence, supported by previous phylogenetic analyses, and gross morphological and ecological differences compared to the other fossorial snake genera of *Antaioserpens*, *Brachyuropis*, *Simoselaps* and *Vermicella*, we allocate both taxa in two monotypic genera. They are phenotypically dissimilar from these other groups, and each other, based on morphometric and meristic attributes, head scalation and details of colour and pattern, as detailed in the following diagnoses. In the following taxonomy section, we assign *bimaculatus* to the

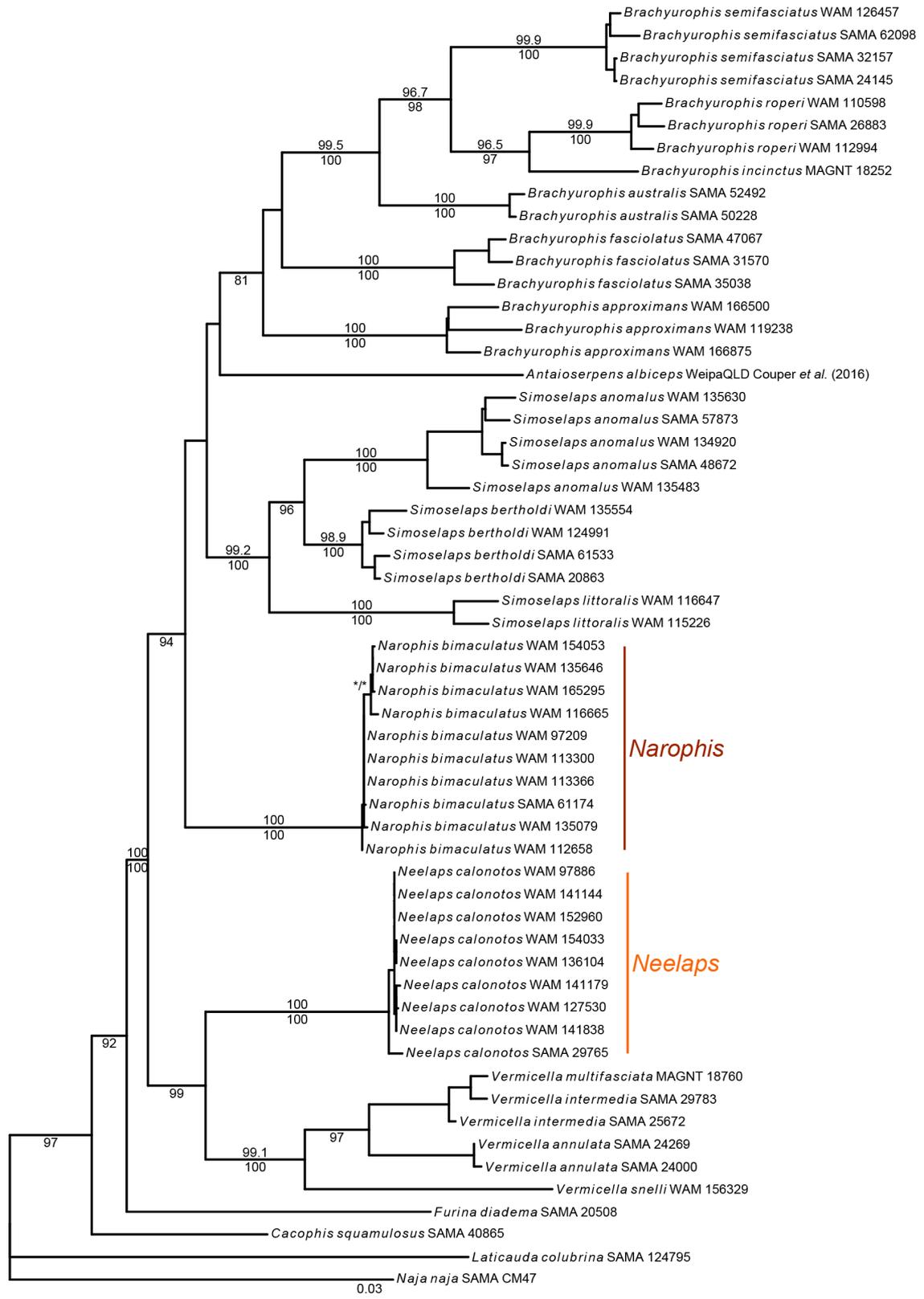


Figure 2. Maximum Likelihood mitochondrial DNA phylogeny of fossorial elapids, including intraspecific variation within *Narophis* and *Neelaps*. Branch lengths and scale bar represents average number of substitutions/site. Branch support values are SH-aLRT (above) and Ultrafast bootstrap (below). Branch support values considered significant in the intraspecific *bimaculatus* clade are indicated with */*. Tree topology is constrained to show monophyly of fossorial elapids.

Table 2. Descriptive statistics for measurements (mm) and meristic counts of female, male and all specimens of *Narophis bimaculatus* and *Neelaps calonotos*. Values shown are the minimum–maximum range, mean (standard deviation). Sample sizes: N is shown at the head of each column. The significance level for t-tests on sexual dimorphism and species differences is ns=not significant, . =0.05, * <0.05, ** <0.009, etc, n/a indicates no tests were performed. Non-meristic and body-length measures were scaled against SVL prior to significance testing, scaled data are in Fig. S3. See Table 1 for abbreviations of measurements and counts. Two specimens of *N. bimaculatus* (WAM R60628, WAM R97209), and MBSR, SupLab and InfLab are excluded.

	<i>N. bimaculatus</i>			<i>N. calonotos</i>			Species Signif.		
	Female	Male	Sex Signif.	All	Female	Male		Sex Signif.	
	N: 23	N: 26		N: 49	N: 12	N: 18		N: 30	
ToL	229–468 354 (79)	251–438 335 (64)	ns	229–468 344 (71)	196–271 239 (22)	154–267 220 (28)	.	154–271 227 (27)	<***
SVL	215–439 331 (74)	224–400 309 (60)	ns	215–439 319 (67)	171–239 211 (20)	134–225 189 (24)	*	134–239 197 (25)	<***
TailL	14–32 24 (5.4)	17–39 30 (5.3)	***	14–39 27 (6.2)	22–32 28 (3.6)	20–42 31 (4.8)	.	20–42 30 (4.6)	*
TailL % of ToL	5.7–9 6.7 (0.7)	5.6–10.8 9 (1)	<***	5.6–10.8 7.9 (1.4)	9.4–13.2 11.7 (1)	12.8–15.9 14.3 (0.9)	<***	9.4–15.9 13.3 (1.6)	<***
HeadL	4.7–8.9 7.2 (1.3)	5.6–8.6 6.9 (1)	ns	4.7–8.9 7 (1.2)	6.1–7.5 6.8 (0.5)	5.4–8.4 6.7 (0.8)	ns	5.4–8.4 6.7 (0.7)	<***
HeadW	3–6.7 4.7 (1.2)	2.5–5.3 4.1 (0.8)	.	2.5–6.7 4.4 (1)	3.8–5.8 4.5 (0.5)	3.4–5.4 4.3 (0.6)	ns	3.4–5.8 4.4 (0.6)	<***
HeadD	2.1–5.3 3.8 (1)	2.2–4.6 3.4 (0.7)	ns	2.1–5.3 3.6 (0.9)	2.7–4 3.4 (0.4)	2.6–3.9 3.2 (0.4)	ns	2.6–4 3.3 (0.4)	<***
SnL	1.6–4.5 2.9 (0.7)	1.9–3.8 2.7 (0.5)	ns	1.6–4.5 2.8 (0.6)	2–3.2 2.6 (0.4)	1.7–3.3 2.4 (0.4)	ns	1.7–3.3 2.5 (0.4)	*
BW	3.3–9.1 6.3 (1.6)	4.2–8.2 5.6 (1)	ns	3.3–9.1 5.9 (1.4)	5.2–7.9 6.3 (0.9)	4.3–8.7 5.9 (1.2)	ns	4.3–8.7 6.1 (1.1)	<***
BD	3.3–8.9 5.9 (1.6)	2.7–7.8 5 (1.3)	*	2.7–8.9 5.5 (1.5)	4.3–6.6 5.6 (0.7)	3.3–7.4 5.5 (1.2)	ns	3.3–7.4 5.6 (1)	<***
IBR	11.1–17.3 13.7 (1.8)	11.2–20.1 14.8 (2.4)	ns	11.1–20.1 14.3 (2.2)	8–10.2 8.9 (0.7)	7–11 8.4 (1.1)	ns	7–11 8.6 (1)	<***
RL	0.9–2.5 1.9 (0.5)	1.1–2.4 1.8 (0.4)	ns	0.9–2.5 1.8 (0.4)	0.6–1.3 0.9 (0.2)	0.7–2.9 1 (0.5)	ns	0.6–2.9 1 (0.4)	*
RW	1.6–3 2.3 (0.5)	1.6–2.9 2.2 (0.3)	ns	1.6–3 2.3 (0.4)	1.7–2.6 2.1 (0.2)	1.7–2.6 2.2 (0.2)	ns	1.7–2.6 2.2 (0.2)	***
RH	1.2–2.5 1.9 (0.4)	1.3–2.1 1.7 (0.3)	ns	1.2–2.5 1.8 (0.4)	1–1.4 1.2 (0.1)	0.8–1.6 1.2 (0.2)	ns	0.8–1.6 1.2 (0.2)	ns
ISL	0.2–0.8 0.5 (0.2)	0.2–0.8 0.5 (0.1)	ns	0.2–0.8 0.5 (0.1)	0.5–0.8 0.7 (0.1)	0.4–0.9 0.6 (0.1)	ns	0.4–0.9 0.6 (0.1)	***
PSL	0.2–0.8 0.5 (0.2)	0.4–0.8 0.5 (0.1)	ns	0.2–0.8 0.5 (0.1)	0.7–1.1 0.8 (0.1)	0.6–1.2 0.9 (0.2)	ns	0.6–1.2 0.8 (0.2)	<***
FrL	1.7–3.4 2.5 (0.5)	1.8–3 2.4 (0.3)	ns	1.7–3.4 2.4 (0.4)	2–2.7 2.4 (0.2)	2–3 2.4 (0.3)	ns	2–3 2.4 (0.2)	<***
FrAW	1.6–3.1 2.3 (0.4)	1.6–2.7 2.1 (0.3)	ns	1.6–3.1 2.2 (0.4)	1.7–2.2 2 (0.2)	1.6–2.5 2.1 (0.2)	ns	1.6–2.5 2 (0.2)	***
FrPW	1.1–2.5 1.8 (0.4)	1.2–2 1.6 (0.2)	*	1.1–2.5 1.7 (0.3)	1.4–2.2 1.6 (0.2)	1.3–2.1 1.6 (0.2)	ns	1.3–2.2 1.6 (0.2)	***
ParL	2.5–4.4 3.5 (0.6)	2.6–3.9 3.2 (0.4)	*	2.5–4.4 3.4 (0.5)	2.9–3.7 3.3 (0.3)	2.7–4.1 3.3 (0.3)	ns	2.7–4.1 3.3 (0.3)	<***
SupOcl	1–2.1 1.5 (0.3)	0.9–1.8 1.4 (0.2)	ns	0.9–2.1 1.5 (0.3)	1.2–1.5 1.3 (0.1)	1.2–1.6 1.3 (0.1)	*	1.2–1.6 1.3 (0.1)	**
SupOcW	0.5–1 0.8 (0.2)	0.5–0.9 0.7 (0.1)	ns	0.5–1 0.7 (0.1)	0.6–0.8 0.7 (0.1)	0.6–0.9 0.7 (0.1)	ns	0.6–0.9 0.7 (0.1)	<***
TempL	0.9–2.8 2.1 (0.5)	1.3–2.4 1.8 (0.3)	ns	0.9–2.8 1.9 (0.4)	1.3–2.4 2 (0.3)	1.6–2.4 1.9 (0.3)	ns	1.3–2.4 1.9 (0.3)	<***
TempW	0.2–1 0.7 (0.2)	0.4–0.8 0.6 (0.1)	ns	0.2–1 0.6 (0.2)	0.6–0.9 0.7 (0.1)	0.4–0.9 0.7 (0.1)	ns	0.4–0.9 0.7 (0.1)	<***
EyeW	0.7–1.3 1 (0.2)	0.7–1.3 1 (0.1)	ns	0.7–1.3 1 (0.2)	0.8–1 1 (0.1)	0.8–1.1 1 (0.1)	ns	0.8–1.1 1 (0.1)	**

	<i>N. bimaculatus</i>				<i>N. calonotos</i>				Species Signif.
	Female	Male	Sex Signif.	All	Female	Male	Sex Signif.	All	
VS	186–226 211 (13)	178–234 204 (13)	.	178–234 207 (13)	130–145 136 (4)	124–140 131 (4)	**	124–145 133 (5)	<***
VertSc	188–232 216 (13)	184–242 209 (13)	.	184–242 212 (13)	134–148 141 (4)	128–142 135 (4)	***	128–148 138 (5)	<***
ScS	18–24 21 (2)	20–33 28 (3)	<***	18–33 24 (4)	23–26 24 (1)	26–34 30 (2)	<***	23–34 28 (3)	***
AntSR	15–16, 15	15–16, 15	n/a	15–16, 15	15–16, 16	15–16, 15	n/a	15–16, 15	n/a
PostSR	13–15, 15	13–15, 15	n/a	13–15, 15	14–15, 15	13–15, 14	n/a	13–15, 15	n/a

available synonym *Narophis* (Worrell 1961: 27), restrict *calonotos* to *Neelaps* (Günther 1863: 24), and provide revised generic diagnoses and descriptions of both species to accommodate this classification.

Discussion

This study has built on previous molecular phylogeny studies and demonstrated the non-monophyly of *Neelaps* (Keogh *et al.* 1998; Sanders *et al.* 2008; Lee *et al.* 2016; Zaher *et al.* 2019). Despite similarities in karyotype (Mengden 1985) and some aspects of anatomy (Scanlon 1985; Keogh 1999), our genetic information unequivocally demonstrates the need to remove *bimaculatus* from *Neelaps* and allocate it in its own genus, resulting in two monotypic genera at the exclusion of the other fossorial snake groups. We thoroughly quantified interspecific differences in the redescrptions of these taxa. These taxa represent the sister groups to the two fossorial snake subclades of *Antaioserpens/Brachyuropis/Simoselaps* and *Vermicella*, and it is likely their similarities are symplesiomorphies present in the common ancestor of the fossorial snake clade. Their previous “lumping” in the same genus was possibly based on these “generalised” fossorial similarities and absence of specialisations found in other groups such as wedge-shaped snouts in *Brachyuropis* and cross-banding along the body in *Simoselaps* (except *S. minimus* (Worrell, 1960)) and *Vermicella*. Interestingly, the combined diminutive size (only *S. anomalus* (Sternfeld, 1919) is smaller) and vertebral stripe of *N. calonotos* makes it one of Australia’s most morphologically distinctive elapids.

Storr (1968) observed geographic variation in *N. bimaculatus* suggesting an inland race should be recognised, but noted this was problematic due to a number of specimens that did not conform to his races. Our molecular phylogeny and morphological data were incongruent with a hypothesis of inland and coastal differentiation, only finding support for a slightly divergent clade that includes individuals on the coast north of Perth. The genetic consistency of our samples spanning a broad area from coastal Western Australia, including the disjunct North West Cape population, across to inland South Australia suggests a single species. However, further detailed sampling is required

to better explore any potential cryptic genetic diversity within *N. bimaculatus*, particularly from inland parts of Western and South Australia.

Southwestern Australia is recognised globally as one of the world’s top biodiversity hotspots (Myers *et al.* 2000; Laurie 2015; Rix *et al.* 2015), based largely on its highly diverse and endemic flora (Beard *et al.* 2000). Despite the overall regional herpetofaunal diversity being considered impoverished due to the cooler climatic conditions (How *et al.* 1987; Chapman & Newbey 1995), the area supports exceptional endemism and by virtue of our new information, *N. calonotos* now joins a list of monotypic genera including frogs (e.g. *Metacrinia nicholli* (Harrison, 1927), *Myobatrachus gouldii* (Gray, 1841) and *Spicospina flammocaerulea* Roberts, Horwitz, Wardell-Johnson, Maxson & Mahony, 1997), turtles (e.g. *Pseudemydura umbrina* Siebenrock, 1901), lizards (e.g. *Hesperoedura reticulata* (Bustard, 1969)), snakes (e.g. *Paroplocephalus atriceps* (Storr, 1980) and *Rhinoplocephalus bicolor* Müller, 1885), and species with very restricted distributions (Kay & Keogh 2012; Doughty & Oliver 2013; Maryan *et al.* 2015; Webster & Bool 2022). The entire southwest is effectively a relatively damp ‘island’ refuge surrounded by oceans and desert (Hopper & Gioia 2004). It has been postulated by Ehmann (1992) that both *Narophis* and *Neelaps* are relicts from earlier wetter times, evidenced by restricted and disjunct distributions in habitats that are more humid than those occupied by other sympatric fossorial species.

Many authors have commented on the conservation status of *N. calonotos* due to its very restricted distribution, centred primarily on the Swan Coastal Plain between Mandurah and Lancelin, an area encompassing the most developed and populated part of Western Australia (Ehmann & Cogger 1985; Jenkins 1985; Wilson & Knowles 1988; Kennedy 1990; Ehmann 1992; Cogger *et al.* 1993; How & Shine 1999; Reed & Shine 2002; Nevill 2005; Bush *et al.* 2010; He 2021; Wilson & Swan 2021). Recent assessments using the IUCN Red List status have classified *N. calonotos* as Near Threatened and Threatened, based on habitat loss and secondarily from fire, and continuing decline in the extent and quality of its habitat that has apparently led to losses of some subpopulations (Chapple *et al.* 2019; Tingley *et al.* 2019). In contrast, under state legislation *N. calonotos* is cur-

rently listed a Priority 3: poorly known species in Western Australia (Department of Biodiversity, Conservation and Attractions 2019), which acknowledges that these species are in need of survey work so that their conservation status can be evaluated (Bush *et al.* 2010). However, the adequacy of surveys to determine the extent of threatening processes used to ascertain a threatened listing is deficient. This results in outdated underlying data that most likely does not reflect the true conservation status of a species. Indeed, the remaining habitat for *N. calanotos* consists of largely the banksia woodlands on the Swan Coastal Plain that have been extensively cleared over the last century or so, initially mostly for agriculture and plantations, but increasingly for the rapidly expanding metropolis of Perth (Ritchie *et al.* 2021; Van Etten & Slee 2022). Despite the listing in 2016 of these woodlands as an endangered ecological community under the Commonwealth Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act), the clearing continues at a rapid rate for urban expansion, particularly on the coast north of Perth (Chapple *et al.* 2019).

Finally, our work provides a comprehensive description of *N. bimaculatus* and *N. calanotos*, supported by molecular and morphological evidence. This evidence necessitates these species be placed in monotypic genera, with the resurrection of *Narophis* Worrell, 1961. This expansion of monotypic genera highlights the prevalence of phylogenetic endemism in southwestern Australia, and the uniqueness of these species within the Australian elapids. This rearrangement increases the urgency to understand the conservation status of these poorly known species.

Taxonomy

Elapidae Boie, 1827

Narophis Worrell, 1961

Type species. *Furina bi-maculata* (= *Narophis bimaculatus*) Duméril, Bibron & Duméril, 1854a: 1240, by monotypy.

Etymology. Worrell (1961: 27) provided no derivation of name, but it is presumably from Latin *naris* meaning the nostrils, or more broadly a snout described in diagnosis by Worrell as “elongate with a large posteriorly acute rostral”, and from Greek *ophis* meaning snake. Since *ophis* is a masculine noun the spelling of *bimaculatus* does not change.

Revised diagnosis. A monotypic genus comprising *N. bimaculatus*, a small, very slender fossorial hydrophiine elapid snake (total length to 468 mm this study, males mean 335 mm, females 354 mm, tail length 6.0–12.1% of SVL mean 8.6%) with: head narrow, depressed and not distinct from neck; protrusive round-shaped snout without cutting edge; no canthus rostralis; frontal not much wider than long; internasals present slightly small-

er than prefrontals, suture between internasal and prefrontal slightly to moderately oblique; preocular in contact with nasal, rarely separated by prefrontal; typically upper primary and secondary temporals fused to form a single elongate scale without deep ventral descent (Fig. 3A), occasionally 1 + 1; rostral as slightly wider than high, posteriorly acute and projecting deeply between internasals; a consistent colour pattern of dark transverse band extends across nape and dark broad band across head forward to level of eyes; tip of snout occasionally dark; variable body colour of shades of reddish, yellowish, orange brown or bright red often with darker margins on posterior facets and pale base forming reticulated pattern; 178–234 ventrals; 184–242 vertebrae; midbody scales very glossy and smooth, in 15 rows occasionally increasing to 16 posterior to the head and decreasing to 14 (rarely 13) anterior to the vent; anal and 18–33 subcaudals divided; supralabials five, last very large possibly through fusion of lower primary temporal with fifth and sixth supralabials; infralabials seven; ventral surface white with glossy shine; eyes are small with pupils indiscernible within black irises (Bush 2017). Other features in the genus are the reversion to the primitive karyotype of 2N = 36 (16M and 20m) (Mengden 1985), and pterygoid tooth row reduced posteriorly such that it does not extend beyond the level of the ectopterygoid-ptyerygoid articulation (Greer 1997).

Most similar to the monotypic genus *Neelaps* in general aspects of morphology and scalation (including cranial, dentition, and hemipenial morphology, Scanlon 1985; Keogh 1999) differs in:

- Larger adult ToL to 468 mm (*versus* to 271 mm) and more slender-bodied indicated by 40% higher IBR values (Table 2), while absolute BW and BD is on average 2.9% and 1.8% narrower.
- Proportionately shorter HeadL and SnL, HeadL 2.2% of SVL (*versus* 3.4%) and SnL 0.8% of SVL (*versus* 1.2%).
- TailL typically < 12% of SVL (*versus* TailL typically > 10% of SVL).
- Rostral as high as wide posteriorly acute and projecting deeply between internasals, Fig. 3A (*versus* rostral much wider than high posteriorly obtuse and only slightly projecting between internasals, Fig. 3B).
- Suture between internasal and prefrontal oblique, Fig. 3A (*versus* suture between internasal and prefrontal transverse, Fig. 3B).
- Much higher ventral and vertebral scale counts of 178–234 and 184–242 (*versus* 124–145 and 128–148).
- Typically five supralabials, Fig. 3A (*versus* typically six supralabials, Fig. 3B).
- Typically extent of the dark head band not behind parietals (except in eastern parts of range in Western Australia), Fig. 3A (*versus* typically behind parietals to partially or

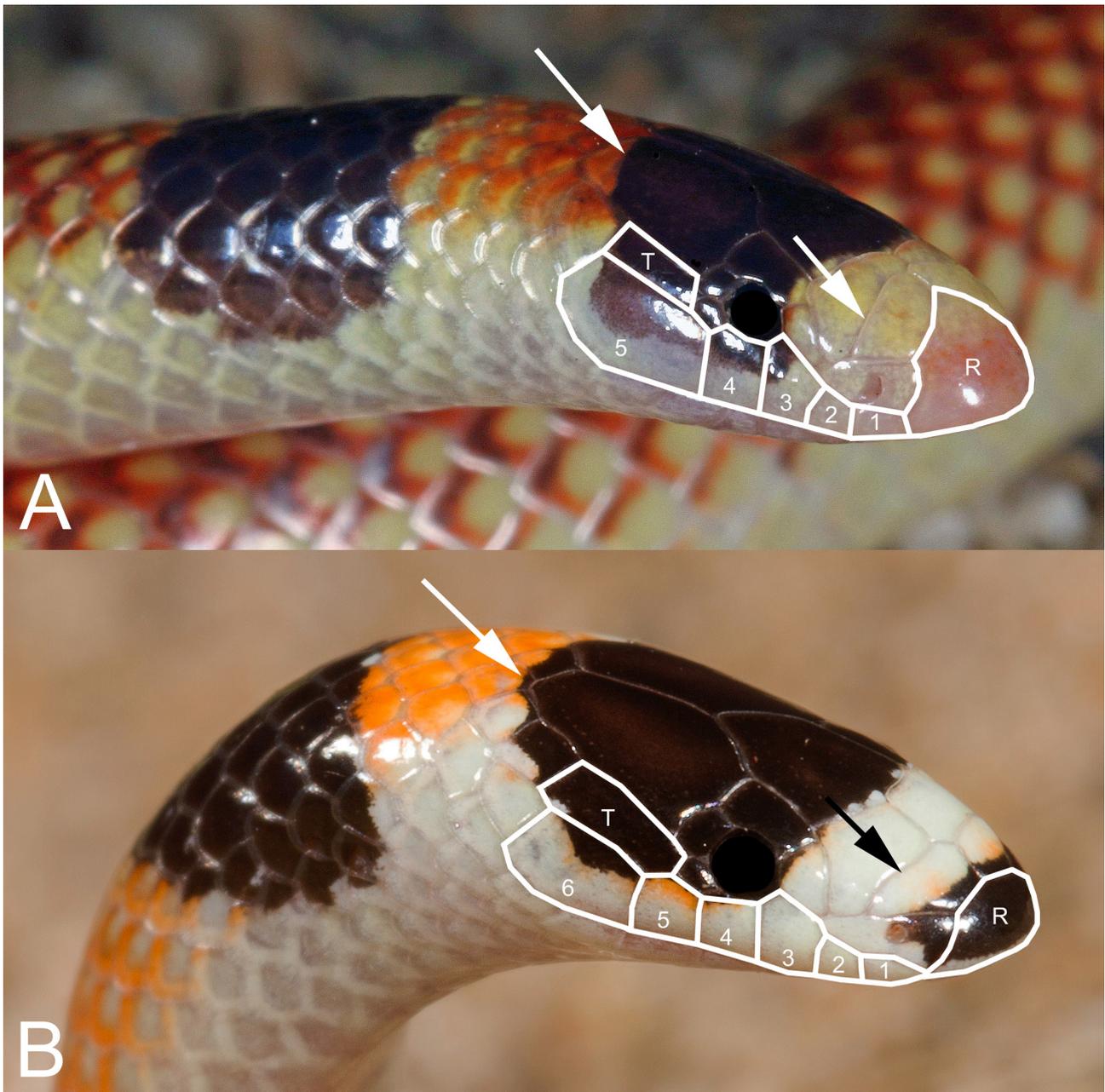


Figure 3. Lateral head views showing the typical extent of the dark head band behind parietals (arrow), suture between internasal and prefrontal (arrow), outlined number of supralabials, single elongate temporal (T) and shape of rostral (R) in live (A) *Narophis bimaculatus* from Neerabup National Park, Western Australia, and (B) *Neelaps calonotos* from Rockingham, Western Australia (photos—A: B. Maryan, B: B. Schembri).

- completely cover first vertebral, Fig. 3B).
- Dark band on nape transverse, Figs. 5A, B, C, D (*versus* dark band on nape crescent-shaped, Figs. 7A, B, C, D).
- Tip of snout occasionally dark and often extending on to ventral edge of rostral (*versus* tip of snout consistently dark and not extending on to ventral edge of rostral).
- Without obvious pattern along the body (*versus* typically vertebral stripe present along the body, or if reduced some indications remain, unstriped individuals share a superficial resemblance).

Based on phylogenetic affinities, *Narophis* is compared with the other fossorial snake genera of *Antaioserpens*, *Brachyuropis* and *Simoselaps* using Storr *et al.* 2002; Cogger 2014; Couper *et al.* 2016 and Wilson & Swan 2021.

Differs from *Antaioserpens* in: larger adult ToL to 468 mm (*versus* to 438 mm), more slender body form (*versus* moderately robust), higher ventral and subcaudal scale counts of 178–234 and 18–33 (*versus* < 159 and < 22), typically one elongate temporal scale (*versus* 2 + 2), protrusive round-shaped snout (*versus* protrusive weakly wedge-shaped snout), five supralabials (*versus* six supralabials), preocular in contact with nasal, rarely sep-

arated by prefrontal (*versus* preocular and nasal separated by prefrontal) and widely allopatric distributions.

Differs from *Brachyuropis* in: larger adult ToL to 468 mm (*versus* to 390 mm), more slender body form (*versus* moderately robust), higher ventral scale counts of 178–234 (*versus* < 190), typically one elongate temporal scale (*versus* typically 1 + 1, but often fused in *B. semifasciatus*), protrusive round-shaped snout without cutting edge (*versus* protrusive wedge-shaped snout with transverse weak to strong cutting edge) and without obvious pattern along the body (*versus* except *B. incinctus* (Storr, 1968) and *B. morrisi* (Horner, 1998) cross-banded along the body, but bands ragged-edged in *B. fasciolatus*). Additionally, *Narophis* feed on small lizards, while most *Brachyuropis* species feed entirely on reptile eggs, having highly modified dentition to accommodate this oophagous diet.

Differs from *Simoselaps* in: larger adult ToL to 468 mm (*versus* to 390 mm), more slender body form (*versus* moderately robust), higher ventral scale counts of 178–234 (*versus* < 135), typically one elongate temporal scale (*versus* 1 + 1, but primary temporal fused with second last supralabial in *S. anomalus* and primary temporal often large contacting oral margin in *S. littoralis* (Storr, 1968) and without bands along the body (*versus* except *S. minimus* encircled by bands along the body).

***Narophis bimaculatus* (Duméril, Bibron & Duméril, 1854) Black-naped Burrowing Snake**

Figs. 1, 3, 4, 5, 6

Holotype. MNHN-RA-0.3942, female, original type locality “Tasmanie” [= Tasmania, Australia] in error, restricted to Perth, Western Australia, *fide* Storr (1968: 85), obtained from J.P. Verreaux and received in Paris, France in 1844 (G. Shea, pers. comm.).

Furina bi-maculata Duméril, Bibron & Duméril 1854a, *Erpétologie Générale ou Histoire Naturelle Complete des Reptiles Tome septieme*: 1240.

Furina bimaculata Duméril, Bibron & Duméril 1854b, *Erpétologie Générale ou Histoire Naturelle Complete des Reptiles Tome neuvième*: 376.

Brachysoma bimaculatum Günther 1858, *Catalogue of Colubrine Snakes in the collection of the British Museum (Natural History)*: 229.

Pseudelaps bimaculatus Jan 1863, *Elenco sistematico degli ofidi descritti e disegnati per l'Iconografia générale*: 116.

Vermicella bimaculata Glauert 1950, *A Handbook of the Snakes of Western Australia*: 37.

Narophis bimaculata Worrell 1961, *Western Australian Naturalist*: 27.

Neelaps bimaculatus Cogger 1975, *Reptiles & Amphibians of Australia*: 391.

Simoselaps bimaculata Underwood 1979, *Classification and Distribution of Venomous Snakes in the World*: 32.

Simoselaps bimaculatus Cogger 1992, *Reptiles & Amphibians of Australia*: 684.

Description of holotype (Fig. 4A). Scallation and proportions as in the diagnosis for the genus. Individual characteristics include: internasals much wider than long angled posteriorly; prefrontals about 1 times wide as long, medial suture slightly offline so that right prefrontal contacts left internasal; single preocular, much wider than high, in contact with nasal; two postoculars, the upper larger and lower much smaller; frontal wider anteriorly, gradually narrowing to rounded point between parietals; parietals almost equal size, right parietal slightly wider; temporals above fifth supralabials contacting both postoculars; five supralabials, first and second much the smallest, third higher in contact with orbit, fourth under orbit in contact with lower postocular and fifth very large; mental triangular between first infralabials; seven infralabials; anterior chin shields in broad contact with infralabials one to three; posterior chin shields in narrow contact with third infralabial only; six rows of intergulars between chin shields and anteriormost broad ventral.

After ≥ 167 years in preservative (Fig. 4A), the holotype has faded to white on the dorsal surface, including tip of snout and interspace between dark bands, with indistinct brown apices extending forward as fine edge on posterior facets of scales along the body, gradually fading posteriorly to tail tip. Head and nape bands have faded to brown.

Colour in life and in preservative. The following description of colour in life is based on Figs. 5A, B, C, D and field observations of *N. bimaculatus* in Western and South Australia. The descriptions in preservative and of variation are based on all specimens of *N. bimaculatus* listed in the Appendix.

In life, variable body colour of shades of reddish brown (Figs. 5A, B), yellowish brown (Fig. 5C), orange brown or bright red (Fig. 5D), with paler interspaces on the head or similar to body colour (Figs. 5A, B, C, D), with pale cream to yellowish base or spots along the body, and dark pigment consisting of dark brown or black narrow to wide margins (almost covering ½ of scale) on the posterior facets, grading to reduced margins or smudging on tail. Dark margins varying in their intensity from clearly defined forming a reticulated pattern (Figs. 5A, B), to relatively indistinct with margins mostly restricted to apex, particularly in pale individuals (Fig. 5C). Occasionally without any indication of dark pigment on the body accentuating the pale bases or spots which tend to be larger lateroventrally (Fig. 5D, see also Storr *et al.* 2002: 130, Plate 30; Allen & Vogel 2019: 92, Plate RS15693–4). Black tip on the snout present (Figs. 5A, B, D) or absent (Fig. 5C). When present extending back before posterior point of rostral often extending on to

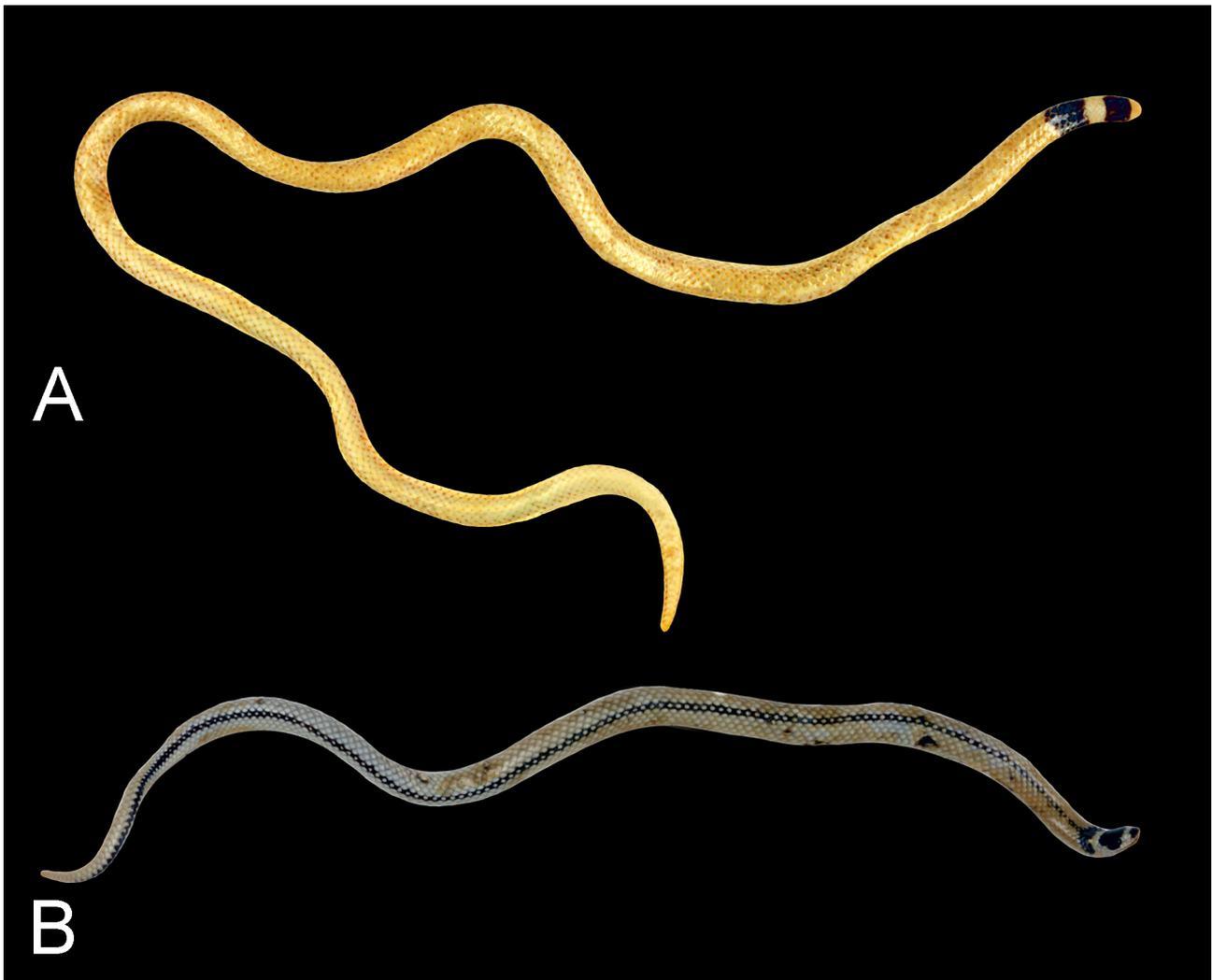


Figure 4. Preserved (A) holotype MNHN-RA-0.3942 of *Furina bi-maculata* and (B) lectotype MNHN-RA-2012.411 of *Furina calonotos* (photos–Muséum National d’Histoire naturelle, Paris (France) Collection: Reptiles and Amphibians (RA)).

ventral edge, and lateral edge partially or narrowly covering internasals ending on nasals. Black band on head commencing on or just before anterior edge of frontal and just forward of eyes, extending back partially or narrowly covering supralabials two to five and ending on or just before posterior edge of parietals. Black band on nape transverse and $3\frac{1}{2}$ –6 scales long, separated from head band by 2– $4\frac{1}{2}$ pale vertebral scales. Occasionally with an indication of a third black blotch on the forebody (Fig. 5A) or reduced black band on the head (Fig. 5C). Eyes are black without discernible pupils. Ventral surface under the head and along the body, including the lateroventral edges, is cream white with glossy shine.

In preservative, body colour fades to white including interspaces on the head. Dark head and nape bands, tips on snouts (when present) and posterior margins on body scales can either be distinct (e.g. SAMA R59348, SAMA R61148, WAM R112153, WAM R118840, WAM R169196) or largely indistinct in the majority of specimens (e.g. SAMA R61174, SAMA R69322, WAM

R60628, WAM R123596, WAM R135079), tending to be clear lateroventrally and grading to smudging on tail. The white ventral surface remains glossy.

Storr (1968: 86) noted geographic variation in colour and patterning between coastal and inland groups representing 45 specimens but his observations are incongruent with the intra-specific genetic variation observed (Fig. 2). Storr observed inland specimens differed in the dark tip on the snout being always present, larger head band, smaller nape band and darker body colour. We observed little correlation between these characters and the coastal and inland groups. Using 134 WAM specimens of *N. bimaculatus* (including those listed in the Appendix), we found the dark tip was present in 42% of individuals from the western and 87% from the eastern parts of range, while the tip was light in 58% of specimens from western parts of the range and only 13% in eastern parts. Five specimens had only a weak indication of a dark spot on the snout. In the South Australian material (see Appendix), a dark tip on the snout is present on all individuals except one specimen (SAMA R61174), the dark head band mostly ended on

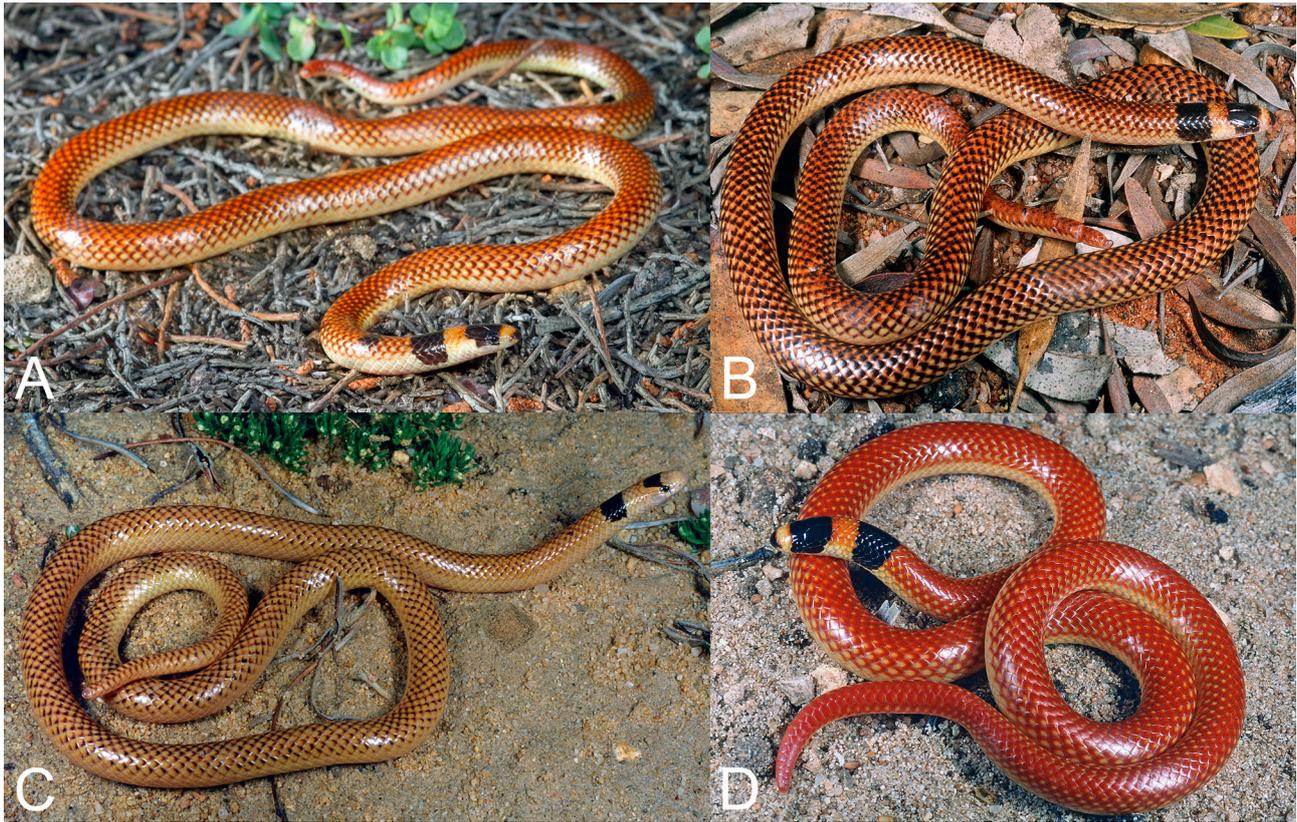


Figure 5. Adult *Narophis bimaculatus* photographed in life from (A) 4 km SW of Ulyerra, Eyre Peninsula, South Australia, (B) 14 km E of Zanthus, Western Australia, WAM R112658, (C) 6 km SW of Coorow, Western Australia, WAM R135079, and (D) Cervantes, Western Australia, showing the variation in body colour and intensity of dark posterior margins (photos—A: B. Schembri, B, C, D: B. Maryan).

or just before posterior edge of parietals (e.g. SAMA R61147–48) and the posterior margins on body scales varied from indistinct smudges (e.g. SAMA R61174, SAMA R69322) to distinct wide margins (e.g. SAMA R59348, SAMA R67492).

The dark head band ending behind posterior edge of parietals was present in 27% of specimens from eastern parts of range including occasional individuals with a third dark blotch on the forebody (e.g. WAM R74220, WAM R147073, WAM R165881, WAM R169106). By contrast, in the western parts of range, we recorded the dark head band typically ending on or just before posterior edge of parietals in 61% of specimens and individuals with a third blotch were rarely seen (WAM R60628, WAM R62367). We observed no appreciable variation in the nature of the nape band between coastal and inland specimens.

Our field observations suggest the degree of the darker body colour in eastern parts of range is affected by the intensity of the posterior margins on scales, and arguably influenced by the subtly different substrates inhabited by these highly fossorial snakes. Individuals from the coastal sands and plains are paler in general appearance when compared to slightly darker individuals occurring on inland sands, a phenomenon regularly observed in other fossorial reptiles (Maryan *et al.* 2013).

Measurements, counts, and scalation. Table 2 presents the minimum–maximum range, means and standard deviations of the characters measured and counted (as defined in Table 1) for each sex and all adult specimens of *N. bimaculatus* listed in the Appendix. Sexual dimorphism is pronounced, where males have longer tails (as found previously by Clarke & How 1995) and higher subcaudal scale counts (Table 2). The widest part of the head is broader in females, indicated by broader total width, broader posterior frontal scale and longer parietal scales (Table 2, Fig. S3).

The head scale configuration in *N. bimaculatus* display minimal intraspecific variation. For illustrations of head scalation in *N. bimaculatus*, see Greer (1997: 169) and Storr *et al.* (2002: 190). All the specimens examined have the nasal contacting the preocular, except for two specimens (WAM R82736, WAM R125965) in which these scales are separated by the prefrontal on both sides and one specimen (SAMA R61147) on the right side. Occasional specimens have the second supralabial contacting the preocular on both sides (WAM R719, WAM R54543, WAM R104313, WAM R172498, WAM R173341). Storr (1968: 85) recorded the typical condition of the upper primary and secondary temporals fused to form a single elongate scale in 92% of specimens. We observed the same typical condition in all specimens on both sides, except in seven specimens: WAM R82736 has 1

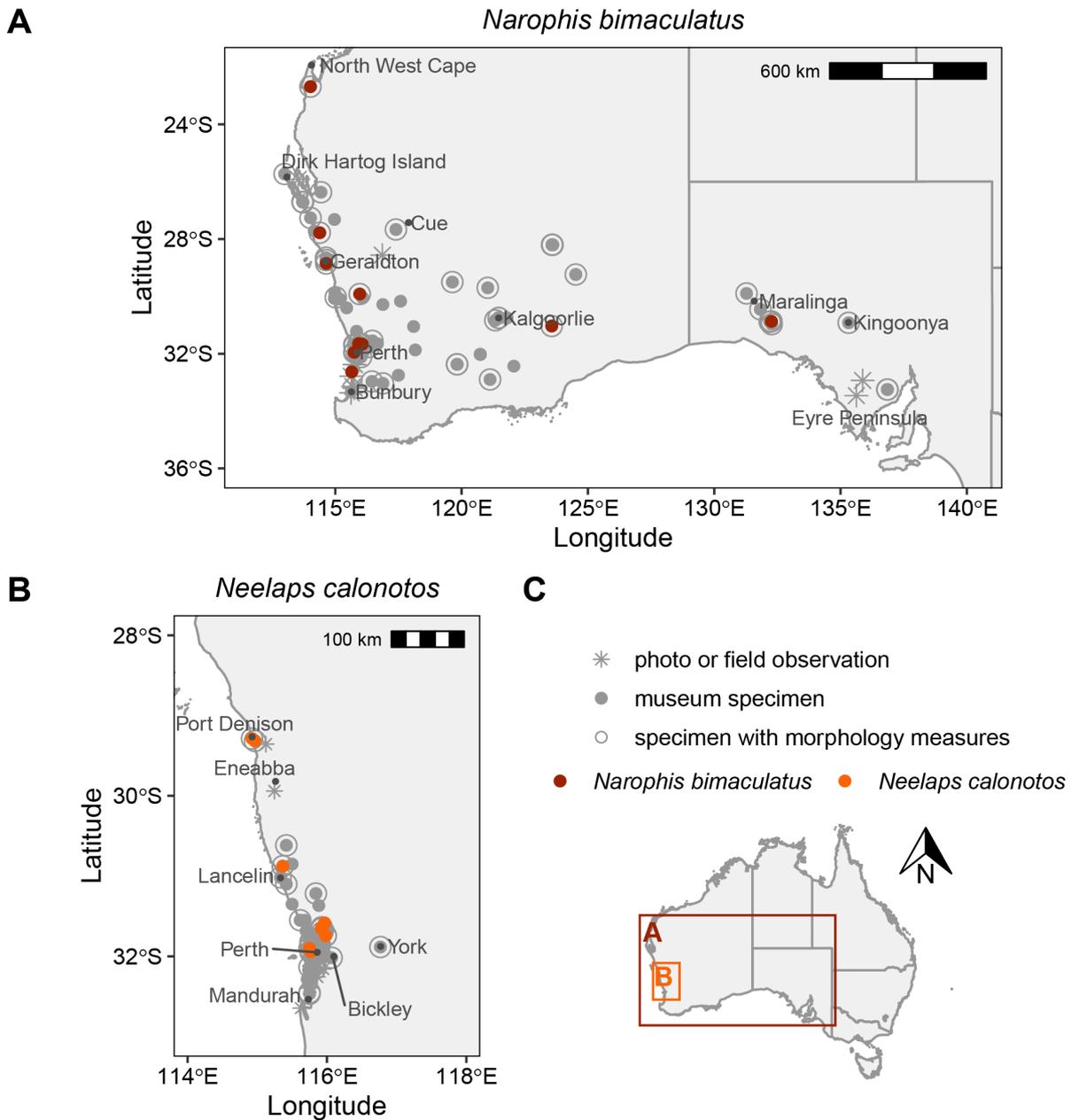


Figure 6. Updated distribution maps for (A) *Narophis bimaculatus* and (B) *Neelaps calonotos* indicated by solid circles and specimens examined in the phylogenetic (coloured) and morphological (encircled) analyses. Stars indicate reliable photo or field observation. Colours within A represent intraspecific genetic variation in *N. bimaculatus*. Specimen locality data derived from OZCAM (2023).

primary + 1 secondary temporals on both sides (the secondary is much smaller), SAMA R61148 and WAM R62367 on the left side and WAM R4722, WAM R125965, WAM R135079, WAM R147076 on the right side.

Other variations of scalation include: one specimen (SAMA R61174) has divided prefrontals; one specimen (SAMA R61147) has four supralabials on the left side, caused by fusion between first and second supralabials and the third supralabial is fused with preocular; two specimens (WAM R147073, WAM R147076) have six supralabials on the right side, caused by an extra scale interposed between fourth and fifth supralabials; three

specimens (WAM R65292, WAM R123596 on the right side, WAM R172498 on the left side) have one postocular, caused by either fusion of lower with fourth supralabial or upper with parietal; one specimen (WAM R165295) has the temporal fused with fifth supralabial on the right side; two specimens (WAM R125965, WAM R165295) have the temporal reduced in size on the left side, caused by the fifth supralabial contacting parietal; one specimen (WAM R135646) has a combination of both divided and undivided subcaudals and a specimen (WAM R60628) has exceptionally high ventral and vertebral scale counts of 263 and 273, respectively.

Distribution. Essentially unchanged from species maps of Schembri (2017: 26) and Chapple *et al.* (2019: 537), *N. bimaculatus* is widespread throughout the temperate, semiarid to arid areas of southern Western Australia and southwestern South Australia (Fig. 6A). In Western Australia, extends north to Denham on the Peron Peninsula at Shark Bay (WAM Photo Database), 22 km SSW of Woodleigh Homestead, 38 km SE of Nerren Nerren Homestead, 29 km SSE of Yalgoo (B. Budrey, pers. comm.) and Lakeside at 48 km SW of Cue, east to 7–8 km WNW of Point Salvation, Tropicana Mine and 14 km E of Zanthus, and south to Bunbury, Mount Saddleback, Williams, 6 km ENE of Lake Cronin and Peak Charles National Park. There is a disjunct population on the North West Cape, represented by a single specimen (WAM R116665) from 2 km W of Bullara Homestead (Maryan 1995; Fig. 6A). Also on Dirk Hartog Island. In South Australia, extends north to 41 km NNW of Maralinga, Ooldea and Kingoonya, east to Secret Rocks, and south to 4 km SW of Ulyerra on the Eyre Peninsula (Schembri 2017).

The apparent allopatric distribution of this species in the Great Victoria Desert of Western and South Australia (Fig. 6A), with collection records indicating a distance of ~688 km between populations, is possibly an artefact of collecting in a poorly surveyed remote region.

Habitat and ecology. *Narophis bimaculatus* occupies a variety of temperate, semiarid to arid vegetation that grow on sandy to loamy soils, including coastal sand dunes and swales, sandplains, dry sclerophyll woodlands of *Banksia* L.f., mallee and/or other *Eucalyptus* L'Hér., heathlands particularly coastal *Acacia* Mill. shrublands and inland hummock grassland dominated sand dunes and plains (Wilson & Knowles 1988; Ehmann 1992; How & Shine 1999; Bush *et al.* 2007, 2010; Schembri 2017; Chapple *et al.* 2019; Wilson & Swan 2021). At the northern extent of its range, the habitat at 2 km W of Bullara Homestead on the North West Cape consists of a red *Triodia* R.Br.-covered sand dune with sparse shrubs (B. Maryan, pers. obs.).

Field observations indicate a preference for sandy soils supporting low open vegetation, and a scarcity of observations on harder substrates such as the clay and granitic soils on the Darling Range (Storr *et al.* 1978; Bush *et al.* 2010). This preference is exemplified by 156 WAM collection records of which the majority are recorded from the Swan Coastal Plain, Great Victoria Desert and Geraldton Sandplains bioregions (OZCAM 2023). In these vegetation associations, specimens of *N. bimaculatus* particularly during cooler weather can be raked from the upper layers of soil beneath leaf litter at base of trees and shrubs, piles of dead vegetation, abandoned stick-ant *Iridomyrmex conifer* Forel, 1902 nests, embedded, decaying logs and stumps and spoil-heaps, consisting of soil, branches and other debris pushed up, usually by machinery, on the side of tracks and firebreaks. Field observations of *N. bimaculatus* on

the surface beneath cover are scarce, apart from one specimen (WAM R64822) found on soil under log.

Additionally, at peak seasonal activity, *N. bimaculatus* can be funnel or pit-trapped in buckets/pipes and nocturnally observed while driving on roads and tracks (How & Shine 1999; Thompson & Thompson 2007; B. Maryan & B. Bush, pers. obs.). Regarding the usefulness of traps in catching small, fossorial snakes, it is generally considered that capture rates are low for snakes poorly suited to moving long distances across open areas (How & Shine 1999). However, the technique of raking can be productive, allowing targeting of particular microhabitats such as spoil-heaps, when on occasions up to 10–15 individuals of *B. semifasciatus* (Günther, 1863), *N. bimaculatus*, *N. calonotos* and *S. bertholdi* (Jan, 1859) can be found in a single day on the Swan Coastal Plain (Maryan 2002; Bush *et al.* 2007: 33).

Sympatry or close parapatry with other fossorial species. Recorded instances of narrow or broad sympatry, occasionally syntopy, involving *N. bimaculatus* include with *B. approximans* (Glauert, 1954) at the southern extremities of its range, *B. fasciolatus* (Günther, 1872), *B. semifasciatus*, and *S. bertholdi* throughout a large area encompassing several bioregions in Western and South Australia, *N. calonotos* on the Swan Coastal Plain and a small area of the Geraldton Sandplains bioregions and *S. littoralis* (Storr, 1968) on the west coast between Shark Bay, including Dirk Hartog Island and Cervantes (Chapman & Dell 1985; Storr *et al.* 2002; Thompson & Thompson 2006; Maryan 2005; Bush *et al.* 2007, 2010; B. Maryan, pers. obs.). At Bold Park in Western Australia, *B. fasciolatus*, *B. semifasciatus*, *N. bimaculatus*, *N. calonotos*, and *S. bertholdi* have all been recorded (How 1998; How & Shine 1999). Based on collection records, *B. approximans*, *S. bertholdi*, and *S. littoralis* are recorded on the North West Cape (Storr *et al.* 2002). Collection records also indicate *N. bimaculatus* and *S. anomalus* occur in sympatry at 7–8 km WNW of Point Salvation in the Great Victoria Desert bioregion. At the boundary between the eastern Eyre Yorke Block and Gawler bioregions in South Australia, collection records suggest *N. bimaculatus* and *V. annulata* (Gray, 1841) occur in close parapatry in the vicinities of Secret Rocks (see Appendix) and Port Augusta (SAMA R2173).

Comparisons with other fossorial species. Diagnostic differences between *N. bimaculatus* and *N. calonotos* are listed under the revised diagnosis for *Narophis*. *Narophis bimaculatus* will be compared with *B. approximans*, *B. fasciolatus*, *B. semifasciatus*, *S. anomalus*, *S. bertholdi*, *S. littoralis*, and *V. annulata* using Storr *et al.* (2002) and Wilson & Swan (2021) with which it occurs in sympatry or close parapatry (see above).

It differs from the listed *Brachyuropis* species in: larger adult total length to 468 mm (*versus* to 390 mm), more slender body form (*versus* moderately robust), higher ventral scale counts of 178–234 (*versus* < 190), typically

one elongate temporal scale (*versus* typically 1 + 1, but often fused in *B. semifasciatus*), 15 midbody scale rows (*versus* 17), protrusive round-shaped snout without cutting edge (*versus* protrusive wedge-shaped snout tipped with transverse weak to strong cutting edge) and without bands along the body (*versus* cross-banded along the body, but bands ragged-edged in *B. fasciolatus*).

It differs from the listed *Simoselaps* species in: larger adult total length to 468 mm (*versus* to 390 mm), more slender body form (*versus* moderately robust), higher ventral scale counts of 178–234 (*versus* < 135), typically one elongate temporal scale (*versus* typically 1 + 1, but primary temporal fused with second last supralabial in *S. anomalus* and primary temporal often large contacting oral margin in *S. littoralis*) and without bands along the body (*versus* encircled by bands along the body).

It differs from *V. annulata* in: smaller adult total length to 468 mm (*versus* to 760 mm), lower ventral scale counts of 178–234 (*versus* 195–257), typically one elongate temporal scale (*versus* 1 + 1, but primary temporal occasionally fused with second last supralabial), protrusive round-shaped snout (*versus* bluntly round-shaped snout) and without bands along the body (*versus* encircled by bands along the body).

Narophis bimaculatus shares a superficial resemblance to the similarly coloured and patterned *Furina ornata* (Gray, 1842) but differs in numerous ways including the protrusive snout (not protrusive in *Furina*), black head band extends forward to level of eyes (black head band extends forward to snout in *Furina*) and one elongate temporal scale (2 + 2 in *Furina*).

Remarks. Strahan *et al.* (1998) and How & Shine (1999) present information on the ecology, reproductive biology and diet of *N. bimaculatus*. In Western Australia, the majority of collection records of *N. bimaculatus* are from the heavily-cleared and modified Swan Coastal Plain that includes the metropolis of Perth; however this species persists in several remnant bushland areas set aside for the conservation of flora and fauna (e.g. How & Dell 1994; How 1998). Due mainly to paucity of records in South Australia, *N. bimaculatus* has a conservation status of Near Threatened and is listed as Rare under state legislation, which is likely due to a combination of remoteness of suitable habitat and the cryptic, fossorial nature of the species (Schembri 2017). In general, *N. bimaculatus* is considered to be Least Concern under the IUCN conservation status owing to its widespread distribution without any perceived threats, occurring in many large, relatively undisturbed nature reserves and national parks (Chapple *et al.* 2019: 537). We note the distinction between categories Least Concern and Data Deficient referring to “inadequate information” is unclear (International Union for Conservation of Nature 2021), especially when this lack of knowledge of population size and structure, ecology, threats and threat ame-

lioration can be equally applied to many Least Concern listed species such as *N. bimaculatus*.

Neelaps Günther, 1863

Type species. *Furina calonotos* (= *Neelaps calonotos*) Duméril, Bibron & Duméril, 1854a: 1241, by monotypy.

Etymology. Günther (1863: 24) provided no derivation of name, but it is presumably from the Greek *neos* meaning new and *Elaps* the type genus of the family Elapidae.

Revised diagnosis. A monotypic genus comprising *N. calonotos*, a very small, slender fossorial hydrophiine elapid snake (total length to 271 mm this study, males mean 239 mm, females mean 220 mm, tail length 10.4–18.9% of SVL mean 15.2%) with: head narrow, depressed and not distinct from neck; protrusive round-shaped snout without cutting edge; no canthus rostralis; frontal not much wider than long; internasals present slightly smaller than prefrontals, suture between internasal and prefrontal transverse; preocular in contact with nasal, rarely separated by prefrontal; typically upper primary and secondary temporals fused to form single elongate scale without deep ventral descent (Fig. 3B), occasionally 1 + 1; rostral much wider than high posteriorly obtuse and only slightly projecting between internasals; a consistent colour pattern of dark crescent-shaped band extends across nape and dark broad band across head forward to level of eyes; tip of snout consistently dark; variable body colour of bright, pale pinkish or orange red with pale anterior portion or spot on each scale, typically distinct feature of a dark vertebral stripe with pale anterior portion or spot forming chain-like pattern extends from nape to tip of tail; 124–145 ventrals; 128–148 vertebrales; midbody scales very glossy and smooth, in 15 rows occasionally increasing to 16 posterior to the head and decreasing to 14 or 13 anterior to the vent; anal and 23–34 subcaudals divided; supralabials six, last the largest; infralabials seven; ventral surface white with glossy shine; eyes are small with pupils indiscernible within black irises (Bush 2017). Other features in the genus are the reversion to the primitive karyotype of 2N = 36 (16M and 20m) (Mengden 1985), and pterygoid tooth row reduced posteriorly such that it does not extend beyond the level of the ectopterygoid-ptyerygoid articulation (Greer 1997). Storr (1968: 85) and B. Maryan record total lengths of 284 mm and 281 mm, respectively in female *N. calonotos*.

Based on phylogenetic affinities, *Neelaps* is compared with the other fossorial snake genus of *Vermicella* using Keogh & Smith 1996; Storr *et al.* 2002; Cogger 2014 and Wilson & Swan 2021.

Differs from *Vermicella* in: substantially smaller adult ToL to 271 mm (*versus* to 760 mm), lower ventral scale counts of 124–145 (*versus* > 195), typically one elongate temporal scale (*versus* 1 + 1, but primary temporal occa-

sionally fused with second last supralabial), protrusive round-shaped snout (*versus* bluntly round-shaped snout), preocular and nasal separated by prefrontal (*versus* preocular in contact with nasal, rarely separated by prefrontal), typically vertebral stripe present along the body, or if reduced some indications remain (*versus* encircled by bands along the body) and widely allopatric distributions. Additionally, *Neelaps* feed on small lizards and at most when threatened raise forebody and thrash, while most (probably all) *Vermicella* species feed entirely on blind snakes (Typhlopidae), contort their bodies into vertically oriented loops, thrash and re-position.

***Neelaps calonotos* (Duméril, Bibron & Duméril, 1854) Black-striped Burrowing Snake**

Figs. 1, 3, 4, 6, 7

Lectotype. MNHN-RA-2012.411 (formerly 3943A), male, the larger of the two syntypes, designated by Wells & Wellington (1985: 46), original type locality “Tasmanie” [= Tasmania, Australia] in error, restricted to Perth, Western Australia, *vide* Storr (1968: 85), obtained from J.P. Verreaux and received in Paris, France in 1844 (G. Shea, pers. comm.).

Paralectotype. MNHN-RA-0.3943, male, same details as lectotype.

Furina calonotos Duméril, Bibron & Duméril 1854a, *Erpétologie Générale ou Histoire Naturelle Complete des Reptiles, Tome septième*: 1241.

Furina calonotus Duméril, Bibron & Duméril 1854b, *Erpétologie Générale ou Histoire Naturelle Complete des Reptiles, Tome neuvième*: 377.

Brachysoma calonotos Günther 1858, *Catalogue of Colubrine Snakes in the collection of the British Museum*: 229.

Neelaps calonotus Günther 1863, *Annals and Magazine of Natural History*: 24.

Pseudelaps calonotus Jan 1863, *Elenco sistematico degli ofidi descritti e disegnati per l'Iconografia Générale*: 116.

Neelaps caledonicus Hoffman 1890, *Klassen und Ordnungen des Their-Reichs, wissenschaftlich dargestellt in Wort und Bild*: 1788. In error for *calonotus*.

Furina calonota Boulenger 1896, *Catalogue of the Snakes in the British Museum (Natural History), Vol III*: 407.

Neelaps neocaledonicus Palacky 1898, *Mémoires de la Société Zoologique de France*: 121. In error for *caledonicus*.

Vermicella calonota Glauert 1950, *A Handbook of the Snakes of Western Australia*: 38.

Melwardia calonota Worrell 1960, *Western Australian Naturalist*: 132.

Vermicella calonotos Storr 1968, *Journal of the Royal Society of Western Australia*: 85.

Simoselaps calonota Underwood 1979, *Classification and Distribution of Venomous Snakes in the World*: 32.

Simoselaps calonotus Cogger 1992, *Reptiles & Amphibians of Australia*: 684.

Neelaps calonotos Storr, Smith & Johnstone 2002, *Snakes of Western Australia Revised Edition*: 191.

Vermicella calonotus Wallach, Williams & Boundy 2014, *Snakes of the World A Catalogue of Living and Extinct Species*: 771.

Confusion regarding spelling of name and the type specimens. The original description in Volume 7 of Duméril, Bibron & Duméril (May 1854a: 1241) is under the name *Furina calonotos* (as also used, as a *nomen nudum*, by Duméril (1853: 517) in a Prodomus to the classification of snakes to be used in 1854). However, in Volume 9 the same authors (September 1854b: 377), in a summary of the entire 9 volumes of the *Erpétologie Générale*, provide a brief redescription under the name *Furina calonotus*. Obviously not aware of this, Cogger *et al.* (1983: 228) incorrectly stated that the species name *calonotos* was validly emended to *calonotus* by Günther (1863: 24); see also remarks by Wallach *et al.* 2014: 771. However, neither Duméril *et al.* (1854b) nor Günther (1863) provided any explanation as to why the species name should change. Hence, under the Code, the change must be considered an incorrect subsequent spelling rather than either a justified or unjustified emendation (an emendation requires a statement that the change has been made; Article 33.2.1 of the Code of Zoological Nomenclature).

David & Ineich (1999: 189) note that the original epithet *calonotos* (“beautiful back”) is a Greek name in apposition, not an adjective, and consider the change to *calonotus* an incorrect subsequent spelling, a conclusion with which we agree. However, under Article 33.3.1 of the Code, when an incorrect subsequent spelling is in prevailing usage and is attributed to the publication of the original spelling, the subsequent spelling is deemed to be a correct original spelling, and is to be maintained. The Code further defines “prevailing usage” as “that usage of the name which is adopted by at least a substantial majority of the more recent authors concerned with the relevant taxon, irrespective of how long ago their work was published”. Based on the literature used here, the spelling *calonotos* (e.g. Storr *et al.* 1978: 196; Clarke & How 1995: 69; Strahan *et al.* 1998: 57; How & Shine 1999: 269; How & Dell 2000: 202; Storr *et al.* 2002: 191; Bush *et al.* 2007: 254, 2010: 149; He 2021: 85; Wilson & Swan 2021: 614; Eipper & Eipper 2022: 96) has been used with similar frequency to *calonotus* (e.g. Shine 1984: 173; Ehmann & Cogger 1985: 443; Wilson & Knowles 1988: 338; Kennedy 1990: 108; Ehmann 1992: 452; Cogger *et al.* 1993: 164; Greer 1997: 182; Reed & Shine 2002: 454; Cogger 2014: 904; Allen & Vogel 2019: 93–94; Chapple *et al.* 2019: 519) without either name having achieved usage over the other. Further, the majority of specimens (86%) are held by the WAM under *calonotos*, hence we argue the original spelling *calonotos* should be maintained. As *calonotos* is a noun, it does not change gender in combination with differing generic names, and hence the spelling *calonota*, used in combination with *Furina* (Boulenger 1896: 407), *Vermicella* (Glauert 1950: 38), and *Melwardia* (Worrell 1960: 132) is also incorrect.

Similarly, there are confusing accounts for the type specimens. Cogger *et al.* (1983: 228) lists 2 specimens as syntypes

under a single MNHP (= MNHN) number 3943, and The Reptile Database (Uetz *et al.* 2021) lists two specimens MNHN 3943 and 3943A as paralectotypes, even though there is only one lectotype and one paralectotype. In the original description it clearly states that there are two specimens of *F. calonotos* with separate colour descriptions provided for each specimen (Duméril, Bibron & Duméril 1854a: 1241). A lectotype designation was made by Wells & Wellington (1985: 46) as “MNHP 3943, being the larger of the two syntypes registered under this number”, apparently without examining the specimens. They presumably based their statement of two syntypes under the number 3943 from the listing by Cogger *et al.* (1983), without realising that the two specimens are independently numbered 3943 and 3943A in the MNHN collection. Hence, it is not clear whether the lectotype is MNHN 3943 (the only specimen actually under that number), or the larger of the two specimens MNHN 3943 or MNHN 3943A. Wallach *et al.* (2014: 771) list MNHN 3943A as lectotype “being the larger of the two syntypes”, following Wells & Wellington (1985), but provide no measurements to support this determination. Designation of a lectotype without having examined it is an unfortunate legacy of Wells & Wellington publications that will continue to cause issues for future researchers (see Dong *et al.* 2021). Fortunately in this case, we received total length measurements from Paris (J. Courtois, pers. comm.) of 250 mm for MNHN 3943 and 252 mm for MNHN 3943A (now catalogued 2012.411, Fig. 4B), confirming the latter specimen is the larger of the two syntypes, so we maintain the application of MNHN 2012.411 as lectotype and MNHN 3943 as paralectotype in accordance with the Muséum National d’Histoire Naturelle database: <http://coldb.mnhn.fr/cataloguenumber/mnhn/ra/2012.411>

Description of lectotype (Fig. 4B). Scapulation and proportions as in the diagnosis for the genus. Individual characteristics include: internasals and prefrontals much wider than long with medial suture much offline so that right internasal contacts left prefrontal; single preocular, slightly higher than wide, in contact with nasal; two postoculars, the upper much larger; frontal much wider anteriorly, gradually narrowing to rounded point between parietals; parietals equal size; temporal above sixth supralabial contacting both postoculars; six supralabials, first and second smallest, third higher in contact with orbit, fourth under orbit in contact with lower postocular, fifth in contact with lower postocular and temporal, sixth much the largest; mental triangular with undulating anterior edge (possibly caused by preservation) between first infralabials; seven infralabials; anterior chin shields in broad contact with infralabials one to three; posterior chin shields in broad contact with fourth infralabials only; six rows of intergulars between chin shields and anterior most broad ventral.

After ≥ 167 years in preservative (Fig. 4B), the lectotype has faded to white on the dorsolateral surface (discoloured where epidermis remains attached), including interspaces behind tip of snout and head band, extending onto anterior portion of supraoculars, with complete narrow black vertebral stripe one scale wide extending from nape to tip of tail (reducing to zig-zag line along tail), each scale within stripe enclosing a white anterior

spot, gradually decreasing in size distally to vanishing along tail. Tip of snout and head and nape bands remain black.

Colour in life and in preservative. The following description of colour in life is based on Figs. 7A, B, C, D, and field observations of *N. calonotos* in Western Australia. The descriptions in preservative and of variation are based on all specimens of *N. calonotos* listed in the Appendix.

In most colour descriptions for *N. calonotos* authors mention a cream or white centre on each body scale including those within the dark vertebral stripe (e.g. Storr *et al.* 2002; Bush *et al.* 2010; Wilson & Swan 2021). After our examination of photos in live individuals (Figs. 7A, B, C, D) and close inspection of the body scales in the specimens (see Appendix) under a microscope, we observed the pale pigment is concentrated more on the anterior portion (= basal, see Scanlon 1985: 51) of each scale and varied in development from a spot to covering up to $\frac{3}{4}$ of the scale.

In life, variable body colour of bright red (Fig. 7A), pale pinkish red (Fig. 7B) or orange red (Figs. 7C, D), with paler or similar colored interspace between dark bands, and more cream to white between dark tip of snout and band on head, each body scale enclosing a yellowish, cream or white anterior portion or spot (covering up to $\frac{3}{4}$ of scale), with dark pigment on the body scales consisting of a typically distinct black vertebral stripe 1–3 scales wide extending from nape to tip of tail (Figs. 7A, B), often broader posteriorly and then reducing to a zig-zag line on tail. Stripe encloses bright cream or white anterior portion or spot on vertebrals forming a chain-like pattern, often gradually decreasing in size distally and vanishing on tail. Dark stripe, varying in development from clearly broad and complete (Fig. 7A) or narrow (Fig. 7B), or occasionally reduced and largely broken, although some indications remain on posterior body or tail (Fig. 7C) and rarely unstriped (Fig. 7D). Black tip on the snout consistently present, variously covering rostral and not extending on to ventral edge, extending back to partially cover or just to edge of internasals, and lateral edge narrowly covering nasals, occasionally extending back to nostrils. Black band on head commencing on or just before anterior edge of frontal and just forward of eyes, extending back partially or narrowly covering supralabials four to six, occasionally supralabials without dark pigment (Fig. 7C), and ending slightly behind posterior edge of parietals to partially or completely cover first vertebral. Black band on nape crescent-shaped and $2\frac{1}{2}$ –5 scales long, separated from head band by 2–3 vertebral scales, occasionally with cream or white anterior portion or spot on scales at rear of band. Eyes are black without discernible pupils. Ventral surface under the head and along the body, including the lateroventral edges is cream white to pale yellow with glossy shine.



Figure 7. Adult *Neelaps calonotos* photographed in life from (A) Casuarina, Western Australia, (B) 5 km SSE of Port Denison, Western Australia, WAM R141838, (C) Ellenbrook, Western Australia, and (D) Ballajura, Western Australia, showing the variation in body colour and the typically complete vertebral stripe of varying width, occasionally reduced or absent as in Figs. 7C, D (photos—B. Maryan).

In preservative, body colour fades to white including interspaces on the head. Dark head and nape bands, tips on snouts and vertebral stripes when present along the body faded to brown but overall retained a black appearance, even in very old specimens (e.g. MNHN-RA-0.3943, MNHN-RA-2012.411). The white ventral surface remains glossy.

Variation includes: development of vertebral stripe from typically broad or narrow and complete up to 3 scales wide, or reduced and largely broken with some indications remaining on posterior body or tail to complete absence. To quantify this intraspecific variation, we examined 93 WAM specimens of *N. calonotos* (including listed in the Appendix), recording the typical condition of a distinct vertebral stripe in 75% of specimens including the lectotype and paralectotype. The next recorded condition of a faint and largely broken stripe was present in 20% of specimens. Only four specimens have the rare unstriped condition. One specimen (WAM R62170, same individual illustrated in Storr *et al.* 2002: 130) has a very broad vertebral stripe extending on to adjacent margins of fourth scale on either side. The pale anterior portion or spot on each body scale within the stripe remain distinct. The dark head band displays varying levels of coverage on some scales such as the frontal, supraoculars and supralabials. The dark tip on the snout is reduced in one specimen (WAM R152960) extending

back to very narrow edge of internasals and upper portion of nasals well separated from nostrils.

Measurements, counts, and scalation. Table 2 presents the minimum–maximum range, means, and standard deviations of the characters measured and counted (as defined in Table 1) for each sex and all adult specimens of *N. calonotos* listed in the Appendix. Sexual dimorphism is pronounced, where females have shorter tails than males (as found previously by Clarke & How 1995), fewer subcaudal scales, yet higher number of ventral and vertebral scales (Table 2).

The head scale configuration in *N. calonotos* display minimal intraspecific variation. For illustration of head scalation in *N. calonotos*, see Storr *et al.* (2002: 191). All the specimens have the nasal contacting the preocular, except in one specimen (WAM R97886) in which these scales are separated by the prefrontal on both sides. One specimen (WAM R127530) has the second supralabial contacting the preocular on the left side; another specimen (WAM R25065) has narrow contact between preocular and frontal on both sides. Storr (1968: 85) recorded the typical condition of the upper primary and secondary temporals fused to form a single elongate scale in 80% of specimens. We observed the same typical condition in all specimens on both sides, albeit in a comparatively smaller sample size (see Appendix),

except in one specimen: WAM R87906 has 1 primary + 1 secondary temporals on both sides.

Other variations of scalation include: two specimens (SAMA R29765, WAM R40287) have five supralabials on the right side, caused by fusion between first and second supralabials; SAMA R29765 also has fused postoculars on the left side forming a single scale; WAM R40287 has the fourth supralabial on the right side contacting the upper postocular bisecting lower postocular and temporal; one specimen (WAM R25065) has one postocular on the left side caused by fusion of lower with fourth supralabial; and a specimen (WAM R62158) has three postoculars on the left side caused by a divided lower postocular.

Distribution. Essentially unchanged from species maps of Storr *et al.* (2002: 191) and Bush *et al.* (2010: 149), *N. calonotos* is endemic and restricted to the temperate Swan Coastal Plain and a small area of the Geraldton Sandplains bioregions of southwestern Western Australia (Fig. 6B). On the Swan Coastal Plain, extends north to 15 km NNE of Lancelin and Cooljarloo at 10 km WNW of Walyering Hill, east to Boonanarring Nature Reserve, Muchea, Maralla Road Nature Reserve at Ellenbrook and Forrestdale Lake Nature Reserve (B. Maryan & G. Gaikhorst, pers. obs.), and south to Singleton, Madora and Dawesville (He 2021) near Mandurah. There are disjunct populations on the Geraldton Sandplains bioregion, represented by two specimens (WAM R127530, WAM R141838) from near Port Denison and field observations from Arrowsmith and 8 km S of Eneabba (M. Bamford, pers. comm.; Ecologia Environment 2008; Fig. 6B).

Two specimens (WAM R3827, WAM R7330) from Bickley and York respectively, the latter mapped by Ehmann (1992: 452) and Storr *et al.* (2002: 191), occur inland from the main coastal plain distribution of this species and require confirmation with additional records (Fig. 6B). Ehmann (1992) noted the York specimen may represent a relictual population isolated by increased aridity in geologically recent times, however the possibility that these distant individuals may have been inadvertently transported to these areas cannot be ruled out.

In general, the occurrence of *N. calonotos* on and east of the Darling Range in the Jarrah Forest and Avon Wheatbelt bioregions is considered doubtful (Cogger *et al.* 1993; Bush *et al.* 2007, 2010; He 2021). Another two more distant specimens (NMV R721, SAMA R2612) with underlying doubt from Katanning and Busselton respectively, are not included on our species map. The Busselton record is possible at the southern extremity of the Swan Coastal Plain bioregion; however it cannot be verified due to an “exchange” entry on the database with no mention of where this specimen was exchanged to (M. Hutchinson, pers. comm.).

Habitat and ecology. *Neelaps calonotos* is restricted to temperate vegetation that grow on sandy soils, includ-

ing coastal and near-coastal sand dunes with heaths and/or *Acacia* thickets, often adjacent to limestone outcropping and dry sclerophyll woodlands of *Banksia/Eucalyptus* with a shrubland understorey (Wilson & Knowles 1988; Ehmann 1992; Cogger *et al.* 1993; How & Shine 1999; Bush *et al.* 2007, 2010; Chapple *et al.* 2019; Wilson & Swan 2021). The habitats near Port Denison and Eneabba consists of near-coastal sand dunes with low heath and dense thickets of *Acacia rostellifera* Benth. and open regenerating kwongan heath on white sandy soils with scattered low shrubs and trees (B. Maryan, pers. obs.; Ecologia Environment 2008).

Field observations and collection records (OZCAM 2023) indicate *N. calonotos* is highly restricted to the sandy soils within the collectively termed claypans of the Swan Coastal Plain Threatened Ecological Community (DPAW 2015). This preference is exemplified by *N. calonotos* being encountered most frequently in banksia woodland on the Cottesloe sands of the Spearwood Dune formation at Bold Park (How & Shine 1999). Based on the results of recurrent surveys, this species appears to prefer mature banksia woodlands, supported by observations that, in several remnant reserves on the Swan Coastal Plain where historically recorded, it persisted only in the larger, more fire-resistant ones (How & Dell 2000).

In these vegetation associations, *N. calonotos*, particularly during cooler weather, can be raked from the upper layers of soil or beneath similar configurations of vegetation and debris as described for *N. bimaculatus*. Field observations of *N. calonotos* on the surface beneath cover are scarce, apart from one individual found ‘amongst a pile of building rubble in bushland’ (True & Reidy 1981). Like *N. bimaculatus*, in peak activity *N. calonotos* can be funnel or pit-trapped or nocturnally observed while driving on roads and tracks (How & Shine 1999; Thompson & Thompson 2007; B. Maryan, pers. obs.). The technique of raking in particular microhabitats can be productive when on occasions up to 5–7 individuals of *N. calonotos* can be found in a single day on the Swan Coastal Plain (Maryan 2002; Bush *et al.* 2007: 33), however it has been extirpated from some remnant bushland areas in recent times by clearing for urbanisation (He 2021; B. Maryan, pers. obs.).

Sympatry with other fossorial species. Broad sympatry, occasionally syntopy, involving *N. calonotos* occurs on the Swan Coastal Plain and a small area of the Geraldton Sandplains bioregions with *B. fasciolatus*, *B. semifasciatus*, *N. bimaculatus*, and *S. bertholdi* (Storr *et al.* 1978; How & Shine 1999; Storr *et al.* 2002; Maryan 2005; Bush *et al.* 2007, 2010; B. Maryan, pers. obs.). Where both *N. calonotos* and *N. bimaculatus* are known to occur, the trapping data suggests population densities are similar (How & Shine 1999). For instance, during a long-term (> 7 years) herpetofaunal survey at Bold Park, the most abundant taxon *S. bertholdi* accounted for 122 trapping captures followed by 22 *B. semifasciatus*, 16 *N.*

calonotos, 10 *N. bimaculatus*, and 7 *B. fasciolatus* (How 1998). In contrast, another survey at Maralla Road Bushland of shorter duration (6 months), yielded the same number of captures for *N. calonotos* and *S. bertholdi* with comparatively low captures for both *Brachyuropis* species and *N. bimaculatus* was not found (Maryan *et al.* 2002). The disjunct populations on the Geraldton Sandplains bioregion from near Port Denison and Eneabba are also regionally sympatric with *S. littoralis* (Storr *et al.* 2002; Maryan 2005).

Comparisons with other fossorial species. Diagnostic differences between *N. calonotos* and *N. bimaculatus* are listed under the revised diagnosis for *Narophis*. *Neelaps calonotos* will be compared with *B. fasciolatus*, *B. semifasciatus*, *S. bertholdi*, and *S. littoralis* using Storr *et al.* (2002) and Wilson & Swan (2021) with which it occurs in sympatry (see above).

It differs from the listed *Brachyuropis* species in: smaller adult total length to 271 mm (*versus* to 390 and 353 mm, respectively), lower ventral scale counts of 124–145 (*versus* 140–172 and 147–188, respectively), typically one elongate temporal scale (*versus* typically 1 + 1, but often fused in *B. semifasciatus*), 15 midbody scale rows (*versus* 17), protrusive round-shaped snout without cutting edge (*versus* protrusive wedge-shaped snout tipped with transverse weak to strong cutting edge) and typically with vertebral stripe along the body, or if reduced some indications remain (*versus* cross-banded along the body, but bands ragged-edged in *B. fasciolatus*).

It differs from the listed *Simoselaps* species in: smaller adult total length to 271 mm (*versus* to 300 and 390 mm, respectively), higher ventral scale counts of 124–145 (*versus* 112–131 and 104–125, respectively), higher subcaudal scale counts of 23–34 (*versus* 15–25 and 16–23, respectively), typically one elongate temporal scale (*versus* typically 1 + 1, but primary temporal often large contacting oral margin in *S. littoralis*) and typically with vertebral stripe along the body, or if reduced some indications remain (*versus* encircled by bands along the body).

Remarks. Shine (1984), Strahan *et al.* (1998) and How & Shine (1999) present information on the ecology, reproductive biology, and diet of *N. calonotos*. *Neelaps calonotos* has a very restricted distribution and is mostly found on the Swan Coastal Plain between Mandurah and Lancelin (see discussion). Records from further north near Port Denison, Arrowsmith and Eneabba suggest it has a much broader distribution. Systematic or targeted fauna surveys to determine the full distributional extent of *N. calonotos* on the Swan Coastal Plain and adjoining Geraldton Sandplains bioregions would greatly improve data used to determine conservation status, particularly in poorly surveyed larger conservation reserves such as Yalgorup, Nambung, Lesueur, and Stockyard Gully National Parks.

Disclosures

The authors declare no conflicts of interest.

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Supplementary Data

Supplementary data:

Appendix (XLSX):

<https://doi.org/10.25573/data.21980903>

Appendix (CSV):

<https://doi.org/10.25573/data.21980915>

Supplementary Figures:

<https://doi.org/10.25573/data.21980963>

APPENDIX CAPTION. Material (all prefixes omitted) examined in this study including GenBank accession numbers. Under the species column: H indicates holotype, L lectotype, PL paralectotype. Abbreviations are: AM Australian Museum, MAGNT Museum and Art Gallery of the Northern Territory, MNHN Muséum National d'Histoire Naturelle, SAMA South Australian Museum, Adelaide, WAM Western Australian Museum, NSW New South Wales, NT Northern Territory, QLD Queensland, SA South Australia, WA Western Australia. Mor. indicates specimens examined as follows: *morphology only, **phylogeny and morphology, ***phylogeny only and ****reliable photo or field observation only. Under the sex column Juv. indicates unsexed juvenile.

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