Zootaxa 3946 (3): 301–330
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3946.3.1
http://zoobank.org/urn:lsid:zoobank.org:pub:91C0214A-7A3D-4DEC-9D24-7B10928AC127

Molecular and morphological assessment of *Delma australis* Kluge (Squamata: Pygopodidae), with a description of a new species from the biodiversity 'hotspot' of southwestern Western Australia

BRAD MARYAN[1,2,7], IAN G. BRENNAN[3,4], MARK ADAMS[5,6] & KEN P. APLIN[2]

[1]*Biologic Environmental Survey, 50B Angove Street, North Perth, Western Australia 6006, AUSTRALIA.*
E-mail: Lerista.2@internode.on.net
[2]*Research Associate, Department of Terrestrial Zoology, Western Australian Museum, 49 Kew Street, Welshpool, Western Australia 6106, AUSTRALIA.*
[3]*Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA*
[4]*Evolution, Ecology and Genetics, Research School of Biology, The Australian National University, Canberra, ACT 0200, AUSTRALIA* [5]*Evolutionary Biology Unit, South Australian Museum, North Terrace, Adelaide, South Australia 5000, AUSTRALIA*
[6]*Australian Centre for Evolutionary Biology and Biodiversity, University of Adelaide, Adelaide, South Australia 5000, AUSTRALIA*
[7]*Corresponding author*

Abstract

The Australian pygopodid lizard genus *Delma* is characterised by morphologically conservative but genetically divergent lineages and species. An initial assessment of molecular and morphological variation in *Delma australis* Kluge, 1974 throughout its main distribution in Western and South Australia reveals at least two undescribed species that are presently included under this epithet. Here we describe the most distinctive and easily diagnosed taxon of these, *D. hebesa* **sp. nov.**, from the proteaceous scrub and mallee heath on the south coast sandplains of southwestern Western Australia. We also foreshadow the need for an expanded genetic framework to assist in unequivocally diagnosing additional candidate species in *D. australis*, which is redescribed herein and shown to be monophyletic for those specimens sampled, albeit displaying geographic variation in a range of molecular and morphological characters. *Delma hebesa* **sp. nov.** differs from all other described *Delma* species, including regional populations of *D. australis*, by a combination of molecular genetic markers, colouration and scalation. Based on phylogenetic affinities and shared morphologies, a *D. australis* species-group is proposed to accommodate *D. australis*, *D. torquata* and the new species described herein. The addition of another new vertebrate species from southwestern Western Australia, recognised globally as a biodiversity 'hotspot', underlines our lack of understanding of genetic diversity and evolutionary histories in this biodiverse region.

Key words: Esperance Plains, heath, *Delma hebesa* **sp. nov.**, endemism, taxonomy, DNA divergence, allozyme electrophoresis

Introduction

There are currently 43 described species of pygopodid lizards known from Australia (Wilson & Swan 2013; Maryan *et al.* 2013a, 2013b). The most diverse genus is *Delma* Gray, 1831 which was last comprehensively revised by Kluge (1974) who described eight new species including *D. australis*. Since that time, several additional species and subspecies have been described (Shea 1987; Storr 1987; Shea 1991; Maryan *et al.* 2007), bringing the current tally to 21 species. In addition, a molecular phylogenetic study of pygopodid lizards has also provided an evolutionary framework for the genus and its relatives (Jennings *et al.* 2003). Despite these advances, knowledge of the taxonomy of the morphologically conservative genus *Delma* is far from complete (Shea 1987; Aplin & Smith 2001).

Delma australis as currently circumscribed is widespread across southern Australia, inhabiting a variety of semi-arid to arid habitats in Western Australia (W.A.), South Australia (S.A.), Victoria (Vic.) and New South Wales (N.S.W.) (Kluge 1974; Ehmann 1992; Wilson & Swan 2013). Geographic variation has been observed in the

Accepted by A. Bauer: 16 Mar. 2015; published: 10 Apr. 2015

intensity of head patterning and in head form (Shea 1991; Aplin & Smith 2001), and several authors have suggested that *D. australis* may contain more than one species (Aplin & Smith 2001; Wilson & Swan 2013). Aplin & Smith (2001: 70) nominated a distinctive sub-population from the southern most parts of W.A. as a probable undescribed species, but the presence of morphological variation among other populations of *D. australis* hindered description of this one sub-population.

Our principal aim in this paper is to resolve the taxonomic status of the distinctive form identified in southern W.A. by Aplin and Smith (2001). To do so we use a combination of molecular and morphological evidence drawn from this region and more widely across the geographic range of *D. australis*, including material collected in proximity to Kluge's type locality at Port Lincoln in S.A. Our results confirm the presence of a second species in southern W.A. which we herein describe and name. In addition, our genetic and morphological analyses identify geographic variation among the remaining populations of *D. australis*. However, further sampling of these populations is required to determine whether or not the variation is taxonomically significant.

Material and methods

Liver samples of those specimens with tissues subsampled for our DNA and allozyme analyses are stored at -70ºC at the Western Australian Museum (WAM) and Evolutionary Biology Unit the Australian Biological Tissue Collection, South Australian Museum, Adelaide (SAMA).

DNA analysis. Genomic DNA was isolated from ethanol-preserved liver samples, via Qiagen DNeasy Tissue Kit (Qiagen) following standard manufacturer's protocol. Mitochondrial (mtDNA) and nuclear (nDNA) loci were amplified by Polymerase chain reaction (PCR). Our molecular dataset consisted of two mitochondrial (16S, ND2) and four nuclear markers (RAG1, MXRA5, DYNLL1, C-mos), reflecting the increased phylogenetic resolution provided by multi-locus, mito-nuclear datasets (Fisher-Reid & Wiens 2011). Primers used for PCR amplification and sequencing are listed in Table 1. Standard 25 μL PCR reactions utilized; distilled H_2O, 5x Taqmaster PCR enhancer, 10x PCR Buffer, deoxynucleotides, forward and reverse primers, Taq polymerase, and genomic DNA, and were carried out on an Eppendorf Nexus gradient thermocycler. Thermocycler amplification programs followed a standard protocol with varying annealing temperatures, relative to the loci and primers; initial denaturation period (95°C, 120 sec) followed by 34 cycles at 95°C (30 s), 48°C (35 s) annealing, and 72°C (150 s) extension. Amplified PCR products were visualized using 1.5% agarose electrophoresis, purified via Agencourt AMPure magnetic bead system (Agencourt Bioscience), and stored in a refrigerator at 4°C until sequenced. We preformed cycle sequencing via BigDye Terminator v3.1 Cycle Sequencing kit using purified PCR product as a template, and sequencing product was purified using Agencourt CleanSeq magnetic bead system (Agencourt Bioscience). Amplified product was sequenced in both forward and reverse directions using an ABI 3730 XL sequencer, to allow for identification of polymorphic sites.

All sequences were aligned by eye, and protein-coding loci were translated to amino acid sequence to maintain proper reading frames and avoid premature stop codons. Transfer RNA (tRNA) secondary structure was addressed and aligned by eye for consistency. Mitochondrial genes were analysed together because of shared evolutionary history as the result of physical linkage. Although trees produced for the combined mitochondrial genes and each nuclear locus exhibited varying degrees of support, the topologies are largely compatible, with no instances of strong conflict. Recognizing congruence between mitochondrial and nuclear datasets, all loci were concatenated into a single mito-nuclear dataset which produced a well-supported evolutionary hypothesis. Final aligned sequences stretched 5,574 bp (16S–796, ND2–1480, DYNLL1–1056, MXRA5–793, RAG1–1071, C-mos–378) respectively. We used maximum likelihood (ML) and Bayesian inference (BI) methods to test for conflict between topologies and support values between analytical programs. ML and BI results returned largely concordant topologies, with comparable Bayesian posterior probability (BPP) and bootstrap support (BSS) values across all datasets. We used the Akaike Information Criterion in jModeltest 2 (Guindon & Gascuel 2003; Darriba *et al.* 2012) to identify the most accurate models of evolution for each gene and codon position (Table 2).

We used the CIPRES Science Gateway *VERSUS*3.3 (Miller *et al.* 2010) as a portal for running all sequenced-based phylogenetic analyses. We used RAxML 8.0 (Stamatakis 2014) for ML analyses, and divided the mito-nuclear dataset into seven partitions; the mitochondrial into three — ND2, tRNA, and 16S; and the nuclear into four — DYNLL1, MXRA5, RAG1, and C-mos. When analysed independently, individual loci were not partitioned

by codon position because of RAxML's limits on evolutionary models, and both individual and concatenated datasets were instead analyzed under GTR+I+Γ. Topology estimates used 100 independent tree searches, and 5000 bootstrap replicates to retrieve support values.

TABLE 1. Primers used for PCR amplification and sequencing.

Gene	Name	Sequence	Source
ND2	MetF1 L4437	5'- AAGCTTTCGGGCCCATACC -3'	Macey *et al*. 1997
	ND2F17	5'-TGACAAAAAATTGCNCC-3'	Macey *et al*. 2000
	TRPR3 H5540	5'-TTTAGGGCTTTGAAGGC-3'	Macey *et al*. 1997
	CO1R1	5'-AGRGTGCCAATGTCTTTGTGRTT-3'	Macey *et al*. 1997
16S	16ScL2189	5'-GTMGGCCTAAAAGCAGCCAC-3'	Reeder 1995
	16SbH2920	5'-GCGCTGTTATCCCTAGGGTAACTTG-3'	Reeder 1995
RAG1	RAG1 396	5'-TCTGAATGGAAATTCAAGCTGTT-3'	Groth & Barrowclough 1999
	RAG1 F700	5'-GGAGACATGGACACAATCCATCCTAC-3'	Bauer *et al*. 2007
	RAG1 R700	5'-TTTGTACTGAGATGGATCTTTTTGCA-3'	Bauer *et al*. 2007
	RAG1 397	5'-GATGCTGCCTCGGTCGGCCACCTTT-3'	Groth & Barrowclough 1999
MXRA5	MXRA5 PF2	5'-AAYATTTTGGCAAAAGTCCGWGGRA-3'	This study
	MXRA5 PR2	5'-GCTTKGGTCTYYTGAACCTATTTGG-3'	This study
DYNLL1	DYNLL1 ex1.F	5'-TGATCAAGAATGCGGATATGTCTGAG-3'	Fujita *et al.* 2010
	DYNLL1 F312	5'-CCCATGAGYGACTGAAGCAAC-3'	This study
	DYNLL1 R1224	5'-TCAAACCACCTCAGTAACTTGCT-3'	This study
	DYNLL1 ex2 R	5'-TCTTCCCACAATACAGTGCCAAGTAG-3'	Fujita *et al.* 2010
C-mos	Cmos G73	5'-GCGGTAAAGCAGGTGAAGAAA-3'	Saint *et al*. 1998
	Cmos G74	5'-GTMGGCCTAAAAGCAGCCAC-3'	Saint *et al*. 1998

TABLE 2. Models of best-fit for data partitioning as determined by AIC in JModeltest.

Gene	Model applied
ND2	
1st position	GTR+I+Γ
2nd position	GTR+I+Γ
3rd position	GTR+Γ
16S	GTR+I+Γ
RAG1	
1st position	HKY+Γ
2nd position	GTR+I+Γ
3rd position	GTR+Γ
MXRA5	
1st position	GTR+I+Γ
2nd position	GTR+Γ
3rd position	GTR+Γ
DYNLL1	GTR+Γ
C-mos	
1st position	GTR+Γ
2nd position	GTR+Γ
3rd position	GTR+Γ

BI analyses were performed using MrBayes 3.2 (Huelsenbeck & Ronquist 2001; Ronquist *et al.* 2012). The mitochondrial dataset was divided into six partitions — ND2, ND2 codons (1st, 2nd, 3rd), tRNA, and 16S; and the nuclear dataset into 13 partitions, each gene receiving 4 partitions (whole locus, three codon positions), with the exception of the non-protein coding nuclear intron DYNLL1 (unpartitioned). Three *versus* six partitions for mtDNA and four *versus* thirteen partitions for nDNA returned identical topologies and did not significantly disrupt

BPP support values. We executed two parallel (two heated and two cold chain) runs for 200 million generations sampled every 1000 generations, with sampling from the first 20 million generations discarded as burn-in.

Allozyme analysis. Allozyme electrophoresis of liver homogenates was undertaken as described in Maryan *et al.* (2013a) and Adams *et al.* (2014). Allozyme genotypes were able to be assigned for the following enzymes: ACON, ADH, AK, CA, DIA, ENOL, EST, FDP, FUM, GAPD, GDA, GDH, GLO, GOT, GPD, GPI, GUK, IDH, LAP, LDH, MDH, ME, MPL, NDPK, NP, PEPA, PEPB, PEPD, 6PGD, PGK, PGM, PK, SOD, SORDH, TPI and UGPP. Enzyme abbreviations are presented in Richardson *et al.* (1986), while enzyme and allozyme nomenclature follow Hammer *et al.* (2007). The details of the 48 individuals screened are presented in the Appendix. Although no frozen tissues of *D. torquata* Kluge were available for the allozyme study, we did include exemplars of the outgroup species *D. butleri* Storr, *D. fraseri* Gray and *D. tincta* De Vis in our tree-based analysis.

We followed the same general methodology as used in previous studies of *Delma* and *Aprasia* (Maryan *et al.* 2007, 2013a, 2013b) in analysing the allozyme data using both individual-based (Principal Coordinates Analysis: PCO) and taxon-based (Neighbour-joining network) assessments of genetic affinities. All procedural details of how these analyses were implemented are presented in these studies and elsewhere (e.g. Hammer *et al.* 2007; Adams *et al.* 2014).

Morphological analysis. We measured and counted meristic features in 34 individuals of the putative new species and 97 specimens of the closely related species, *D. australis*, from Western and South Australia, the latter selected on the basis of preservational condition, whether or not a tissue sample had been genotyped and for geographic coverage (Appendix and type lists in Taxonomy section). All specimens are from the collections of the Western Australian Museum, Perth (WAM) and South Australian Museum, Adelaide (SAMA). Sex of individuals was determined by visual inspection of everted hemipenes in males, presence of eggs in heavily gravid females, or internal examination of gonads.

Head scale definitions for supraciliary, parietal, occipital and upper temporal scales follow those used by Shea (1987), and for rostral, supranasal, postnasal, prefrontal, frontal, supraloreal, loreal, supraocular, labial and mental scales follow those used by Storr *et al.* (1990). All head scales are labelled in Fig. 6A, B. Linear measurements and meristic counts follow those used by Kluge (1974).

For the purpose of this study the following linear measurements reported in millimetres (mm) were taken with digital calipers or plastic ruler: snout-vent length (SVL) measured from tip of snout to vent, tail length (TL) measured from tip of tail to vent and including both potentially original and regenerated tails (see further comments below), head depth (HD) measured from dorsal surface of head and ventral surface of throat at point immediately behind eye, head length (HL) measured from tip of snout to posterior margin of ear, head width (HW) measured from a point between the ears, hindlimb length (HLL) measured from junction of limb flap with body to distal tip of flap, mouth length (ML) measured from tip of snout to extreme angle of mouth (determined by probe of calipers under the upper lip and moving posteriorly), rostral length (RL) measured from midline anterior to posterior point of scale, rostral width (RW) measured across from lateral extremities of scale, snout length (SL) measured from tip of snout to anterior margin of transparent spectacle and eye width (EW) horizontal distance measured from anterior to posterior extremities of transparent spectacle (measurement not including the circumocular granules). Three meristic counts were taken: number of hindlimb scales (HLS) counted from distal extreme and origin with body, number of midbody scale rows (MSR) counted completely midway around body and number of ventrals (VE) counted from immediately behind mental scale to vent. Specimens preserved in a circular or twisted position were straightened on a flat surface when measured for snout-vent and tail length.

We exclude tail length from our summary descriptive statistics and analyses, as the majority of tails in specimens were either recently broken or obviously regenerated, as indicated by a clear break in colouration. X-rays are necessary to reliably distinguish between original and fully regenerated tails in pygopodid lizards (G. Shea, pers. comm.) and these were not taken during this study. For the formal descriptions, we provide only tail length (TL), for the longest TL/SVL recorded in each species.

For statistical analysis, we subdivided the total sample into four populations: 1) the putative new species from southern W.A., as defined *a priori* by its distinctive head form and colour pattern; 2) *D. australis* from remaining areas of W.A.; 3) *D. australis* from S.A. with the exception of specimens from localities in the Murray-Darling River catchments (henceforth 'the Riverina'); and 4) *D. australis* from the Riverina. As will be described in the Results, each of populations 2 and 3 contain significant genetic variation and both may be composite samples, either of the same two species or of different species in each case. While subdivision of these samples is clearly

desirable, there are at present too few genotyped individuals of each group to support statistical analysis of morphological variation. Accordingly, the samples are left as composites and diagnosis of the putative new species is made against each of the regional populations. In addition, diagnosis is made against the holotype of *D. australis* which comes from Port Lincoln in South Australia and is the only previously named form in this group of Delmas.

For each of the regional samples, we used T-tests (alpha = 0.05) to test for significant sexual dimorphism in the individual body, head and limb measurements and in the meristic scale counts; these were calculated without prior assumption of equal variances. We then used single factor Analysis of Variance (ANOVA; alpha = 0.05) to test for any significant differences among the four regional populations in any measurement or count. Where significant sexual dimorphism was present in any one of the four populations, the ANOVA was conducted separately on each sex.

Otherwise the ANOVA was conducted on combined-sex samples. Before conducting each ANOVA, we tested for equality of variances using 95% Bonferroni Confidence Intervals for Standard Deviations and Levene's test (alpha = 0.05), as implemented in Minitab vers. 17.1.0. ANOVA was conducted only if there was no significant contrast in variance among the four populations. Where the overall ANOVA was significant, we used Tukey's post-hoc test (alpha = 0.05) to determine which populations differed significantly from each other. Bivariate plots were used to identify potentially diagnostic combinations of measurements and scale counts. All statistical and graphical operations were implemented in Minitab vers. 17.1.0.

Results

DNA analysis. Four individuals of the putative new species, three *D. torquata*, and eleven *D. australis*, in addition to three outgroup *D. concinna* (Kluge) and six *D. butleri* were genotyped for all six loci, and sequences generated have been deposited in Genbank (accession numbers): ND2 (KP851394–KP851426), 16S KP851427–KP851456), RAG1 (KP851227–KP851299), MXRA5 (KP851300–KP851363), DYNLL1 (KP851364–KP851393), C-mos (KP851198–KP851226). An additional five specimens of the putative new species (WAM R129674, WAM R131902, WAM R144237, WAM R154234, WAM R156978) were identified by the mitochondrial marker ND2, but were not sequenced for all loci, and so were excluded from analyses.

Phylogenetic analyses of mtDNA and nDNA assessed individually and as a concatenated dataset support the paraphyly of *D. australis sensu lato* with respect to the morphologically similar *D. torquata* (Fig. 1). Additionally, there is high support in the mito-nuclear dataset (100/100) for the monophyly of the putative new species, *D. torquata*, and remaining *D. australis* in Western and South Australia (Fig. 1). The putative new species genotyped for the intron DYNLL1 (n = 4) are molecularly diagnosable by a fifteen base-pair insertion, followed closely by another three base-pair insertion near the beginning of the intronal sequence. Excluding samples of the putative new species, the remaining sequences of *D. australis* are divided between two sub-lineages, each of which includes samples from Western and South Australia but with a geographic segregation that for convenience will be termed 'southern' (= generally more peripheral) *versus* 'northern' (= more inland) (Fig. 1; Appendix).

Allozyme analysis. The primary allozyme dataset for this study comprised the inferred genotypes for 48 *D. australis sensu lato* at 49 presumptive allozyme loci. The following loci were monomorphic: *Adh2, Ak, Gapd, Gda, Gdh, Got1, Got2, Lap, Mdh1, Np, Pk and Ugpp*. Data for the 37 variable loci are summarised in Table 3 as allozyme frequencies by locus for each final lineage. An initial PCO on all individuals (Fig. 2) clearly demonstrated the presence of three primary genetic lineages, all diagnosable by fixed differences at multiple loci (Table 4). As predicted by our DNA datasets, the first PCO dimension unequivocally separated the putative new species from all other individuals referable to *D. australis* (reflecting a minimum of nine fixed allozyme differences: Tables 3 and 4). Importantly, the second PCO dimension assigned all remaining *D. australis* into one of two discrete genetic groups that are diagnosable by fixed differences at two loci (*Ldh1* and *Ndpk1*: Table 3). Only two individuals of *D. australis* are currently characterised for both DNA and allozymes but in each case these show a concordance between the 'southern' and 'northern' attributions from each analysis (Fig. 1).

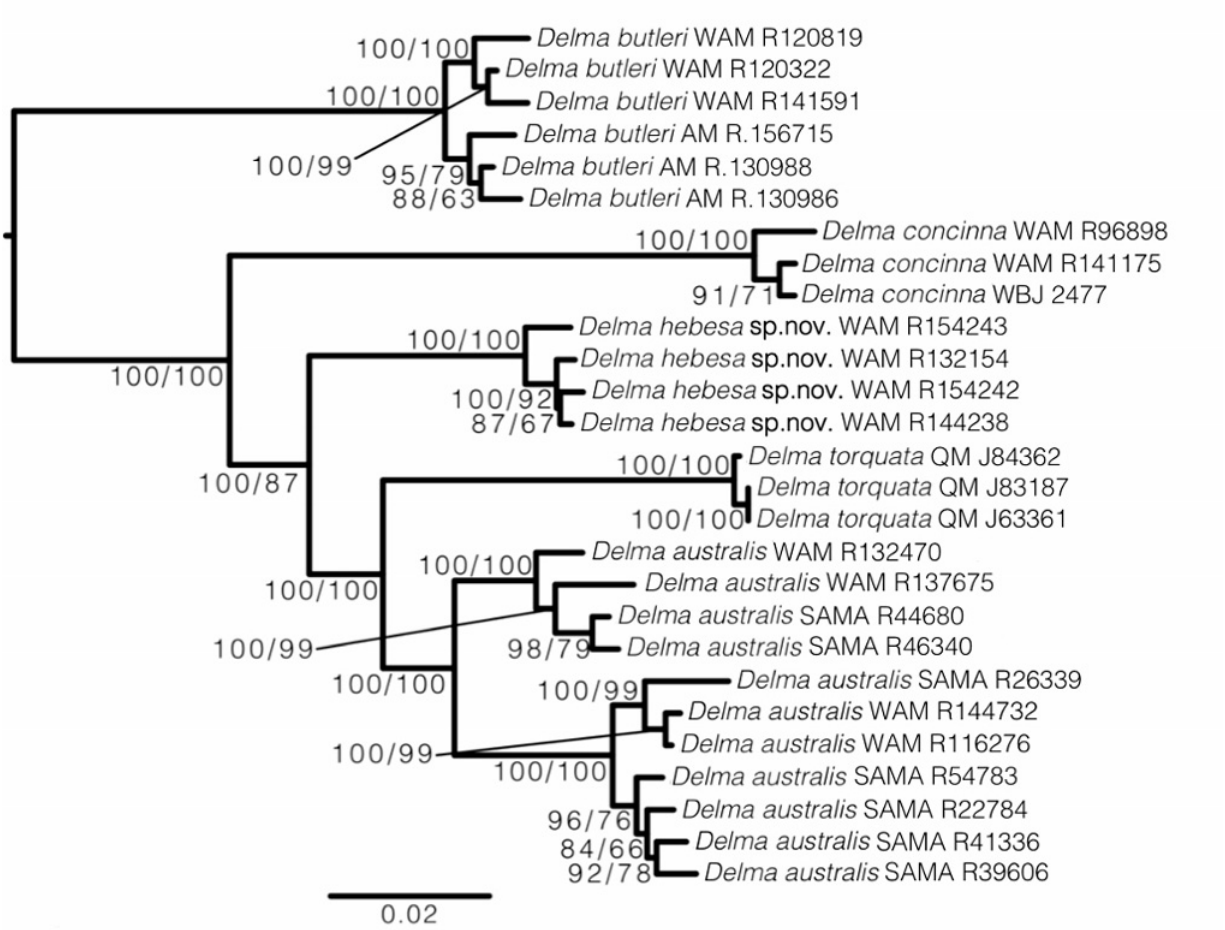

FIGURE 1. Maximum likelihood tree based on the combined mitochondrial (ND2 and flanking tRNAs, 16S) and nuclear genes (RAG1, MXRA5, DYNLL1, C-mos) showing relationships among the *D. australis* species-group, and the outgroup species *D. butleri* and *D. concinna*. This tree highlights the paraphyly of *D. australis* sensu lato, with respect to *D. torquata*, and identifies *D. hebesa* **sp. nov.** as sister taxa to a *D. australis* + *D. torquata* clade. Values indicated at branches are Bayesian posterior probabilities/ maximum likelihood bootstrap support.

Follow up PCOs on each of the three primary genetic clusters (analyses not presented) found no evidence of strong genetic sub-structure within either the putative new species or *D. australis* 'southern', but did contain a suggestion of genetic differentiation among the various widely separated sampled populations of *D. australis* 'northern'. However, sampling of this genetic group is currently too limited (n = 11 overall, with most putative diagnosable lineages comprising only 1–4 individuals) to support any further analysis or conclusions. A neighbour-joining network assessing the genetic affinities of our three primary genetic lineages in comparison to three other species of *Delma* is presented in Figure 3. Concordant with the DNA-based phylogenetic tree, this analysis supports the sister relationships of both the 'southern' and 'northern' lineages within *D. australis* and of the putative new species and *D. australis*.

Morphological analysis. The putative new species from southern W.A. displays significant sexual dimorphism in four variables (Tables 5 and 6). Females average larger values and attain higher maxima for SVL and VE, whereas males average larger values and attain higher maxima for HLL and HLS. For all variables there is broad overlap in values between the sexes. The W.A. population of *D. australis* also displays significant sexual dimorphism in four variables (Tables 5 and 6). Females average larger values and attain higher maxima for SVL, VE and EW. Males average larger values and attain higher maxima for HLL. There is broad overlap in values between the sexes for all variables. South Australian populations of *D. australis* exclusive of those from the Riverina are sexually dimorphic in only two variables (Tables 5 and 6). Females average higher counts and attain higher maxima for VE. Males average larger values and attain higher maxima for HLL. The Riverina sample *D. australis* contains too few females to test for sexual dimorphism (Table 5).

TABLE 3. Allozyme frequencies at all variable loci for the three genetic lineages identified by PCO in *D. australis* sensu lato. For polymorphic loci, the frequencies of all but the rarest allele is expressed as a percentage and shown as a superscript. Sample sizes are given in brackets for each lineage. Loci displaying fixed differences between lineages (allowing a cumulative 10% tolerance for shared alleles, as advocated by Maryan *et al.* 2013a) are asterisked.

Locus	*D. australis* 'southern' (N = 28)	*D. australis* 'northern' (N = 11)	*D. hebesa* **sp. nov.** (N = 9)
*Acon1**	$a^{88}\,c^{11}\,b$	$a^{91}\,b$	c
Acon2	$b^{84}\,a^{11}\,d^{4}\,e$	$b^{85}\,c^{10}\,e$	b
*Acp1**	$d^{96}\,b$	$d^{91}\,a$	c
*Acp2**	b	$c^{67}\,b$	a
Acyc	$b^{91}\,c^{5}\,a^{2}\,d$	b	$b^{94}\,d$
Ada	$b^{96}\,a^{2}\,d$	$b^{91}\,c$	$b^{89}\,d$
Adh1	$a^{98}\,c^{2}$	$a^{80}\,b^{20}$	a
Ca	b	$b^{95}\,a^{5}$	b
Dia	$c^{34}\,e^{30}\,h^{10}\,a^{7}\,g^{4}\,d^{4}\,i^{4}\,j^{3}\,b^{2}\,f$	$f^{45}\,d^{32}\,i^{18}\,c$	$i^{44}\,k^{28}\,e^{22}\,c$
Enol	$b^{96}\,a^{2}\,c$	b	b
Est	$a^{95}\,c$	$a^{91}\,c$	$a^{94}\,b$
Fdp	a	a	$b^{78}\,a$
Fum	$a^{98}\,c$	a	$a^{56}\,b$
Glo	$b^{83}\,a^{13}\,c$	$d^{55}\,b$	b
Gpd	$b^{98}\,a$	$b^{95}\,a$	$b^{94}\,a$
Gpi	a	a	a
Guk	$c^{48}\,d^{40}\,a^{6}\,b^{4}\,e$	$b^{60}\,d^{35}\,c$	d
Idh1	b	b	$b^{94}\,a$
*Idh2**	b	$b^{95}\,a$	a
*Ldh1**	a	b	b
Ldh2	$a^{98}\,b$	a	a
Mdh2	b	b	$b^{94}\,a$
Me	$a^{96}\,b$	a	a
*Mpi**	$b^{52}\,a^{43}\,d^{3}\,e$	$b^{35}\,c^{25}\,e^{15}\,a^{10}\,f^{10}\,g$	c
*Ndpk1**	$b^{95}\,e^{3}\,c$	$e^{46}\,a^{27}\,c^{18}\,d$	a
Ndpk2	$b^{95}\,a$	b	b
*PepA1**	$c^{95}\,b^{2}\,e^{2}\,d$	$c^{86}\,d$	a
*PepA2**	$d^{94}\,b^{2}\,c^{2}\,a$	d	e
*PepB**	$c^{77}\,g^{12}\,a$	$e^{55}\,g^{15}\,f^{10}\,h$	$e^{89}\,f$
PepD	$i^{89}\,f^{7}\,c$	$f^{52}\,c^{23}\,i^{22}\,d^{8}\,b^{5}\,h^{5}\,e$	$d^{44}\,a^{22}\,i^{17}\,g^{6}\,f^{6}\,j$
6Pgd	$b^{48}\,c^{46}\,a^{2}\,d^{2}\,f$	$c^{70}\,b^{15}\,a$	$c^{94}\,e$
Pgk	$b^{98}\,a$	b	b
*Pgm1**	$b^{66}\,c^{29}\,e$	$b^{86}\,a$	d
Pgm2	$a^{98}\,c$	$a^{77}\,b^{18}\,c$	a
Sod	$a^{96}\,b$	a	a
Sordh	$b^{84}\,a$	$b^{95}\,c$	b
*Tpi**	b	b	a

TABLE 4. Pairwise genetic distance values among species and lineages of *Delma* based on the allozyme data. Lower left-hand triangle = number of loci displaying a fixed allozyme difference; upper right-hand triangle = unbiased Nei distance.

Taxon	*D. australis* 'southern'	*D. australis* 'northern'	*D. hebesa* **sp. nov.**	*D. tincta*	*D. fraseri*	*D. butleri*
D. australis 'southern'	-	0.09	0.34	0.58	0.61	0.53
D. australis 'northern'	2	-	0.26	0.59	0.61	0.54
D. hebesa **sp. nov.**	11	8	-	0.55	0.61	0.48
D. tincta	20	18	16	-	0.45	0.38
D. fraseri	21	20	18	15	-	0.37
D. butleri	17	19	16	13	14	-

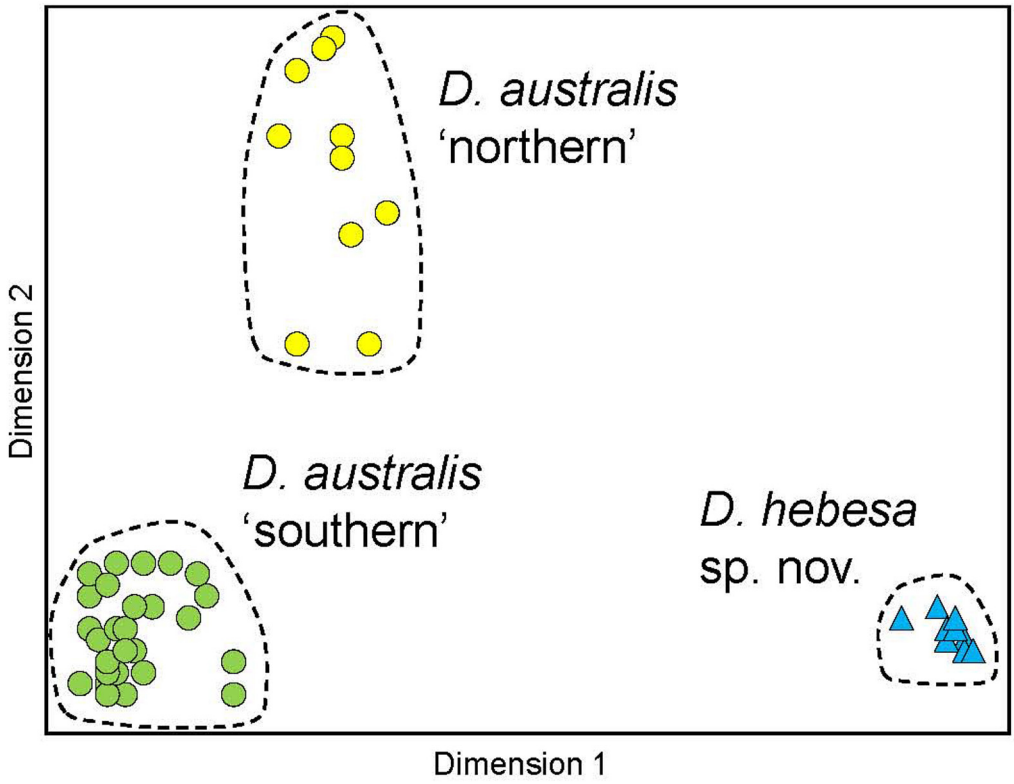

FIGURE 2. Principal Coordinates Analysis of the 48 individuals surveyed in the allozyme study. The relative PCO scores have been plotted for the first and second dimensions, which individually explained 37% and 12% respectively of the total multivariate variation present in 47 dimensions. Taxon symbols as for Figure 8.

Based on these results, inter-populational contrasts were carried out separately for each sex for SVL, VE, HLL, HLS and EW and on combined-sex samples for all other variables. Significantly unequal variances were present in two cases only—the female sample for SVL and the male sample for HLS. ANOVA results (Table 7) identify overall significant inter-populational variation in SVL (males; females not tested), VE (both sexes), HLL (males only), HLS (females; males not tested), HD (sexes pooled), ML (sexes pooled), SL (sexes pooled), RL (sexes pooled), and RW (sexes pooled). EW alone showed no significant contrasts (sexes tested separately).

Tukey pairwise comparisons (Table 7) identify the following significant contrasts between the putative new species and the geographically proximate W.A. population of *D. australis*: higher average values for VE (both sexes, tested separately); higher average values for HLL in males; higher average values for HLS in females (males show an equivalent degree of contrast but unequal variances prohibit significance testing); and higher average values for RW (sexes pooled).

A bivariate plot of VE by HLS (Fig. 4) provides the best illustration of morphological distinction between these geographically adjacent populations. Less pronounced contrasts are observed in head proportions and rostral proportions. As illustrated in Figure 5, relative head depth does not give as clear segregation between the species as anticipated from observation of living animals. This may reflect variable distortion of head shape as a result of fixation. Tukey pairwise comparisons also identify significant contrasts between the southern W.A. and S.A. populations of *D. australis* (Table 6), most notably in VE (both sexes), ML (sexes pooled), SL (sexes pooled), RL

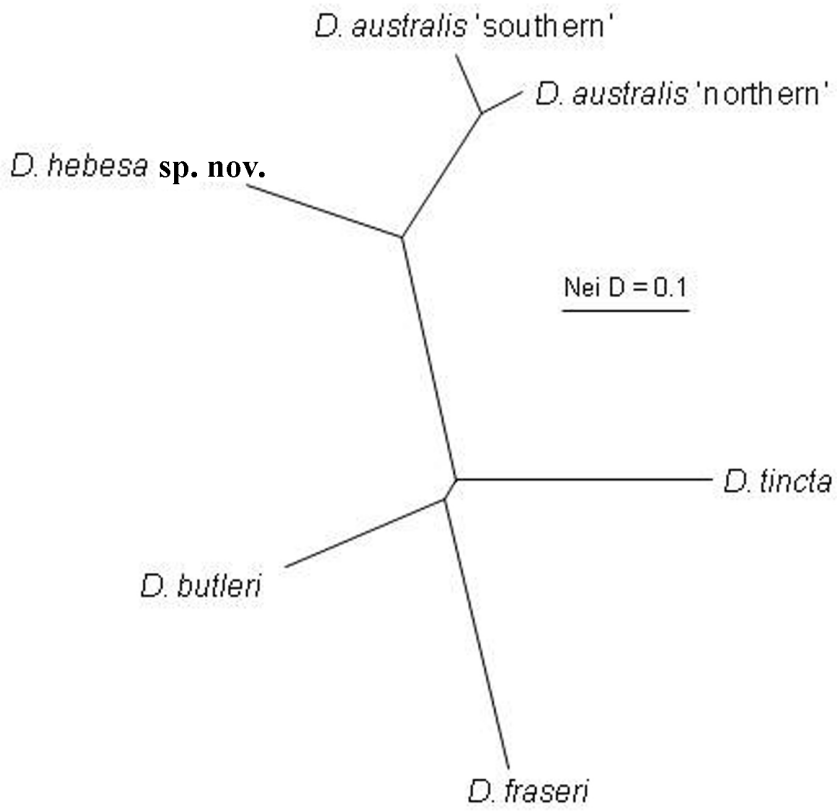

FIGURE 3. Unrooted neighbour-joining network among six species or lineages of *Delma*, based on the pairwise matrix of unbiased Nei's distances presented in Table 4.

TABLE 5. Descriptive statistics for *D. hebesa* **sp. nov.** and each of three regional populations of *D. australis***.** Values shown are the sample size (N), the mean, ± one standard deviation (S.D.), and the minimum (Min.) and maximum (Max.) values. See Material and Methods for abbreviations of measurements and counts.

D. hebesa **sp. nov.**						
	Sex	N	Mean	S.D.	Min.	Max.
SVL	♂	19	61.1	6.5	49	75
	♀	15	69.5	6.5	51	79
HD	♂	19	2.8	0.4	1.5	3.4
	♀	15	2.8	0.3	2.3	3.5
HL	♂	19	6.8	0.7	5.5	7.9
	♀	15	7.1	0.5	5.8	7.7
HW	♂	19	4.2	0.5	2.8	4.9
	♀	15	4.4	0.4	3.7	5.0
HLL	♂	19	3.3	0.3	2.4	3.7
	♀	15	2.1	0.2	1.5	2.4

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TABLE 5. (Continued)

	Sex	N	Mean	S.D.	Min.	Max.
ML	♂	19	4.6	0.5	3.6	5.8
	♀	15	4.7	0.4	3.6	5.4
RL	♂	19	0.9	0.1	0.7	1.1
	♀	15	0.9	0.1	0.7	1.0
RW	♂	19	1.4	0.1	1.2	1.7
	♀	15	1.3	0.1	1.2	1.6
SL	♂	19	2.8	0.2	2.3	3.4
	♀	15	2.8	0.3	2.3	3.4
EW	♂	19	1.2	0.0	1.0	1.3
	♀	15	1.2	0.1	0.9	1.4
HLS	♂	19	10.1	0.4	9	11
	♀	15	9.6	0.7	8	10
MSR	♂	19	18.0	0.2	18	19
	♀	15	18.0	0.3	17	19
VE	♂	19	76.8	1.9	73	81
	♀	15	85.5	3.8	78	92
Southwest W.A. *D. australis* (* = sex unknown)						
	Sex	N	Mean	S.D.	Min.	Max.
SVL	♂	19	58.4	7.0	45	69
	♀	22	66.7	5.2	60	78
	*	2	42.0	11.3	34	50
HD	♂	19	3.1	0.4	2.3	4.1
	♀	22	3.1	0.3	2.4	3.7
	*	2	2.0	0.2	1.8	2.1
HL	♂	19	6.5	0.7	4.9	7.8
	♀	22	7.0	0.5	6.0	7.8
	*	2	5.0	0.7	4.5	5.6
HW	♂	19	4.3	0.6	3.2	5.8
	♀	22	4.5	0.4	3.7	5.5
	*	2	3.1	0.4	2.8	3.4
HLL	♂	19	2.6	0.4	1.5	3.3
	♀	22	1.9	0.2	1.5	2.3
	*	2	1.3	0.3	1.1	1.5
ML	♂	19	4.5	0.3	4.0	5.0
	♀	22	4.7	0.4	3.9	5.5
	*	2	3.6	0.1	3.5	3.7
RL	♂	19	0.8	0.1	0.6	1.0
	♀	22	0.9	0.0	0.7	1.0
	*	2	0.6	0.1	0.5	0.7
RW	♂	19	1.2	0.1	0.9	1.5
	♀	22	1.2	0.0	1.1	1.4
	*	2	0.8	0.2	0.6	1.0

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TABLE 5. (Continued)

	Sex	N	Mean	S.D.	Min.	Max.
SL	♂	19	2.7	0.3	2.1	3.3
	♀	22	2.8	0.2	2.3	3.2
	*	2	2.2	0.1	2.1	2.3
EW	♂	19	1.1	0.0	1.0	1.2
	♀	22	1.2	0.0	1.1	1.5
	*	2	1.0	0.1	0.9	1.1
HLS	♂	19	6.2	1.1	5	9
	♀	22	5.9	1.3	3	8
	*	2	6	1.4	5	7
MSR	♂	19	18.5	0.9	18	20
	♀	22	18.6	0.9	18	20
	*	2	18	0.0	18	18
VE	♂	19	73.5	3.0	68	78
	♀	22	79.6	3.3	72	85
	*	2	77.5	0.7	77	78
S.A. *D. australis* except 'Riverina'						
	Sex	N	Mean	S.D	Min.	Max.
SVL	♂	21	65.0	5.5	55	72
	♀	22	70.1	11.0	53	93
HD	♂	21	3.1	0.4	2.1	4.0
	♀	22	3.1	0.5	2.0	4.2
HL	♂	21	6.9	0.6	6.0	8.2
	♀	22	6.8	0.9	5.2	9.0
HW	♂	21	4.5	0.4	3.9	5.5
	♀	22	4.5	0.6	3.5	6.1
HLL	♂	21	3.0	0.4	1.6	3.8
	♀	22	2.0	0.4	1.3	2.9
ML	♂	21	5.5	0.4	4.7	6.6
	♀	22	5.5	0.8	4.4	7.5
RL	♂	21	0.9	0.1	0.7	1.2
	♀	22	0.9	0.1	0.6	1.3
RW	♂	21	1.3	0.1	1.0	1.7
	♀	22	1.3	0.1	1.1	1.7
SL	♂	21	2.9	0.2	2.5	3.6
	♀	22	2.9	0.4	2.3	4.0
EW	♂	21	1.2	0.1	1.0	1.5
	♀	22	1.2	0.1	0.9	1.6
HLS	♂	21	5.9	1.4	4	10
	♀	22	5.3	1.0	3	7
MSR	♂	21	18.3	0.8	17	20
	♀	22	18.2	0.7	18	20
VE	♂	21	77.9	3.7	71	86
	♀	21	87.6	2.5	84	92

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TABLE 5. (Continued)

D. australis 'Riverina'						
	Sex	N	Mean	S.D.	Min.	Max.
SVL	♂	9	66.1	5.7	55	75
	♀	2	66.0	11.3	58	74
HD	♂	9	3.2	0.3	2.8	3.8
	♀	2	3.0	0.1	2.9	3.1
HL	♂	9	7.1	0.5	6.5	8.1
	♀	2	7.0	1.2	6.2	7.8
HW	♂	9	4.6	0.4	4.1	5.3
	♀	2	4.1	0.6	3.7	4.6
HLL	♂	9	3.1	0.3	2.5	3.6
	♀	2	2.0	0.1	1.9	2.1
ML	♂	9	5.8	0.2	5.3	6.1
	♀	2	5.1	0.5	4.7	5.4
RL	♂	9	0.9	0.1	0.8	1.1
	♀	2	0.9	0.0	0.9	1.0
RW	♂	9	1.4	0.1	1.1	1.6
	♀	2	1.3	0.2	1.2	1.5
SL	♂	9	2.9	0.2	2.6	3.2
	♀	2	2.9	0.3	2.7	3.1
EW	♂	9	1.2	0.1	1.1	1.4
	♀	2	1.2	0.0	1.1	1.2
HLS	♂	9	6.1	0.3	6	7
	♀	2	5.5	0.7	5	6
MSR	♂	9	18.0	0.00	18	18
	♀	2	18.0	0.00	18	18
VE	♂	9	78.5	2.6	74	82
	♀	2	84.0	0.0	84	84

(sexes pooled), and RW (sexes pooled). However, the presence of two genetic groups within each of these regional samples cautions against any taxonomic interpretation of these differences. The holotype of *D. australis* (WAM R27359) is an adult male. Its mensural and meristic attributes generally fall within the range of both the putative new species and the S.A. regional sample currently attributed to *D. australis* (population 3). However, the holotype's ventral count of 71 falls below the documented range for the putative new species (73–81) but within the range for population 3 (68–78).

Consistent differences in body colouration and head pattern are present between the putative new species and southwestern Australian populations of *D. australis*: *D. australis* have a more distinctly patterned head and forebody that contrasts sharply with an overall brownish body and tail, while the putative new species has a weakly patterned head and overall greyish head and tail (Figs. 7C, D; 10A, B). The head patterning in southwestern Australian *D. australis* typically comprises strong, dark narrow bars (sometimes reticulating) on the head (including lower labials), nape and lateral scales of the forebody. By contrast, the putative new species has a uniform greyish head with weakly developed dark bars or smudges present on the lower labials and lateral scales of the forebody. A further point of distinction concerns the patterning of the lower labials: in *D. australis* the sutures between the mental and anterior two lower labial scales typically fall within unpigmented areas, while in the putative new species these sutures typically fall within pigmented bars (Figs. 11A, B). These differences are most pronounced in immature animals but remain apparent in life at all stages of maturity. The differences in body

colouration are less apparent in preserved specimens due to the leaching of colours in ethanol. Also more obvious in life is a difference in body texture between the two species, consisting of a more polished appearance in all populations of *D. australis*, compared to a dull matt-textured appearance in the putative new species.

TABLE 6. Results of T-tests for sexual dimorphism in each of *D. hebesa* **sp. nov.** and regional populations of *D. australis*. See Material and Methods for abbreviations of measurements and counts. Results that satisfy the $p < 0.05$ criterion for statistical significance are in bold.

	D. hebesa **sp. nov.** 19♂, 15♀	Southwest W.A. *D. australis* 19♂, 22♀	S.A. *D. australis* 21♂, 22♀
SVL	**t=3.7, df=31**	**t=4.21, df=38**	t=1.96, df=40
	p <0.001	**p <0.001**	p=0.059
HD	t=0.28, df=31	t=0.06, df=38	t=0.18, df=40
	p=0.781	p=0.95	p=0.856
HL	t=1.11, df=31	**t=2.15, df=38**	t=0.47, df=40
	p=0.274	**p=0.04**	p=0.644
HW	t=1.43, df=31	t=1.12, df=38	t=0.38, df=40
	p=0.162	p=0.273	p=0.704
HLL	**t=11.04, df=31**	**t=5.74, df=38**	**t=7.24, df=40**
	p <0.001	**p <0.001**	**p <0.001**
ML	t=0.39, df=31	t=1.55, df=38	t=0.09, df=40
	p=0.697	p=0.13	p=0.926
RL	t=0.72, df=31	t=1.55, df=38	t=0.38, df=40
	p=0.479	p=0.13	p=0.704
RW	t=1.02, df=31	t=0.43, df=38	t=0.27, df=40
	p=0.315	p=0.672	p=0.789
SL	t=0.61, df=31	**t=1.73, df=38**	t=0.18, df=40
	p=0.544	**p=0.094**	p=0.857
EW	t=0.81, df=31	**t=2.28, df=38**	t=0.18, df=40
	p=0.428	**p=0.028**	p=0.857
HLS	**t=2.32, df=31**	t=0.81, df=38	t=1.68, df=40
	p=0.03	p=0.42	p=0.102
VE	**t=8.07, df=31**	**t=6.06, df=38**	**t=9.79, df=40**
	p <0.001	**p <0.001**	**p <0.001**

TABLE 7. Results of ANOVA for inter-populational differences between *D. hebesa* **sp. nov.** and each of three regional populations of *D. australis*. See Material and Methods for abbreviations of measurements and counts. Results that satisfy the $p < 0.05$ criterion for statistical significance are in bold. Populations are numbered as follows: 1 = Southwest W.A. *D. australis*; 2 = S.A. *D. australis* (except Riverina); 3 = Riverina *D. australis*; 4 = *D. hebesa* **sp. nov.** UV = unequal variances precluded ANOVA.

Populations	ANOVA RESULTS			Tukey's Pairwise Comparisons between populations					
Males only	F	df	p	2 *versus* 1	3 *versus* 1	4 *versus* 1	3 *versus* 2	4 *versus* 2	4 *versus* 3
SVL (1–4)	4.98	3	**0.004**	**0.009**	**0.019**	0.543	0.971	0.228	0.221
EW (1–4)	1.58	3	0.203	0.4	0.22	0.439	0.887	1	0.833
HLL (1–4)	7.14	3	**> 0.001**	0.087	0.082	**> 0.001**	0.944	0.11	0.602
HLS (1–4)	UV								
VE (1–4)	9.07	3	**> 0.001**	**> 0.001**	**0.001**	**0.007**	0.958	0.651	0.5
Females only									
SVL (1,4)	2.06	1	0.16			0.16			
EW (1,2,4)	0.09	2	0.912	0.994		0.943		0.909	
HLL (1,2,4)	1.67	2	0.197	0.532		0.177		0.683	
HLS (1,2,4)	77.23	2	**> 0.001**	0.133		**> 0.001**		**> 0.001**	
VE (1,2,4)	36.19	2	**> 0.001**	**> 0.001**		**> 0.001**		0.127	
Pooled sexes									
HD (1–4)	3.39	3	**0.02**	0.92	0.843	0.115	0.975	**0.026**	0.105
HL (1–4)	1.33	3	0.268	0.767	0.325	0.439	0.698	0.934	0.909
HW (1–4)	1.482	3	0.223	0.204	0.293	0.613	0.793	0.068	0.114
ML (1–4)	26.21	3	**> 0.001**	**> 0.001**	**> 0.001**	0.984	0.818	**> 0.001**	**> 0.001**
SL (1–4)	3.61	3	**0.015**	**0.013**	0.193	0.602	1	0.346	0.673
RL (1–4)	4.35	3	**0.006**	**0.007**	0.081	0.543	0.99	0.303	0.465
RW (1–4)	7.83	3	**> 0.001**	**0.007**	**0.022**	**> 0.001**	0.849	0.541	1

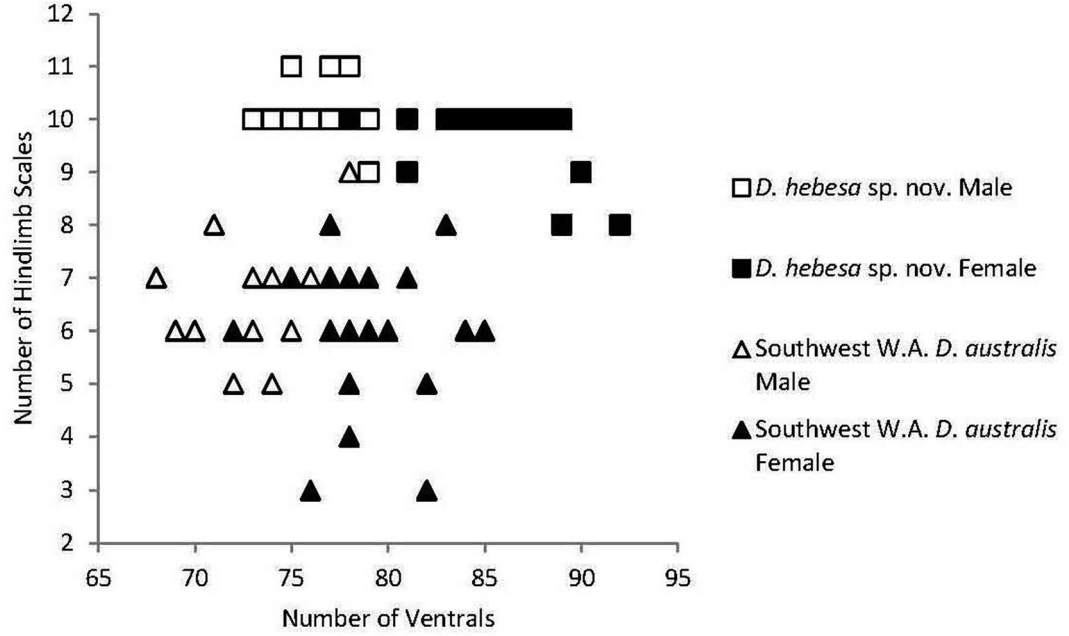

FIGURE 4. Bivariate plot of number of ventral scales *versus* number of hindlimb scales in males and females of each of the southwest W.A. population of *D. australis* and *D. hebesa* **sp. nov.**

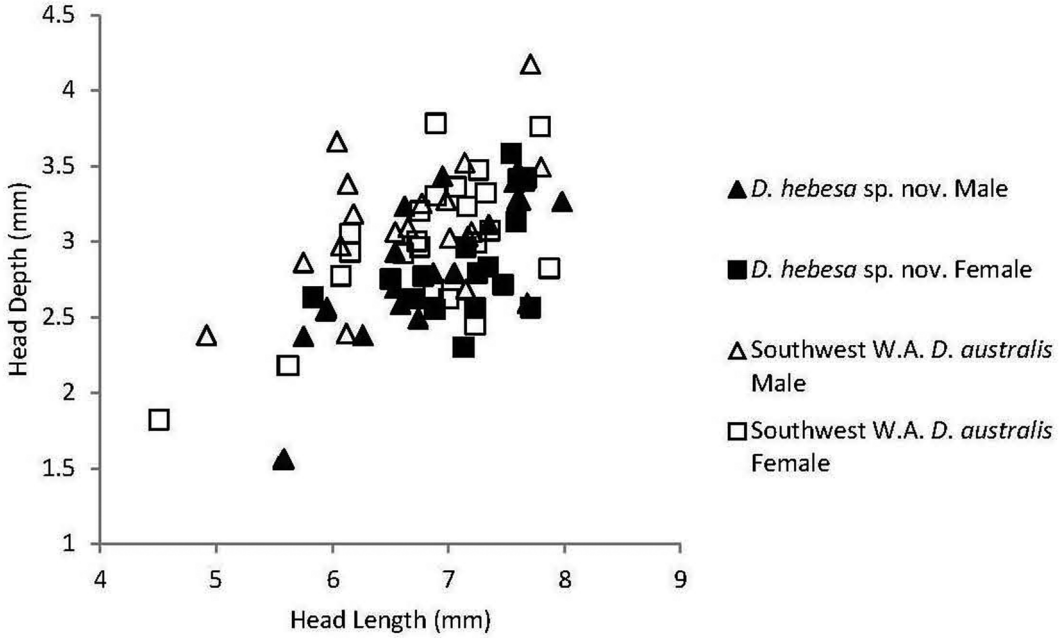

FIGURE 5. Bivariate plot of measurements of head length *versus* head depth in males and females of each of the southwest W.A. population of *D. australis* and *D. hebesa* **sp. nov.**

Taxonomic conclusions. Each of the three datasets examined here – molecular sequences, allozymes and morphological characters—support the conclusion that the southern-most W.A. populations previously referred to *D. australis* represent a distinct species. The molecular sequence dataset clearly differentiates this population from the sampled *D. australis* and from another closely related taxon, *D. torquata* of eastern Australia. Furthermore, the recovered molecular phylogeny points to a possible sibling relationship between *D. australis* and *D. torquata* to the exclusion of the new species (Fig. 1). The allozyme dataset shows a total of nine fixed differences between *D. australis* and the new species (Tables 3 and 4). This is compelling evidence for a long historical separation of two

evolutionary lineages and for a lack of geographically widespread, contemporary gene flow between the two lineages, despite their geographic proximity in the southwestern corner of Western Australia. While further sampling may reveal localized loci of genetic interaction or narrow hybrid zones, the genetic consequences of any such interaction clearly are insufficient to cause breakdown of the genetic identities of these evolutionary distinct species. The morphological dataset documents consistent differences between the new species and all regional populations of *D. australis* including the geographically proximate populations in W.A. Although the two species are essentially similar in body size and head scalation (Table 5), there are consistent differences in body colouration, scalation texture, head pattern and body meristics (ventral and hindlimb scale counts) (Figs. 7, 10, 11) that distinguish the two species.

Below we provide a brief generic description for *Delma*, a composite description of the *D. australis* species-group, redescribe *D. australis*, and describe *D. hebesa* **sp. nov.** from the south coast sandplains and interspersed granitic outcrops of southwestern Western Australia.

Taxonomy

Pygopodidae Boulenger, 1884

Delma Gray, 1831

Type species: *Delma fraseri* Gray, 1831, by monotypy.

Diagnosis. *Delma* differs from all other pygopodid lizard genera in possessing the following combination of characters: head scales, including the parietals, enlarged and symmetrical; anterior nasal scales nearly always in contact; first pair of lower labials in contact behind mental scale; nostril usually bordered by more than two scales (except in some *D. impar*); external ear opening large; 20 or fewer midbody scale rows; dorsal and ventral scales smooth; precloacal pores absent; tail about three times as long as body (except in the *D. australis* species-group).

Delma australis species-group

Diagnosis. Based on the molecular analysis of Jennings *et al.* (2003) and this study we formally propose a *D. australis* species-group, currently comprising *D. australis*, *D. hebesa* **sp. nov.** and *D. torquata*. The morphological characteristics of this species-group are relatively small-size (SVL to 93 mm); ventral scales usually not markedly larger than adjacent lateral scales (enlarged in some *D. torquata*); one pair of supranasal scales; modally 16 or 18 midbody scales (occasionally 17, 19 or 20); loreal scale row usually interrupted by a ventral extension of supraloreal scale that contacts upper labials. For comparisons of ventral body scale size between *D. australis* and *D. fraseri* see Kluge (1974: 9).

Delma australis Kluge, 1974

Marble-faced Delma

(Figs. 6, 7, 11)

Holotype: WAM R27359, male**,** Port Lincoln (34º44'S 135º52'E), South Australia, Australia, collected by G.M. Storr, 19 October 1966.

Paratype: WAM R24528, female, 37 km ENE of Wirrula (32º22'S 134º54'E), South Australia, Australia.

Other material examined: A full list of material examined is provided at the end of the paper.

Revised diagnosis. A small species of *Delma* (SVL to 93 mm) with: ventral scales not markedly larger than adjacent lateral scales; one pair of supranasals; typically 18 midbody scales; 68–92 ventral scales (males average 76.3, females 83.5); six upper labials typically with fourth below eye; loreal scale row typically interrupted by a ventral extension of supraloreal scale that contacts upper labials; modally 5–7 hindlimb scales in both sexes; strong dark variegations on upper surface of head; narrow dark bars on side of head (extending onto labial scales), nape

and forebody. This revised diagnosis is essentially unchanged from those provided by previous authors (Kluge 1974; Storr *et al.* 1990; Shea 1991), despite the exclusion herein of *D. hebesa* **sp. nov.**

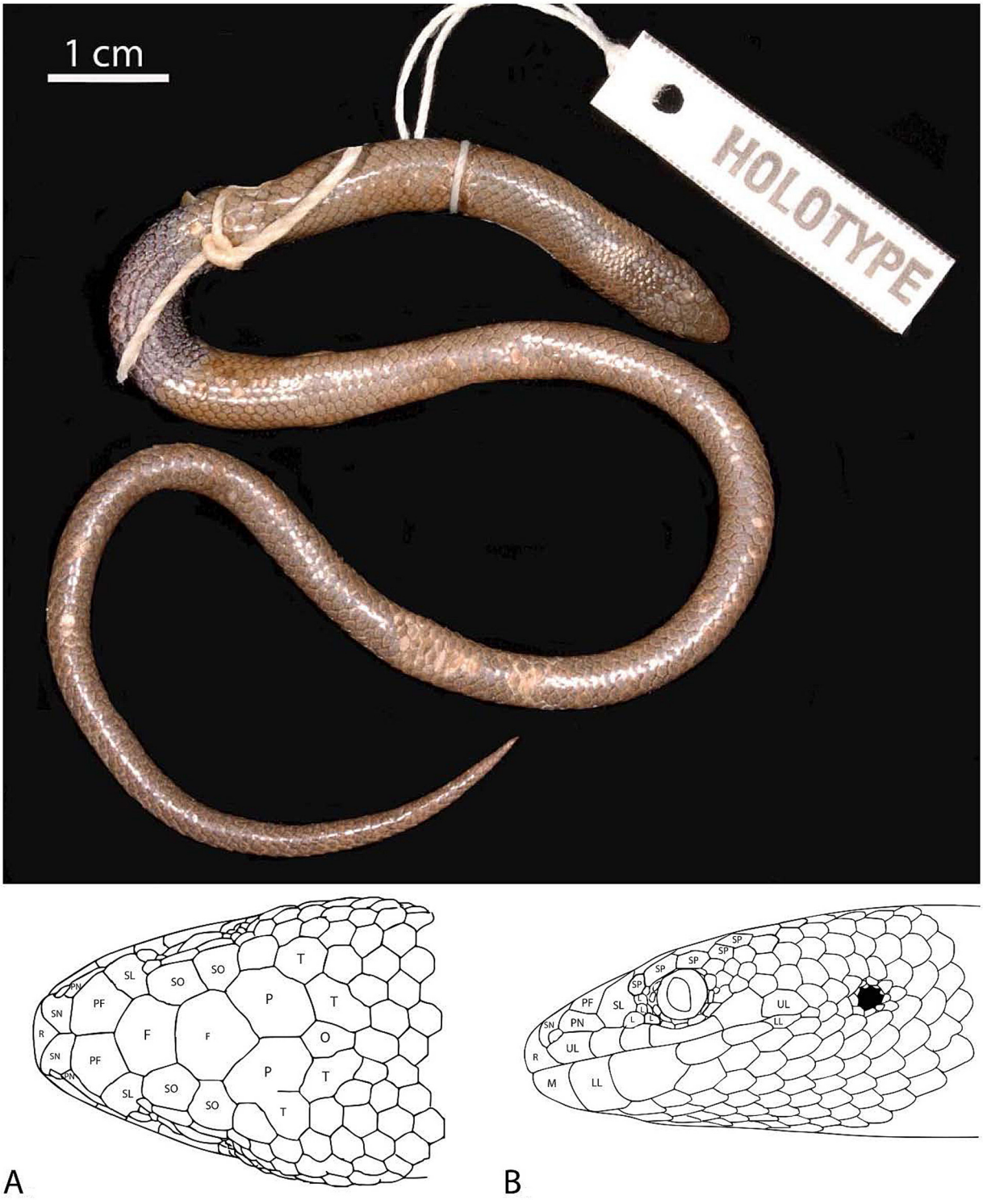

FIGURE 6. Preserved holotype WAM R27359 of *D. australis* and head scalation in (A) dorsal and (B) lateral views; F = frontals, L = loreals, LL = lower labials, M = mental, O = occipital, P = parietals, PN = postnasals, PF = prefrontals, R = rostral, SP = supraciliaries, SL = supraloreals, SN = supranasals, SO = supraoculars, UL = upper labials, T = upper temporals.

FIGURE 7. Adult *D. australis* photographed in life from (A) Cowell, Eyre Peninsula, South Australia, (B) 14 km NW of Coober Pedy, South Australia, (C) Buningonia Spring, Coolgardie Goldfields bioregion, Western Australia, (D) 30 km NW of Salmon Gums, Mallee bioregion, Western Australia, (E) Rat Island, Houtman Abrolhos, Western Australia, (F) 22 km WSW of Hamelin Homestead, Shark Bay and (G) Cape Range, North West Cape, Western Australia, showing the variation in body colouration and intensity of head pattern (images–A, B, C, E, F, G: B. Maryan, D: R. Lloyd).

Delma australis differs from the closely related *D. torquata* of southeastern Queensland in: larger adult size (SVL to 93 mm *versus* to 63 mm); three precloacal scales (*versus* two); the fourth upper labial scale typically below the eye (*versus* typically the third below the eye); modally 18 midbody scale rows (*versus* 16); and dark variegations or narrow bars (if present) on head, neck and forebody (*versus* broad dark bands). It differs from *D. hebesa* **sp. nov.** in: hindlimb scale counts in both sexes modally 5–7 (*versus* > 9); body colour brownish on head and tail (*versus* greyish on head and tail); head, nape and lateral scales of forebody with strong dark variegations or narrow barring (*versus* weak variegations); dark barring on head typically extends ventrally onto the chin and throat (*versus* indistinct dark bars or smudges present on the lower labials); and dark pigment on rostral and lower labials not aligned with sutures (*versus* dark smudges positioned over sutures between rostral and lower labials).

Description of holotype (Fig. 6). Measurements (in mm) and meristic values, as determined during this study: SVL 65, HD 3.5, HL 7.5, HW 5.0, HLL 3.2, ML 4.7, RL 1.0, RW 1.7, SL 2.8, EW 1.3, HLS 10, MSR 19, VE 71.

Head short and blunt, narrowing very gradually forward of eyes, of equal width to body posteriorly; obvious tympanic aperture, indicated by round opening directly posterior to corner of mouth; snout blunt and rounded in dorsal profile, rounded in lateral profile; body moderately robust of equal width and round in cross-section; hindlimbs visible as well-developed elongate, rounded flaps adpressed to body at lateral extremes of vent; tail relatively short, tapering very gradually distally to a pointed tip.

Head scales smooth, non-imbricate and heterogeneous; large rostral blunt anteriorly, wider than long, with obtuse apex projecting between supranasals; one pair of supranasals in broad contact, angled backwards posteromedially behind rostral and in short contact with first upper labial anterior to nostril; nostril positioned on posterior junction of supranasal with first upper labial and postnasal; one postnasal, much wider than high and narrower posteriorly, slightly angled posteroventrally and in broad contact with second upper labial; prefrontals symmetrical, in broad contact; one supraloreal, much higher than wide and in broad contact with second upper

labial; four loreals, the anterior most much larger; five supraciliaries, first and fourth the smallest, second the largest; two supraoculars, first slightly larger and wider than second; two frontals, the posterior most slightly wider and larger; two parietals, one on left side fused (partial suture evident) with upper temporal; occipital present; two upper temporals; six upper labials, fourth the widest and positioned below eye, third the smallest and fifth the highest; five lower labials, second the largest and widest, fifth the smallest; mental wider than long with suture starting half-way along the first upper labial. General form of head and details of scalation illustrated in Fig. 6A, B.

Body scales smooth, non-imbricate, homogeneous, and arranged in parallel longitudinal rows; ventral scales only very marginally wider than the adjacent lateral body scales; three precloacal scales.

After more than 40 years in preservative (Fig. 6), the holotype is light brown on the dorsal surface with a slightly darker head bearing dense black variegations. Lower labials whitish with distinct black bars positioned centrally on first to third lower labial scales. Black bars continue on to corner of mouth, around ear opening and on the lateral scales of forebody. A faint dark bar is also present within mental scale. Dark bars extend ventrally onto chin and throat. Ventral surface under head and along body is whitish.

Variation in measurements and scalation. Table 5 presents the means, standard deviations and ranges of the characters counted and measured for each of the three geographic populations of *D. australis*, as defined in Material and Methods. Data are presented separately for each sex. Most head scales in *D. australis* display minimal intraspecific variation. However, the condition of the supraloreal (described as a prefrontal by Shea 1991) extending ventrally to contact the upper labials, thereby interrupting the row of small loreals, is variable in this species. The most common condition is contact with the upper labials, as noted by Storr *et al.* (1990: 115), Shea (1991: 115) and shown in Figure 6B. Our examination of 97 specimens of *D. australis* from Western and South Australia recorded the supraloreal (sometimes the postnasal and prefrontal) contacting the upper labials in over 70% of specimens. The opposing condition of no contact between the supraloreal and upper labial scales was mostly caused by the presence of either one large loreal (sometimes with elongate postnasal), or two smaller loreals extending continuously from the postnasal to the subocular upper labial.

We observed 0–5 loreals in this species, with one loreal being the typical condition, as reported by Storr *et al.* (1990). Most specimens had six upper labials with the 4th below the eye but we saw occasional individuals with five (3rd below the eye) or seven (5th below the eye), mostly unilaterally. Over 70% of specimens examined had the typical 18 midbody scales. Most others had 20 midbody scales, with occasional counts of 17 and 19, corresponding to the range given by Storr *et al.* (1990). One specimen (SAMA R36487) has extensively fused head scales, with the supraloreal and prefrontal fused on the left side only and only four upper labials on the right side. The longest tail measured was 162 mm (245% of SVL) on WAM R112667. Kluge (1974: 78) and Storr *et al.* (1990: 115) illustrate the general form of the head and details of scalation of *D. australis*.

Variation in colouration and pattern. Shea (1991: 72–73) documented geographic variation in the intensity of the head pattern in this species in South Australia. He distinguished and mapped a 'patterned' form from the southern half and northwest of the state (Fig. 7A; Cogger 2014: 388) and an 'unpatterned' form from the western Lake Eyre drainage (Fig. 7B). The holotype and 15 paratypes of *D. australis* from the Eyre Peninsula (south of the Gawler Ranges) in South Australia (Kluge 1974) are considered representative of the 'patterned' form (Shea 1991: Fig. 1) in having strong dark variegations on the head, although the pattern is reduced, particularly laterally, in a few specimens. The 'patterned' form is contiguous and similar to populations in northwestern Victoria and southwestern New South Wales (Swan *et al.* 2004: 49; Swan & Watharow 2005: 26; Wilson & Swan 2013: 145). Kluge (1974: 78) illustrates a preserved adult male specimen (SAMA R10375) of the 'patterned' form from near Kokatha in South Australia. In addition, strongly patterned individuals of *D. australis* have been illustrated by Ehmann (1992: 87) and Henkel (2010: 141).

Western Australian populations of *D. australis* also display geographic patterning in colouration. Strongly patterned individuals with dark variegations and narrow bars on the lateral scales of forebody occur throughout the eastern Coolgardie Goldfields (Fig. 7C) and Mallee bioregions (Fig. 7D) (Thackway & Cresswell 1995). Particularly strongly patterned individuals are found on the Houtman Abrolhos (Fig. 7E), while the population found to the immediate north around Shark Bay has very reduced patterning, with some individuals almost having dark brown uniform heads (Fig. 7F), similar in many respects to the unpatterned form from South Australia. By contrast, a unique representative of the group (WAM R132470) from the North West Cape has a rich brick-red body with an intensely black head flecked with small pale spots (Fig. 7G).

Distribution and sympatry. *Delma australis* is widespread throughout the subhumid to arid areas of southern

Australia, from northwestern Victoria, and southwestern New South Wales, through most of South Australia and adjacent southern Northern Territory to southern and central west Western Australia (Wilson & Knowles 1988; Shea 1991; Swan *et al.* 2004; Wilson & Swan 2013; Fig. 8). In Western Australia, it extends north to Shark Bay (base of Peron Peninsula), Meedo Station, Weld Range, Paynes Find, Windarling Hill and Buningonia Spring, south through the Avon Wheatbelt, Mallee and Coolgardie Goldfields bioregions, and east to Cocklebiddy. There is a disjunct population on the North West Cape, represented by a single specimen from Shothole Canyon in the Cape Range (Fig. 8). Other possible outlier populations in the mid-west of Western Australia are Walyering Hill, Oakajee and near Kalbarri. Insular populations occur on Rat and Middle Islands in the Houtman Abrolhos.

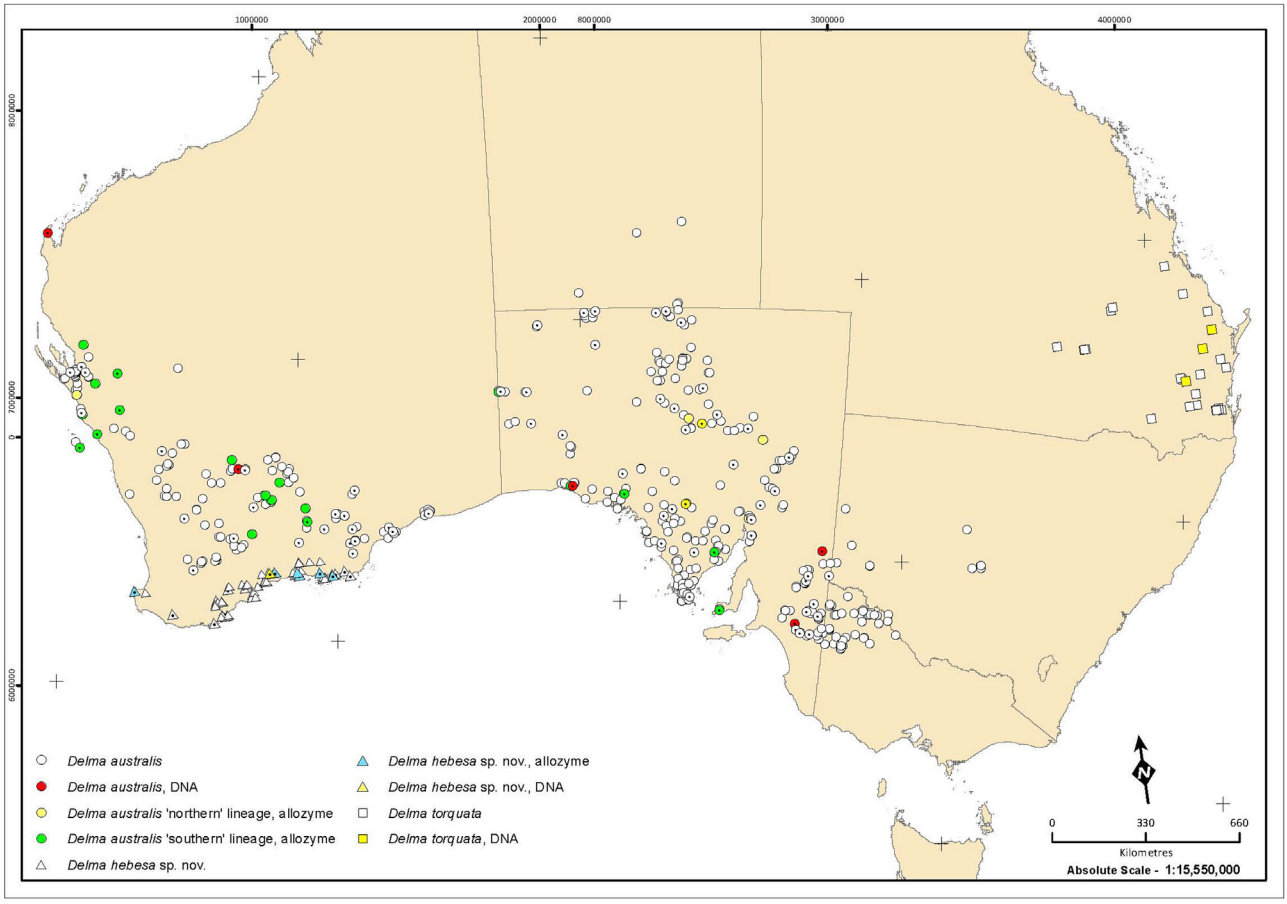

FIGURE 8. Map of Australia showing distribution of the *D. australis* species-group and specimens examined in the DNA and allozyme analyses. Specimens examined in the morphological analysis are indicated by a symbol with a central dot.

Recorded instances of sympatry involving *D. australis* include *D. butleri*, *D. fraseri*, *D. grayii* Smith, *D. nasuta* Kluge and *D. petersoni* Shea (Dell & Chapman 1981; Dell & How 1984; Chapman & Dell 1985; Shea 1991; Mckenzie *et al.* 1993; B. Maryan & G. Shea, per. obs.). For instance, in the vicinity of Poochera in South Australia, *D. australis*, *D. butleri* and *D. petersoni* have all been recorded (Shea 1991: 82). Four other species of *Delma* are recorded on the North West Cape. *Delma nasuta* and *D. tincta* are known from several localities (Maryan et al. 2007), while *D. tealei* Maryan, Aplin & Adams has been collected at Shothole Canyon and other localities on the Cape Range. *Delma butleri* is known from a single specimen collected at the Learmonth Air Weapons Range, immediately south of the Cape Range National Park.

Habitat. In northwestern Victoria and southwestern New South Wales *D. australis* mainly occupies mallee habitats with a spinifex (*Triodia*) understorey (Swan *et al.* 2004; Swan & Watharow 2005). This habitat association is repeated in South Australia where the majority of the southern and western populations are from *Triodia* or mallee habitats, or combination of both (Shea 1991). The western Lake Eyre Basin population lives on gibber plain with *Atriplex*, on watercourses lined with *Eucalyptus*, and on low, stony hills with drainage channels and *Acacia* (Shea 1991; B. Maryan, pers. obs.).

In Western Australia, *D. australis* occupies a variety of habitats growing on different soils, including mallee

and/or other *Eucalyptus* woodlands and *Acacia* with a spinifex (*Triodia* and *Plectrachne*) or shrubland understorey (Storr *et al.* 1990; Smith *et al.* 1997; Bush *et al.* 2007). The habitat at Cape Range on the North West Cape consists of a heavily dissected limestone plateau sparsely vegetated with *Triodia*, shrubs and low eucalypts; gorges within the range are more heavily vegetated (Storr & Hanlon 1980).

These diverse vegetation communities provide ample cover for *D. australis*, where most specimens have been pit-trapped, found in and under spinifex and sedge tussocks, raked from leaf litter, spoil-heaps, mats of dead vegetation and found under logs, mallee roots, rocks (including coral slabs on the Houtman Abrolhos) and rubbish, especially pieces of corrugated iron in disturbed areas adjacent to uncleared vegetation. When found in sympatry with other *Delma* species, *D. australis* tends to occur in moister microhabitats (Shea 1991; Wilson & Swan 2013). Interestingly, nocturnal observations of *D. australis* on sealed roads or tracks are rare, unlike other, larger-bodied species of *Delma.*

Remarks. Using morphology alone, Kluge (1974) recognized and assessed differences between three geographic samples of male *D. australis*: a southwestern Western Australia sample (south of 32°30'S, west of 120°E), an Eyre Peninsula of South Australia sample (south of 32°S), and a Victorian sample. He found significant mean differences in number of preorbital, preanal, hindlimb and caudal scales; as well as throat pattern and visceral pigmentation. A multivariate analysis of these six characters also revealed significant differentiation among the three regions. However, Kluge's character definitions were different to those used in this study, and were based on a very small sample size (n=3 per locality = 7, 8 and 12 respectively, with the Western Australian sample potentially including both *D. australis* and *D. hebesa* **sp. nov.**). Further studies in the laboratory and field are needed to determine whether or not the geographic sub-populations identified in each of South Australia and Western Australia correspond with the 'northern' and 'southern' groups distinguished by allozyme differences in the present study. Large gaps remain in the geographic sampling of all regional populations and the collection of additional specimens at or near potential contact zones would be particularly valuable to establish the status of the various forms.

***Delma hebesa* sp. nov.**
Heath Delma
(Figs. 9, 10, 11)

Holotype: WAM R144237, male, Bandalup Hill, Ravensthorpe Range (33º40'29"S 120º23'54"E), Western Australia, Australia, collected by R. Teale & G. Harold, 14 October 2000. Fixed in 10% formalin, stored in 70% ethanol, liver sample stored in –80ºC ultrafreezer at WAM.

Paratypes: All from Western Australia. WAM R129674, male, 3.8 km W of Kundip, (33º41'S 120º09'E); WAM R131902, female, Hellfire Bay, Cape Le Grand National Park, (34º00'15"S 122º10'20"E); WAM R132154, female, Duke of Orleans Bay, Wharton Beach, (33º56'S 122º33'E); WAM R144238, male, same details as holotype; WAM R154234, male, Kundip, (33º40'26"S 120º11'45"E); WAM R156978, male, Canal Rocks, (33º39'46"S 115º00'45"E).

Other material examined: A full list of material examined is provided at the end of the paper.

Diagnosis. A small species of *Delma* (SVL to 79 mm) with: ventral scales not markedly larger than adjacent lateral scales; one pair of supranasals; modally 18 midbody scales; modally 10 hindlimb scales in both sexes; 73–92 ventral scales (males average 76.8, females 85.5); six upper labials with fourth typically below eye; loreal scale row typically interrupted by a ventral extension of supraloreal scale that contacts upper labials; essentially unpatterned head, sometimes with weak dark variegations on sides of head and indistinct narrow bars or smudges on labial scales, nape and forebody. Diagnostic differences between *D. hebesa* **sp. nov.** and *D. australis* are listed under the foregoing species account.

Delma hebesa **sp. nov.** differs from *D. torquata* from southeastern Queensland in having a larger adult size (SVL to 79 mm *versus* to 63 mm), three precloacal scales (*versus* two), the fourth upper labial typically below the eye (*versus* typically the third below the eye), modally 18 midbody scale rows (*versus* 16) and only dark variegations (if present) on head and neck (*versus* broad dark bands).

Delma hebesa **sp. nov.** differs from all other Australian species (except *D. australis*, *D. torquata* and *D. concinna*) in having ventral scales not markedly larger than adjacent lateral scales (*versus* markedly larger).

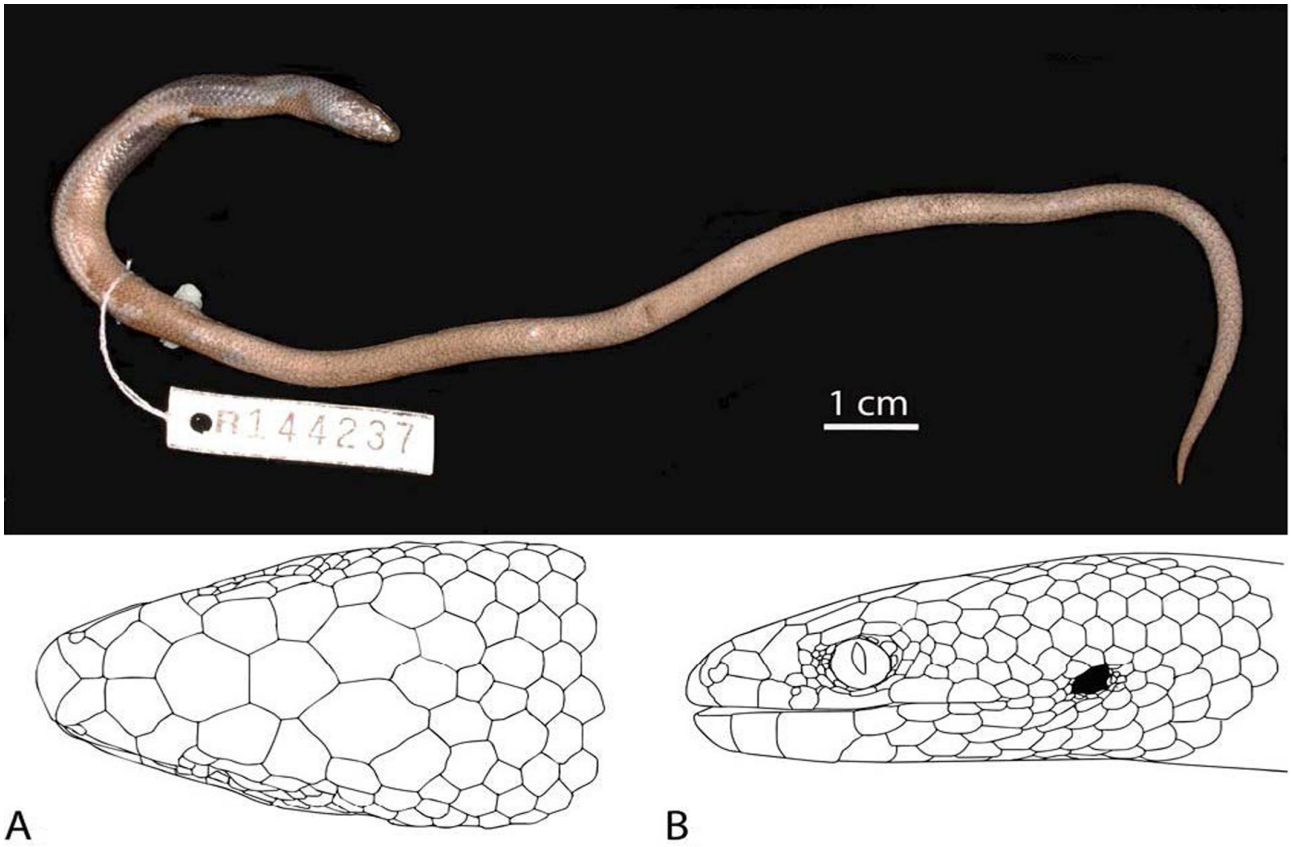

FIGURE 9. Preserved holotype WAM R144237 of *D. hebesa* **sp. nov.** and head scalation in (A) dorsal and (B) lateral views.

Delma hebesa **sp. nov.** differs from *D. fraseri* with which it occurs in sympatry (see below) in having a smaller adult size (SVL to 79 mm *versus* to 140 mm, Bush *et al.* 2007), one pair of supranasals (*versus* two pairs), modally 18 midbody scale rows (*versus* 16), ventral scales not markedly larger than adjacent lateral scales (*versus* markedly larger) and only dark variegations (if present) on head and neck (*versus* broad dark bands, often faded in adults).

Description of holotype (Fig. 9)**.** Measurements (in mm) and meristic values: SVL 57, HD 3.4, HL 6.9, HW 4.5, HLL 3.3, ML 4.9, RL 0.9, RW 1.3, SL 2.6, EW 1.1, HLS 10, MSR 18, VE 75.

Head short and narrowing gradually forward of eyes, of equal width to body posteriorly; obvious tympanic aperture, indicated by round opening posterior to corner of mouth, opening is more narrow on right side; snout moderately long and rounded in dorsal and lateral profiles; body moderately robust of equal width and round in cross-section; hindlimbs visible as well-developed elongate, rounded flaps adpressed to body at lateral extremes of vent; tail relatively short, tapering very gradually distally to a pointed tip.

Head scales smooth, non-imbricate and heterogeneous; rostral rounded anteriorly, wider than long, with obtuse apex projecting between supranasals; one pair of supranasals in broad contact, angled backwards posteromedially behind rostral and in short contact with first upper labial; nostril positioned on posterior junction of supranasal with first upper labial and postnasal; one postnasal, wider than high, angled posteroventrally and in short contact with second upper labial; prefrontals symmetrical and in broad contact; supraloreal much higher than wide, and in broad contact with second upper labial; four loreals, the anterior most slightly larger; five supraciliaries, first and fourth the smallest, second and fifth the largest; two supraoculars, first slightly larger than second; two frontals, the anterior most slightly wider and larger; two parietals, one on left side is slightly larger and longer; occipital present; two upper temporals; six upper labials, fourth the widest and positioned below eye, third the smallest, on left side a small scale intersects suture between second and third upper labial; five lower labials, second the largest and widest, fifth the smallest; mental wider than long with suture starting half-way along first upper labial. General form of head and details of scalation illustrated in Fig. 9A, B.

Body scales smooth, non-imbricate, homogeneous, and arranged in parallel longitudinal rows; ventral scales only very marginally wider than the adjacent lateral body scales; three precloacal scales.

In preservative, due to the leaching of colours in ethanol after 14 years, the holotype (Fig. 9) has lost the grey colouration on the dorsal surface which is now light brown. All other aspects of dark bars or smudges on lower labials and obscure variegations on body remained.

Colouration in life. The following description of colouration in life is based on Figs. 10A, B, 11A and field observations of *D. hebesa* **sp. nov.** from the Esperance Plains. Top of head bluish to light grey and unpatterned or with weak dark variegations. Lower labials whitish with blackish bars or smudges, centred on sutures of mental and anterior two lower labial scales, corner of mouth, grading to obscure variegations or weak bars around ear opening and on lateral scales of forebody. There is only very weak ventral extension of black bars or smudges on to chin and throat. Dorsal body surface bluish to light grey anteriorly, gradually merging to light brown body than to light grey tail. Lower flanks are slightly pinkish to reddish brown. Dorsal surface is uniform, except for some indication of obscure dark spots or variegations, particularly on some sutures of body scales. Ventral surface under head and along body whitish, with blackish variegations, becoming less pigmented under tail. The longest tail measured was 140 mm (208% of SVL) on WAM R131902.

FIGURE 10. Adult *D. hebesa* **sp. nov.** photographed in life from (A) Scaddan and (B) Mettler Lake, Western Australia (images–B. Maryan).

For comparisons of both *D. hebesa* **sp. nov.** and *D. australis* in life see Thompson & Thompson (2006: 44, 'grey morph' and 'brown morph'), Bush *et al.* (2007: 135) and Henkel (2010: 141).

Variation. Table 5 presents the means, standard deviations and ranges of the characters counted and measured for each sex of *D. hebesa* **sp. nov.** Table 8 presents the individual measurements and meristic counts for the type series of *D. hebesa* **sp. nov.** As noted in *D. australis*, the variation in the contact of the supraloreal with the upper labials and interrupting the loreal scale row or not, is similarly recorded in *D. hebesa* **sp. nov.** as the following conditions: the supraloreal contacts second upper labial on both sides (as in holotype) in WAM R129674 and WAM

R154234; it contacts second and third upper labial on both sides in WAM R131902 and WAM R144238, and is separated from upper labials by either one large loreal and an elongate postnasal or two smaller loreals in WAM R156978. One specimen (WAM R154234) has five upper labials unilaterally, with the third under eye. All the type material has 18 midbody scales and 2–4 loreals.

TABLE 8. Individual measurements (mm) and meristic counts for the type series of *D. hebesa* **sp. nov.** The holotype is marked with an asterisk.

WAM #	Sex	SVL	HD	HL	HW	HLL	ML	RL	RW	SL	EW	HLS	MSR	VE
129674	♂	61	3.2	6.6	4.3	3.1	5.2	0.9	1.5	2.8	1.2	10	18	76
131902	♀	67	2.6	6.6	3.7	2.2	5.4	0.7	1.3	2.3	1.1	10	18	84
132154	♀	78	3.4	7.6	5	2.1	5.3	1	1.4	3.2	1.3	10	18	85
144237*	♂	57	3.4	6.9	4.5	3.3	4.9	0.9	1.3	2.6	1.1	10	18	75
144238	♂	66	3.2	7.5	4.7	3.6	5.8	1	1.7	2.9	1.2	10	18	78
154234	♂	49	2.5	5.9	3.7	2.4	4.4	0.8	1.3	2.6	1.2	10	18	77
156978	♂	66	3.2	7.6	4.4	3.6	5	1	1.3	3.1	1.1	11	18	78

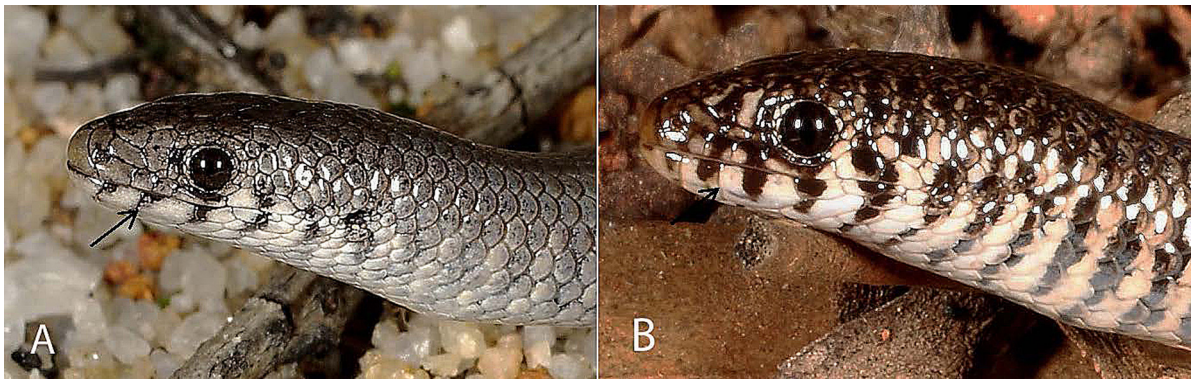

FIGURE 11. Head patterning of (A) *D. hebesa* **sp. nov.** adult from Kundip, Western Australia and (B) *D. australis* adult from Cowell, Eyre Peninsula, South Australia, and arrows indicating pigmented or clear suture on lower labials (images–B. Maryan).

Variation in colouration and pattern. Most specimens are similarly coloured to the holotype in life and in preservative. Occasional preserved individuals (e.g. WAM R131902) have more pronounced dark bars on the lower labials and lateral scales of forebody, while others (e.g. WAM R154234) are a very uniform dark grey on head, body and tail. In life, hatchlings of *D. hebesa* **sp. nov.** have a similar colour and head pattern to adults (B. Bush, pers. comm.).

Etymology. The specific name *hebesa* is derived from the Latin adjective *hebes*, meaning dull, alluding to the matt body texture, without much shine, of this species.

Distribution and sympatry. *Delma hebesa* **sp. nov.** is widespread on the Esperance Plains bioregion and patchily distributed on the Warren and southern Jarrah Forest bioregions (Thackway & Cresswell 1995) in southwestern Western Australia (Fig. 8). Records extend east to the vicinity of Thomas River and Cape Arid, west to Canal Rocks and near Busselton, and inland to Stirling Range National Park, Ongerup, Ravensthorpe Range, Scaddan and Mount Burdett.

The geographic distributions of *D. hebesa* **sp. nov.** and *D. australis* appear to be parapatric (Fig. 8). Currently the two species are known to occur within 80 km of each other in the east: WAM R91740 of *D. hebesa* **sp. nov.** from Cape Arid *versus* WAM R36229 of *D. australis* from Pine Hill and within 130 km in the west: WAM R42637 of *D. hebesa* **sp. nov.** from Ongerup *versus* WAM R12604 of *D. australis* from Wagin. Specimens from these parapatric localities do not show any indication of morphological intermediacy. The only recorded instance of sympatry involving *D. hebesa* **sp. nov.** is with *D. fraseri* (Bush 1981, 1984, as *D. australis*).

Habitat. *Delma hebesa* **sp. nov.** occupies the proteaceous scrub and mallee heath on south coast sandplains

(Beard 1990; Comer *et al.* 2001; Fig. 12). This habitat preference is exemplified of 65 records of *D. hebesa* **sp. nov.** from 18 sites, in which 79% were recorded from mallee heath (Sanders *et al.* 2012, as *D. australis*). These diverse vegetation communities provide ample cover for *D. hebesa* **sp. nov.**, where most specimens, including the type series, have been pit-trapped and raked from leaf litter, spoil-heaps, and mats of dead vegetation and inside abandoned stick-ant (*Iridomyrmex conifer* Forel) nests . It has also been found under logs, mallee roots, rocks and rubbish, especially pieces of corrugated iron in disturbed areas adjacent to uncleared heath (Bush 1981). It also occupies the granitic heath where it is occasionally found under exfoliated granite slabs (B. Maryan, pers. obs.). There are no habitat data associated with specimens from the lower southwestern corner of Western Australia (WAM R129003, WAM R156978, WAM R172507).

FIGURE 12. The habitat of *D. hebesa* **sp. nov.**, dense scrub heath on sandplain at Stirling Range National Park, Western Australia (image–B. Maryan).

Remarks. Bush (1981: 21), Wilson & Knowles (1988: 246) and Bush *et al.* (2007: 135a) illustrated *D. hebesa* **sp. nov.** as *D. australis*. Additionally, Wilson & Knowles (1988: 96) and Wilson & Swan (2013: 144) refer to *D. australis* individuals from the far southwest of range as bluish grey, a colouration feature consistent with *D. hebesa* **sp. nov.** Historically, *D. australis* has been documented as not occurring in the humid deep southwest of Western Australia (Kluge 1974; Wilson & Knowles 1988; Storr *et al.* 1990). However, there are a few records of *D. hebesa* **sp. nov.** in this area where they appear to be scarce when compared to the Esperance Plains. This apparent scarcity is documented by How *et al.* (1987), who recorded '*D. australis*' from only Two Peoples Bay in a survey of herpetofauna between Busselton and Albany.

Biological surveys conducted on the Esperance Plains to date indicate *D. hebesa* **sp. nov.** to be widespread and locally abundant in areas of suitable habitat (Chapman & Dell 1975; Bush 1985; Chapman & Newbey 1995; Sanders *et al.* 2012, as *D. australis*). Bush (1983, 1984, as *D. australis*) provides additional information on reproduction in captivity and field observations of winter aggregations of *D. hebesa* **sp. nov.** from the Esperance Plains. The Esperance Plains bioregion is a biogeographically significant area rich in endemic plants, rare ecosystems, and vulnerable and specially protected fauna (Comer *et al.* 2001). Approximately 87% of the Esperance Plains bioregion has been cleared and developed for intensive agriculture. However, much of the

remaining vegetation is afforded statutory protection, including many nature reserves and national parks (Cape Arid, Cape Le Grand, Stokes, Fitzgerald River and Stirling Range National Parks) where *D. hebesa* **sp. nov.** is known to occur.

Discussion

The present study has partially clarified the taxonomic status of *D. australis*. Our main contribution is the confirmation of a new species, *D. hebesa* **sp. nov.**, that inhabits southwestern Western Australia. This species is well-differentiated genetically from *D. australis* and other congeners, with reciprocal monophyly to close relatives on combined mtDNA and nuclear gene sequences, and >12 fixed genetic differences to *D. australis* as revealed by allozyme electrophoresis. It is also morphologically distinct from regional populations of *D. australis*; however, the two species are closely similar and apart from a clear difference in hindlimb scale count, there are few points of absolute distinction. Our DNA, allozyme and morphological analyses also provide firm indications that *D. australis* as redefined herein to exclude *D. hebesa* **sp. nov.** remains polytypic. Reflecting this, we are now working to collect and genetically characterise additional specimens from key geographic regions and morphotypic forms. This will allow us to generate the detailed genetic framework required to define how many additional candidate species are likely to be present, before ultimately assessing these for morphological diagnosability.

The geographic ranges of *D. australis* and *D. hebesa* **sp. nov.** appear to be parapatric, with current records suggesting gaps of 80–130 km between populations of the two species. This gap appears to coincide with the long and abrupt boundary between the cooler southerly Esperance Plains and drier northerly Mallee bioregions. However, considering the long interface between the two bioregions (Thackway & Cresswell 1995) and the variable nature of the transition in terms of vegetation communities and soil structures (Beard 1990), it seems likely that instances of sympatry or immediate parapatry between *D. australis* and *D. hebesa* **sp. nov.** will be found. These should be actively sought to investigate the nature and extent of genetic interactions between these species.

Southwestern Australia is recognised globally as one of the world's top 25 biodiversity hotspots (Myers *et al.* 2000), based largely on its highly diverse and endemic flora (Beard *et al.* 2000). The entire area is effectively a relatively damp 'island' refuge surrounded by oceans and desert (Hopper & Gioia 2004). 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 with several monotypic species including frogs (e.g. *Metacrinia nichollsi* (Harrison), *Myobatrachus gouldii* (Gray) and *Spicospina flammocaerulea* Roberts, Horwitz, Wardell-Johnson, Maxson & Mahony), turtles (e.g. *Pseudemydura umbrina* Siebenrock), lizards (e.g. *Hesperoedura reticulata* (Bustard)) and snakes (e.g. *Paroplocephalus atriceps* (Storr) and *Rhinoplocephalus bicolor* Müller) and species with very restricted distributions (e.g. Kay & Keogh 2012; Doughty & Oliver 2013).

Our assessment of *D. australis* adds yet another vertebrate species, *D. hebesa* **sp. nov.**, to the growing number of regional endemics. The continual documentation of endemic species resulting from the re-evaluation of previously known taxa demonstrates that we are still far from completing the inventory of the vertebrates that inhabit the highly fragmented natural habitats of southwestern Western Australia.

Acknowledgements

We are grateful to A. Heidrich for preparing the distribution map and the figures. We thank R. Lloyd for the use of his image. For allowing access to specimens at the Western Australian Museum we thank C. Stevenson (formerly), L. Umbrello and P. Doughty, and at the South Australian Museum we thank C. Kovach and M. Hutchinson. We further thank M. Hutchinson for regular discussions and his observations of *D. australis* in South Australia and for helpful comments on the manuscript. For data on collection records we thank R. Sadlier at the Australian Museum. B. Bush and P. Oliver provided helpful advice and suggestions throughout this study. Lastly, we thank Glenn Shea for his thorough and insightful comments on the draft manuscript.

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APPENDIX. Additional material examined. Unless otherwise indicated all localities are in Western Australia and South Australia, Australia. Also included in one or more of the molecular analyses are indicated (both *DNA and ^allozyme analyses; #DNA only; ^^allozymes only).

Delma australis WAM: 12604, Wagin, (33º19'S 117º21'E); 30706, 30749, 12 km E of Fraser Range, (32º02'S 122º55'E); 36229, Pine Hill, (33º18'S 123º23'E); 53461, Newman Rock, (32º07'S 123º11'E); 57909, 11.5 km NE of Charlina Rock, (32º33'S 123º26'E); 58045, Clear Streak Well, (32º29'S 122º24'E); 59745, 20 km ESE of Mount Newmont, (32º59'S 123º18'E); 66844, Coragina Rock, (32º55'S 123º30'E); 66999–00, 13 km W of Eyre Homestead, (32º15'S 126º10'E); 67369, 14 km E of Hyden, (32º27'S 119º00'E); 72505, 11.5 km NE of Buningonia Spring, (31º20'30"S 123º37'00"E); 77765, Toolina Rockhole, (32º45'05"S 124º58'50"E); 94091, 25 km NW of Toolina Rockhole, (32º35'S 124º48'E); 94092, 7 km NW of Toolina Rockhole, (32º42'30"S 124º55'00"E); ^^112665 'northern', 11.5 km NE of Buningonia Spring, (31º20'30"S 123º37'00"E); ^^112666 'southern', Ponier Rock, (32º56'S 123º30'E); 112667, Ponier Rock, (32º56'S 123º30'E); *^116276 'southern', 22 km S of Kalbarri, (27º51'S 114º10'E); 116277, 22 km S of Kalbarri, (27º51'S 114º10'E); 116744, 5 km W of Overlander Roadhouse, (26º24'S 114º25'E); 117102, 23 km ESE of Overlander Roadhouse, (26º36'S 114º32'E); ^^117388 'southern', 25 km S of Woolgangie, (31º23'16"S 120º33'13"E); 117389, Toomey Hills, (31º33'26"S 119º51'38"E); ^^119002 'southern', 4 km SSE of Boorabbin, (31º14'12"S 120º19'50"E); ^^120886 'southern', Nerren Nerren Station, (27º00'21"S 114º47'57"E); 122450, 24 km WSW of Hamelin Homestead, (26º31'21"S 114º00'09"E); ^^122613 'southern', 6 km SW of Meedo Homestead, (25º42'38"S 114º35'58"E); ^^123583 'northern', 53 km NNW of Kalbarri, (27º15'33"S 114º04'03"E); 126345, Aurora Range, (30º21'16"S 119º42'09"E); ^^127370 'southern', Higginsville, (31º45'S 121º45'E); ^^129773–76 'southern', 22 km S of Kalbarri, (27º51'S 114º10'E); ^^131015 'northern', 22 km WSW of Hamelin Homestead, (26º31'S 114º00'E); ^^131778 'southern', 12 km WNW of Wandina Homestead, (27º56'S 115º32'E); #132470, Shothole Canyon, Cape Range National Park, (22º03'S 114º01'E); ^^135108 'southern', Bullabulling, (30º51'59"S 120º54'24"E); 135196, Camel Soak, (29º26'S 116º48'E); ^^136283 'southern', Muggon Station, (26º46'44"S 115º37'40"E); ^^136406–07 'southern', Norseman area, (32º12'S 121º47'E); *^137675 'northern', 74 km NW of Balladonia Roadhouse, (32º02'S 122º55'E); ^^137676 'northern', 74 km NW of Balladonia Roadhouse, (32º02'S 122º55'E); 144087, 5 km E of Cunderdin, (31º39'S 117º17'E); ^^144587 'southern', Windarling Hill, (29º59'53"S 119º16'05"E); #144732, Bungalbin Hill, (30º19'S 119º29'E); R151125, Eyre Bird Observatory, (32º13'28"S 126º18'10"E); 151210, Salmon Gums area, (32º49'12"S 121º24'36"E); 151218, Salmon Gums area, (32º49'59"S 121º24'50"E); ^^151219 'southern', Salmon Gums area, (32º49'59"S 121º24'50"E); ^^152638 'southern', Middle Island, Houtman Abrolhos Islands, (28º54'35"S 113º54'53"E); ^^156274 'southern', 40 km NE of Holt Rock, (32º24'50"S 119º41'22"E); ^^166866 'southern', Oakajee, (28º34'25"S 114º35'04"E).

SAMA: *^22784 ‘southern’, Mount Remarkable National Park, (32º50'S 138º05'E); 23091, Mount Remarkable National Park, (32º50'S 138º05'E); 25072, 5 km NW of Quorn, (32º18'S 138º00'E); 25349, Hambidge Conservation Park, (33º26'25"S 136º02'01"E); #26339, Yalata Roadhouse, (31º28'10"S 131º35'30"E); 28138, W of Marree, (29º38'S 137º44'E); 28172, Beresford Rail Siding, (29º14'00"S 136º39'30"E); 28248, Abminga Rail Siding, (26º07'S 134º51'E); 28540, 77.5 km N of Minnipa, (32º09'S 135º11'E); 30401, 25 km NNW of Coober Pedy, (28º48'00"S 134º40'52"E); 32278, 50 km SW of Halinor Lake, (29º31'30"S 130º09'00"E); 36487, Courtabie Station, (33º12'30"S 134º51'20"E); 38434, 1.5 km WSW of Tanah Merah Homestead, (34º58'S 140º16'E); 39341, 1 km SE of Alawoona, (34º44'27"S 140º30'43"E); 39420, 5 km NW of Tauragat Hill, (35º33'14"S 139º56'49"E); 39421, 1 km W of Nulungery, (35º38'49"S 140º06'18"E); 39569, 15 km SE of Baan Hill, (35º38'06"S 140º28'55"E); #39606, 3 km S of Buccleuch, (35º21'54"S 139º52'51"E); 40473, Mount Crispe, (26º27'S 135º22'E); 40905, Carmeena Well, (27º07'55"S 132º25'33"E); 41277, Box Tree Waterhole, (33º50'30"S 140º56'50"E); #41336, Oakbank Outstation, (33º07'40"S 140º36'20"E); 41453, Atkindale Homestead, (34º03'30"S 140º08'60"E); 41471, Middle Dam, (33º54'30"S 140º12'20"E); 44405, 8.4 km NW of Mount Kintore, (26º29'57"S 130º26'20"E); ^^44426 ‘northern’, 8 km NW of Mount Kintore, (26º30'01"S 130º26'13"E); #44680, 44885, 4 km SSW of Mount Cuthbert, (26º08'09"S 132º03'60"E); ^^44763 ‘northern’, 7 km WNW of Wilpoorinna Homestead, (29º56'24"S 138º15'45"E); 45193, Karte Conservation Park (35º05'02"S 140º41'06"E); 45567, Jellabinna Rocks, (31º06'41"S 133º22'40"E); ^^45576 ‘southern’, 5 km NNE of Inila Rock, (31º43'50"S 133º27'02"E); *^46340 ‘northern’, 6.5 km WNW of Johnson Bore, (29º30'49"S 136º09'21"E); 46438, 15 km NW of Backadinna Hill, (29º05'00"S 135º10'00"E); ^^46505 ‘northern’, 3.8 km SSE of Mungutana Dam, (29º22'49"S 135º40'55"E); 46529, 5 km WNW of Mount Margaret, (28º28'30"S 136º01'37"E); 46980, 5.6 km SSE of Mosquito Camp Dam, (26º09'28"S 134º30'49"E); 47178, Peake Station, (28º26'10"S 136º07'41"E); 48961, Andamooka Station, (30º44'31"S 137º18'49"E); 50181, 1.4 km SW of Sentinel Hill, (26º05'35"S 132º26'37"E); 51992, 4.1 km N of Warden Hill, (30º24'23"S 139º13'29"E); 52032, Quorn Nature Reserve (32º21'S 138º02'E); 52270, 4.3 km ENE of Willow Springs Homestead, (31º26'25"S 138º48'12"E); 52484, 20.1 km SSE of Port Lincoln, (34º54'16"S 135º55'08"E); 52485, 11.5 km SE of Port Lincoln, (34º47'53"S 135º57'27"E); 53079, 1 km E of Mount Elm, (31º54'27"S 138º19'43"E); ^^53107 ‘northern’, 3.2 km SSW of Dutchmans Peak, (32º20'33"S 137º56'31"E); *^54783, Port Lincoln ‘southern’, (34º54'16"S 135º55'08"E); ^^57677 ‘southern’, 2.4 km ESE of Sheoak Hill, (33º24'44"S 136º45'21"E); 59330, 43.8 km WNW of Maralinga, (29º54'05"S 131º14'06"E); ^^59664 ‘southern’, Yorke Peninsula, (35º09'44"S 137º05'16"E); ^^61993 ‘northern’, 9 km SE of Moonaree Hill, (31º58'56"S 135º40'01"E); ^^62235 ‘southern’, 184 km SSW of Watarru, (28º30'28"S 129º00'17"E); 62277, 180 km SSW of Watarru, (28º30'09"S 129º04'49"E); 62372, 166 km SSE of Watarru, (28º32'58"S 129º59'53"E); 62622, 2.8 km S of Prominent Hill, (29º42'45"S 135º35'39"E); ^^63423 ‘southern’, 30.3 km WNW of Yalata Roadhouse, (31º28'52"S 131º29'47"E).

Delma butleri AM: #130986, #130988, 19.7 km N of Coombah Roadhouse, New South Wales, (32º49'S 141º37'E); #156715, 35 km from Mount Hope on Eubalong Road, New South Wales, (32º56'48"S 146º11'32"E). WAM: #120322, 7 km E of Cape Cuvier, (24º13'26"S 113º27'41"E); #120819, 25 km SSE of Peron Homestead, (26º03'S 113º37'E); ^^129758, 2 km W of Yellowdine, (31º17'59"S 119º37'44"E); #141591, 5 km WSW of Boolathana Homestead, (24º35'21"S 113º32'10"E).

Delma concinna WAM: #96898, 7 km NE of Tamala Homestead, (26º40'S 113º47'E); #141175, 15 km NNE of Lancelin, (30º57'43"S 115º21'53"E). #W. Bryan Jennings 2477, Lesueur National Park, (30º14'S 115º10'E).

Delma fraseri WAM: ^^129670, 10 km S of Quairading, (32º07'S 117º24'E); ^^129686–87, Lort River, (33º45'S 121º14'E).

Delma hebesa **sp. nov.** WAM: 42637, 9.6 km SE of Ongerup, (34º02'S 118º03'E); 43858, Duke of Orleans Bay, (33º54'S 122º40'E); 43859–60, 1.6 km W of Duke of Orleans Bay, (33º55'S 122º34'); 46262, 46268, Mississippi Bay, Cape Le Grand National Park, (33º59'S 122º16'E); 51769, 51772, Bluff Knoll, Stirling Range National Park, (34º23'S 118º15'E); 57742, Thomas River, (33º49'S 123º02'E); 75620, 6 km ENE of Manypeaks (34º49'S 118º13'E); 86666, 86669, 86671–72, Lort River Station, (33º45'S 121º15'E); 86988, Gordon Inlet, (34º17'S 119º28'E); 89358, East Mount Barren, Fitzgerald River National Park, (33º54'S 119º58'E); 91089, 4 km W of Mount Trio, Stirling Range National Park, (34º21'S 118º04'E); 91740, NE of Cape Arid, (33º59'S 123º12'E); 91742, East Mount Barren, Fitzgerald River National Park, (33º55'S 120º01'E); 95434, Albany, (35º02'S 117º53'E); 96253, Lort River Station, (33º27'S 121º21'E); 129003, Shannon Basin, (34º34'20"S 116º19'19"E); ^^129682, Quagi Beach, (33º50'S 121º17'E); ^^129690, ^^129692, ^^129708, Lort River, (33º45'S 121º14'E); ^^131899, Mount Merivale, (33º48'45"S 122º06'15"E); *^132154, Duke of Orleans Bay, (33º56'S 122º33'E); 137203, Stirling Range National Park, (34º51'S 118º25'E); 144236, *^144238, Bandalup Hill, (33º40'29"S 120º23'54"E); *^154242, Kundip, (33º40'01"S 120º12'03"E); #154243, Kundip, (33º40'01"S 120º12'03"E); ^^156978, Canal Rocks, (33º39'46"S 115º00'45"E).

Delma tincta SAMA: ^^22867, 5 km E of Carnarvon, (24º52'S 113º42'E); ^^29302, Carnarvon, (24º53'S 113º40'E); ^^44804, Cordillo Downs, (26º19'05"S 140º20'10"E).

Delma torquata QM: #63361, Kilkivan, Queensland, (26º05'S 152º14'E); #83187, Biggenden, Queensland, (25º30'S 152º02'E); #84362, Nanango, Queensland, (26º40'S 152º00'E).