

Two new species of the *Delma tincta* group (Squamata: Pygopodidae) from northwestern Australia

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Abstract – Analysis of allozyme and morphological variation has revealed that two pygopodid lizard species are presently confused under *Delma pax* Kluge, 1974. *Delma pax* is redescribed and shown to be confined to the Pilbara region, while a closely related, new species is described from the arid deserts of western and central Australia. A second new species, endemic to the Cape Range Peninsula, is also described. Among Western Australian specimens previously referred to *D. borea* Kluge, 1974, those from the Pilbara islands are confirmed; however, all specimens from the Pilbara mainland and arid desert localities are reallocated to other taxa. Both of the newly described species belong to an expanded *Delma tincta* group which displays a complex biogeographic pattern in northwestern Australia. An updated key to the *Delma* spp. of Western Australia is provided.

INTRODUCTION

There are currently 25 described species of pygopodid lizard known from Western Australia (Wilson and Swan 2003). Of these, *Delma* is the most speciose genus with ten species, five of which were described in a comprehensive taxonomic revision by Kluge (1974a). Since this revision, several additional species and subspecies have been recognized in Western Australia, including *D. butleri* Storr, 1987, *D. haroldi* Storr, 1987 and *D. fraseri petersoni* Shea, 1991. Shea (1991) advocated synonymy of *D. haroldi* and *D. butleri* and this view is supported in a recent phylogenetic study of pygopodid lizards by Jennings *et al.* (2003). These authors also elevated *D. f. petersoni* to full species status and advocated transfer of *Aclys concinna* Kluge, 1974 to *Delma* [as suggested also by Kluge (1976)]. Aplin and Smith (2001) highlighted further taxonomic complexity in the widespread *D. australis* Kluge, 1974 and in *D. butleri*, with preliminary investigations suggesting that both are composites.

Shea (1991) proposed a *Delma tincta* group to include *D. tincta*, *D. borea* and *D. pax*, based on their similar patterning, the usual presence of a single large temporal scale bordering each parietal scale, and their largely allopatric pattern of geographic distributions. The integrity of this grouping was strongly supported by Jennings *et al.*

(2003) analysis of DNA sequence variation among pygopodid lizards and by their combined morphological and molecular analysis. However, neither dataset was able to resolve the relationships among the three species.

Problems with the taxonomy of the *Delma tincta* group were noted by field herpetologists working in the Pilbara region in Western Australia. Application of a published key (Storr *et al.* 1990) resulted in some Pilbara specimens being identified as *D. borea* Kluge, 1974, which is otherwise known from the Kimberley region, Northern Territory, western Queensland (Kluge 1974; Shea 1987; Shea 1991) and northwestern South Australia (Ehmann 2005). Similar identification problems were apparent on the Cape Range Peninsula, where specimens initially identified as *D. pax* from the Exmouth region (Storr and Hanlon 1980) were subsequently transferred to *D. tincta* De Vis, 1888 (Storr *et al.* 1990).

This study presents molecular and morphological evidence for the recognition of two new species of *Delma* in northwestern Australia, both of which were previously confused with *D. pax* and/or *D. tincta*. The results further reinforce the opinion of Shea (1987) and others (e.g. Aplin and Smith 2001) that our knowledge of the taxonomy of the morphologically conservative genus *Delma* is far from complete.

METHODS

Morphological analysis

This study is based on the examination of material held in the Western Australian Museum (WAM), Northern Territory Museum (NTM), Australian Museum (AM) and South Australian Museum (SAM). The "R" prefix has been omitted for all WAM, NTM, AM and SAM specimens and, unless otherwise indicated, specimen registration numbers refer to the herpetological collection of the Western Australian Museum. Sex of individuals was determined by dissection and inspection of gonads; some immature or poorly preserved individuals were left unsexed. Head scale terminology, methods of scale counting and morphometric measurements follow those used by Shea (1987), except that all scales between postnasal and circumocular granules are counted as loreals (after Storr *et al.* 1990). Bilateral loreal counts were averaged if different.

For the purpose of this study the following morphometrics data were taken with digital vernier calipers and plastic ruler: snout-vent length (SVL), tail length (Tail L), head depth immediately behind eye (Head D), head length from tip of snout to posterior margin of ear (Head L), head width between ear (Head W), hindlimb length from junction of limb flap with body to distal tip of flap (Hindlimb L), mouth length from tip of snout to oral rictus (Mouth L), rostral depth between dorsal and ventral extremes of scale (Rostral D), rostral width between lateral extremes of scale (Rostral W), snout length from tip of snout to anterior margin of eye (Snout L) and eye width between anterior and posterior extremes of transparent cornea (Eye W). All measurements are reported in millimeters (mm) and characters recorded from the right side only. Specimens preserved in a circular or twisted position were straightened on a flat surface when measured for snout-vent and tail length. Tails were not measured if they were recently broken or obviously regenerated, as suggested by a clear break in colouration or patterning. However, x-rays are necessary to reliably distinguish original and fully regenerated tails and these were not taken during this study. Accordingly, tail measurements are not used in any taxonomic sense and statistical data are provided for descriptive purposes only.

For each species, the possibility of sexual dimorphism in body measurements and scale counts were explored by Analysis of Variance (ANOVA), following tests for normality and homogeneity of variance. Pairwise interspecific statistical comparisons were similarly conducted, using pooled-sex or single sex samples as appropriate. Contrasts are regarded as statistically significant if *p* values were less than 0.05.

Because significant sexual dimorphism was

observed in SVL for most species, variation in the size and proportions of the head was further examined by Analysis of Covariance (ANCOVA). For each taxon, Head L was first regressed against SVL for each sex and ANCOVA used to test for equality of the slopes and intercepts. All other dimensions were then regressed against Head L to test for differences in head proportions between the sexes.

Interspecific differences were explored by first preparing bivariate plots of all dimensions against SVL, separately for each sex. The head dimensions were then combined using Principal Component Analyses (PCA; based on covariance matrices) to produce a simplified representation of the morphometric variation. All analyses were performed on untransformed data after bivariate plots showed essentially linear patterns of relative growth among the various measures and no significant growth-related increase in variance in any dimension. Statistical analyses were performed with MINITAB Release 14.20 or GenStat Release 6.1.

All WAM specimens of *D. borea* and *D. tincta* collected subsequent to Kluge (1974) were assessed for three characters; supranasal scale division, midbody scale row count and the identity of the supralabial scale positioned beneath the eye to quantify the intraspecific variation and determine the effectiveness of these characters for identification. Due to their geographic proximity to the new species described herein, all specimens from the Western Australian Pilbara islands plus all available *D. borea* from the southern sector of the Northern Territory were also examined (see Appendix 1).

Allozyme analysis

Frozen liver or heart tissues for allozyme electrophoresis were obtained from the frozen tissue collections of the Western Australian and South Australian Museums for 12 specimens of typical *D. pax*, six specimens of the 'desert' morphotype, four specimens of the 'Cape Range' morphotype, and three specimens of each of *D. tincta* and *D. borea* from localities in northwestern Australia. We also included samples identified as *D. butleri* (*n* = 9) and *D. haroldi* (*n* = 4), drawn from across the geographic range of this sibling pair (or geographically variable taxon; Shea 1991). A total of 41 specimens were represented in the study (see Appendix 2 for voucher details). We used allozyme electrophoresis to test the hypothesis that each of the identified morphotypes within the *Delma tincta* group represents a distinct evolutionary species. The samples of *D. butleri* and *D. haroldi* were included as members of a second species group to provide a perspective on genetic diversity within the *D. tincta* group.

Allozyme electrophoresis was carried out on cellulose acetate gels (Cellogel®) using the principles and procedures detailed in Richardson *et al.* (1986). The following enzymes or non-enzymatic proteins displayed sufficient activity and resolution to allow allozymic interpretation:— aconitase hydratase (ACON, EC 4.2.1.3), acid phosphatase (ACP, EC 3.1.3.2), aminoacylase (ACYC, EC 3.5.1.14), adenosine deaminase (ADA, EC 3.5.4.4), alcohol dehydrogenase (ADH, EC 1.1.1.1), carbonate dehydratase (CA, EC 4.2.1.1), diaphorase (DIA, EC 1.6.99), enolase (ENOL, EC 4.2.1.11), esterase (EST, EC 3.1.1), fructose-bisphosphatase (FDP, EC 3.1.3.11), fumarate hydratase (FUM, EC 4.2.1.2), glyceraldehyde-3-phosphate dehydrogenase (GAPD, EC 1.2.1.12), guanine deaminase (GDA, EC 3.5.4.3), lactoylglutathione lyase (GLO, EC 4.4.1.5), aspartate aminotransferase (GOT, EC 2.6.1.1), glycerol-3-phosphate dehydrogenase (GPD, EC 1.1.1.8), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), guanylate kinase (GUK, EC 2.7.4.8), isocitrate dehydrogenase (IDH, EC 1.1.1.42), cytosol aminopeptidase (LAP, EC 3.4.11.1), L-lactate dehydrogenase (LDH, EC 1.1.1.27), malate dehydrogenase (MDH, EC 1.1.1.37), "malic" enzyme (ME, EC 1.1.1.40), mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), nucleoside-diphosphate kinase (NDPK, EC 2.7.4.6), dipeptidase (PEPA, EC 3.4.13), tripeptide aminopeptidase (PEP-B, EC 3.4.11), proline dipeptidase (PEPD, EC 3.4.13), phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44), phosphoglucomutase (PGM, EC 5.4.2.2), pyruvate kinase (PK, EC 2.7.1.40), superoxide dismutase (SOD, EC 1.15.1.1), L-idoitol dehydrogenase (SRDH, EC 1.1.1.14) and triose-phosphate isomerase (TPI, EC 5.3.1.1). The nomenclature used to refer to loci and allozymes follows Adams *et al.* (1987).

The allozyme data were analysed in several ways. In the first instance, Principal Co-ordinates Analysis (PCoA) was employed to assess the genetic affinities of individuals, independently of any *a priori* grouping based on morphology. Following an initial PCoA on all 41 specimens analysed, subsequent PCoAs were then undertaken on each of the three subsets of specimens which clustered together and comprised more than one morphotypic form. The rationale underlying this 'stepwise' use of multiple PCoAs to identify genetic groups from first principles, plus the methodological details involved, are presented in Smith and Adams (2006).

Having defined the major genetic groupings using PCoA, the phylogenetic relationships among these groups were explored by constructing a Neighbor Joining tree from pairwise Nei's genetic distances. This analysis was undertaken using the NEIGHBOR computer program contained with PHYLIP 3.5c (Felsenstein 1993), and the resultant

tree drawn using TREEVIEW (Page 1996). A measure of the robustness of clades was obtained by bootstrapping the allele frequency data for 100 pseudoreplicates, using a BASIC program written by M. Adams.

A second measure of genetic divergence was obtained by calculating the percentage fixed differences (% FDs) among groups. As argued by Richardson *et al.* (1986), the number of "fixed" or diagnostic differences between populations is more biologically relevant when determining species boundaries than are Nei D values, which may be quite large even in the absence of any genuinely diagnostic loci.

RESULTS

Morphological analysis

Initial recognition of the potential new species emerged during a careful examination of all *D. pax* specimens and of *D. borea* specimens from the southern Kimberley in Western Australia and from southern Northern Territory. During this morphological survey, special attention was paid to the identity of the supralabial scale positioned beneath the eye and the detail and intensity of head patterning at various stages of maturity. Using these characters in combination, it was possible to detect subtle but consistent differences between three morphologically diagnosable geographic entities. These were: (i) true *D. pax* from the Pilbara with strong juvenile head pattern that fades early in ontogeny, (ii) a distinctive, inornate 'Cape Range' morphotype with similarities to each of *D. pax* and *D. borea* and (iii) a widespread 'desert' morphotype with a persistent well-developed head pattern. Each of these taxa appeared to be quite distinct from each of *D. borea* and *D. tincta*.

Before undertaking any morphometric comparisons, we examined the linear measurements and scale counts from each of the putative taxa and geographically proximate samples of *D. borea* and *D. tincta* for evidence of sexual dimorphism. Statistically significant sexual dimorphism was observed in each species but with contrasting expression in each (Tables 1 and 2).

In all putative taxa, females are significantly longer bodied (SVL) than males. In typical *D. pax* and the 'desert' morphotype the mean SVL of females is 109% and 112% larger than that of conspecific males (Table 1). This value is slightly lower in *D. borea* (107%). The small sample of the 'Cape Range' morphotype gives an estimate of dimorphism of 112%. These observations are consistent with Kluge's (1974: 34) observation for pygopodids that "the female of a given species almost always attains a larger size than the male."

In each of *D. pax*, the 'desert' morphotype and *D.*

Table 1 Summary of mensural and meristic data gathered in this study, presented separately for each sex. The 'desert' and 'Cape Range' morphotypes are listed in this and all subsequent tables as *D. desmosa* and *D. tealei*, respectively, reflecting the ultimate taxonomic arrangement. Also shown are data for the redefined *D. pax* and for geographically proximate samples of *D. borea* and *D. tincta*. Values are mean \pm one standard deviation, range and sample size (n).

		<i>D. tealei</i>	<i>D. desmosa</i>	<i>D. pax</i>	<i>D. borea</i>	<i>D. tincta</i>
SVL	♂	73.7 \pm 1.49 70–77 (4)	70.0 \pm 1.47 60–80 (24)	74.1 \pm 1.42 55–93 (42)	70.0 \pm 1.10 54–88 (42)	66.6 \pm 1.72 58–72 (9)
	♀	82.2 \pm 2.56 77–88 (4)	78.4 \pm 2.53 56–90 (15)	81.0 \pm 1.46 58–98 (39)	74.8 \pm 1.18 54–95 (50)	79.4 \pm 4.62 66–92 (5)
Tail L	♂	146.3 \pm 33.0 107–212 (3)	198.2 \pm 10.7 85–275 (24)	184.4 \pm 7.67 109–271 (32)	172.9 \pm 6.86 57–240 (35)	189.3 \pm 17.61 102–263 (9)
	♀	142.2 \pm 29.7 87–210 (4)	187.5 \pm 13.0 80–257 (14)	198.5 \pm 6.31 117–257 (33)	176.5 \pm 9.21 53–259 (42)	228.6 \pm 11.87 200–260 (5)
Ventrals	♂	50.5 \pm 0.5 50–52 (4)	51.8 \pm 0.30 48–56 (24)	54.2 \pm 0.30 50–58 (43)	53.7 \pm 0.46 47–62 (42)	48.7 \pm 0.78 44–52 (9)
	♀	51.5 \pm 0.5 50–52 (4)	52.9 \pm 0.45 50–58 (15)	56.0 \pm 0.32 52–60 (39)	54.3 \pm 0.34 50–58 (50)	52.4 \pm 0.68 50–58 (5)
Head L	♂	8.50 \pm 0.09 8.36–8.77 (4)	8.04 \pm 0.13 7.08–9.28 (24)	8.51 \pm 0.10 6.96–9.88 (43)	8.13 \pm 0.09 6.79–9.39 (42)	7.58 \pm 0.16 6.96–8.22 (9)
	♀	8.81 \pm 0.27 8.18–9.39 (4)	8.52 \pm 0.16 7.21–9.65 (15)	8.72 \pm 0.10 7.45–9.78 (39)	8.34 \pm 0.10 6.68–9.89 (50)	8.20 \pm 0.35 7.16–9.02 (5)
Head W	♂	5.55 \pm 0.09 5.35–5.75 (4)	4.76 \pm 0.08 3.91–5.54 (24)	5.11 \pm 0.08 3.96–6.48 (43)	4.82 \pm 0.08 3.91–5.99 (42)	4.52 \pm 0.16 3.88–5.24 (9)
	♀	5.53 \pm 0.23 5.11–6.16 (4)	5.11 \pm 0.15 3.85–6.06 (15)	5.34 \pm 0.10 3.71–6.73 (39)	5.01 \pm 0.07 3.69–6.06 (50)	4.77 \pm 0.32 3.97–5.59 (5)
Head D	♂	4.49 \pm 0.27 3.85–5.04 (4)	4.39 \pm 0.08 3.60–5.13 (24)	4.52 \pm 0.07 3.51–5.97 (43)	3.91 \pm 0.07 3.16–5.04 (42)	3.79 \pm 0.10 3.35–4.39 (9)
	♀	4.44 \pm 0.13 4.11–4.73 (4)	4.70 \pm 0.15 3.61–5.65 (14)	4.68 \pm 0.12 3.33–6.25 (39)	4.07 \pm 0.07 3.06–5.45 (49)	3.94 \pm 0.22 3.44–4.52 (4)
Mouth L	♂	5.89 \pm 0.14 5.51–6.18 (4)	5.83 \pm 0.12 4.88–6.84 (24)	6.29 \pm 0.12 5.24–8.40 (43)	5.65 \pm 0.08 4.63–6.79 (42)	6.23 \pm 0.21 4.87–6.99 (9)
	♀	5.85 \pm 0.11 5.59–6.13 (4)	6.19 \pm 0.14 4.99–6.93 (15)	6.49 \pm 0.10 5.02–7.99 (39)	5.80 \pm 0.07 4.51–6.82 (50)	6.71 \pm 0.34 5.76–7.89 (5)

tincta the number of enlarged ventral scales is significantly higher in females than males (Table 2), with mean ventral scale counts in females being 1.8, 1.1 and 3.7 (scales) greater than the conspecific male

values, respectively (Table 1). In contrast, *D. borea* and the 'Cape Range' morphotype do not show significant sexual dimorphism in this feature, although in each case the mean value for females is

Table 1 (cont.)

		<i>D. tealei</i>	<i>D. desmosa</i>	<i>D. pax</i>	<i>D. borea</i>	<i>D. tincta</i>
Snout L	♂	3.53 ± 0.11 3.32–3.78 (4)	3.19 ± 0.06 2.33–3.86 (24)	3.46 ± 0.05 2.74–4.76 (43)	3.28 ± 0.04 2.69–4.07 (42)	3.06 ± 0.10 2.76–3.76 (9)
	♀	3.51 ± 0.11 3.35–3.84 (4)	3.39 ± 0.09 2.61–3.93 (15)	3.52 ± 0.05 2.96–4.29 (39)	3.40 ± 0.04 2.63–4.09 (50)	3.39 ± 0.21 2.76–4.00 (5)
Rostral W	♂	1.88 ± 0.05 1.77–2.01 (4)	1.62 ± 0.04 0.93–1.88 (24)	1.66 ± 0.02 1.26–2.06 (43)	1.54 ± 0.02 1.23–1.84 (42)	1.44 ± 0.03 1.28–1.66 (9)
	♀	1.85 ± 0.08 1.63–2.06 (4)	1.79 ± 0.04 1.51–2.27 (15)	1.78 ± 0.03 1.40–2.19 (38)	1.58 ± 0.02 1.17–1.98 (50)	1.61 ± 0.06 1.48–1.87 (5)
Rostral D	♂	0.92 ± 0.07 0.76–1.10 (4)	0.95 ± 0.02 0.52–1.24 (24)	1.03 ± 0.02 0.81–1.25 (43)	0.87 ± 0.01 0.71–1.16 (42)	1.00 ± 0.03 0.81–1.14 (9)
	♀	1.09 ± 0.06 0.93–1.25 (4)	1.00 ± 0.03 0.67–1.18 (15)	1.06 ± 0.01 0.84–1.33 (38)	0.89 ± 0.01 0.64–1.21 (50)	0.98 ± 0.06 0.73–1.06 (5)
Eye W	♂	1.73 ± 0.13 1.48–2.04 (4)	1.46 ± 0.04 0.83–1.74 (24)	1.56 ± 0.02 1.23–1.84 (42)	1.50 ± 0.02 1.34–1.79 (42)	1.55 ± 0.07 1.16–1.88 (9)
	♀	1.97 ± 0.14 1.56–2.13 (4)	1.54 ± 0.04 1.16–1.79 (15)	1.56 ± 0.02 1.28–1.93 (39)	1.49 ± 0.02 1.19–1.81 (50)	1.60 ± 0.08 1.39–1.79 (5)
Hindlimb L	♂	3.20 ± 0.21 2.91–3.81 (4)	3.63 ± 0.10 2.59–4.42 (24)	3.60 ± 0.09 1.70–4.92 (43)	2.61 ± 0.05 1.73–3.43 (41)	2.63 ± 0.14 1.73–3.16 (9)
	♀	2.89 ± 0.27 2.08–3.31 (4)	2.89 ± 0.13 1.95–3.53 (15)	2.62 ± 0.06 1.95–3.80 (39)	2.10 ± 0.04 1.46–2.95 (49)	2.38 ± 0.16 1.99–2.95 (5)
Loreals	♂	7.25 ± 0.66 6–9 (4)	6.85 ± 0.22 5–9 (24)	7.37 ± 0.18 5–10 (43)	7.50 ± 0.19 4–9 (40)	4.96 ± 0.20 4–6 (9)
	♀	6.25 ± 0.48 5–7 (4)	6.87 ± 0.29 5–8 (15)	7.54 ± 0.19 5–10 (39)	7.24 ± 0.19 4–11 (50)	5.30 ± 0.46 4.5–7 (5)
Hindlimb scales	♂	8 ± 0.00 8 (4)	8 ± 0.00 8 (24)	8.51 ± 0.88 8–10 (43)	8.00 ± 1.25 5–10 (41)	5 ± 0.00 5 (9)
	♀	8 ± 0.00 8 (4)	8 ± 0.00 8 (15)	8.56 ± 0.91 8–10 (39)	7.66 ± 1.17 5–9 (50)	5 ± 0.00 5 (5)

higher than that for males. Kluge (1974) reported significant sexual dimorphism in mean ventral counts (always greater in females than males) in four species of *Delma* [*D. australis*, *D. impar* (Fischer, 1882), *D. nasuta* Kluge, 1974, and *D. tincta*], with means differing by 3–5 scales in each case. Species that Kluge (1974) found to be non-dimorphic in this attribute include *D. borea*, *D.*

fraseri Gray, 1831, *D. grayii* Smith, 1849, *D. inornata* Kluge, 1974, *D. molleri* Lütken, 1863 and *D. plebeia* De Vis, 1888. Kluge's (1974) samples of *D. nasuta* and *D. inornata* were both composites as they both included specimens subsequently referred to *D. butleri* (Storr 1987; Shea 1991).

Sexual dimorphism in hindlimb length is expressed in each of *D. pax*, the 'desert'

Table 2 Statistical analysis (ANOVA) of intraspecific sexual dimorphism in selected mensural and meristic characters for each of *D. tealei*, *D. desmosa*, *D. pax*, *D. borea*, and *D. tincta*.

	<i>D. tealei</i>	<i>D. desmosa</i>	<i>D. pax</i>	<i>D. borea</i>	<i>D. tincta</i>
SVL	F = 8.218 d.f. = 1,7 P = 0.029	F = 9.600 d.f. = 1,38 P = 0.004	F = 11.380 d.f. = 1,80 P = 0.001	F = 8.311 d.f. = 1,91 P = 0.005	F = 9.753 d.f. = 1,13 P = 0.009
Tail L	F = 0.008 d.f. = 1,6 P = 0.931	F = 0.387 d.f. = 1,37 P = 0.538	F = 2.027 d.f. = 1,64 P = 0.160	F = 0.093 d.f. = 1,76 P = 0.761	F = 2.364 d.f. = 1,13 P = 0.150
Ventrals	F = 2.000 d.f. = 1,7 P = 0.207	F = 5.231 d.f. = 1,38 P = 0.028	F = 17.595 d.f. = 1,81 P <0.001	F = 1.175 d.f. = 1,91 P = 0.281	F = 10.105 d.f. = 1,13 P = 0.008
Head L	F = 1.108 d.f. = 1,7 P = 0.330	F = 4.933 d.f. = 1,38 P = 0.033	F = 1.995 d.f. = 1,81 P = 0.162	F = 2.274 d.f. = 1,91 P = 0.135	F = 3.407 d.f. = 1,13 P = 0.090
Head W	F = 0.008 d.f. = 1,7 P = 0.931	F = 4.464 d.f. = 1,38 P = 0.041	F = 2.967 d.f. = 1,81 P = 0.089	F = 2.839 d.f. = 1,91 P = 0.096	F = 0.576 d.f. = 1,13 P = 0.463
Head D	F = 0.0296 d.f. = 1,7 P = 0.869	F = 3.741 d.f. = 1,37 P = 0.061	F = 1.246 d.f. = 1,81 P = 0.268	F = 2.591 d.f. = 1,90 P = 0.111	F = 0.498 d.f. = 1,12 P = 0.495
Mouth L	F = 0.047 d.f. = 1,7 P = 0.835	F = 3.296 d.f. = 1,38 P = 0.078	F = 1.508 d.f. = 1,81 P = 0.223	F = 1.706 d.f. = 1,91 P = 0.195	F = 1.543 d.f. = 1,13 P = 0.238
Snout L	F = 0.016 d.f. = 1,7 P = 0.904	F = 3.044 d.f. = 1,38 P = 0.089	F = 0.536 d.f. = 1,81 P = 0.466	F = 2.955 d.f. = 1,91 P = 0.089	F = 2.513 d.f. = 1,13 P = 0.139
Rostral W	F = 0.084 d.f. = 1,7 P = 0.781	F = 5.659 d.f. = 1,38 P = 0.023	F = 7.498 d.f. = 1,80 P = 0.008	F = 1.582 d.f. = 1,91 P = 0.212	F = 6.231 d.f. = 1,13 P = 0.028
Rostral D	F = 2.894 d.f. = 1,7 P = 0.140	F = 1.354 d.f. = 1,38 P = 0.252	F = 1.320 d.f. = 1,80 P = 0.254	F = 0.837 d.f. = 1,91 P = 0.363	F = 0.101 d.f. = 1,13 P = 0.756
Eye W	F = 1.555 d.f. = 1,7 P = 0.259	F = 1.622 d.f. = 1,38 P = 0.211	F = 0.001 d.f. = 1,80 P = 0.979	F = 0.149 d.f. = 1,91 P = 0.700	F = 0.208 d.f. = 1,13 P = 0.657
Hindlimb L	F = 0.839 d.f. = 1,7 P = 0.395	F = 18.702 d.f. = 1,38 P <0.001	F = 65.496 d.f. = 1,81 P <0.001	F = 49.009 d.f. = 1,89 P <0.001	F = 1.103 d.f. = 1,13 P = 0.314
Loreals	F = 1.500 d.f. = 1,7 P = 0.267	F = 0.001 d.f. = 1,38 P = 0.973	F = 0.405 d.f. = 1,81 P = 0.526	F = 0.887 d.f. = 1,89 P = 0.349	F = 0.641 d.f. = 1,13 P = 0.439

morphotype and *D. borea*, with males having longer hindlimb flaps in each taxon (Table 1). Bivariate plots of this measurement against SVL for each of these taxa (Figure 1A–C) show that variance in hindlimb length is low at early growth stages (low SVL) and that sexual dimorphism emerges through life as a result of more rapid growth of the hindlimb, relative to SVL, in males than females. The different relative growth trajectory of each sex is confirmed by results of ANCOVA for each of *D.*

pax and *D. borea* (Table 3). Results for the 'desert' morphotype are not statistically significant but this may be due to the lack of smaller females in the sample. Too few individuals of the 'Cape Range' morphotype were available and too few specimens of *D. tincta* were examined to determine the extent of hindlimb sexual dimorphism in each of these taxa. Somewhat surprisingly, the number of hindlimb scales is not sexually dimorphic in any of the studied species (Table 1). Kluge (1974) did not

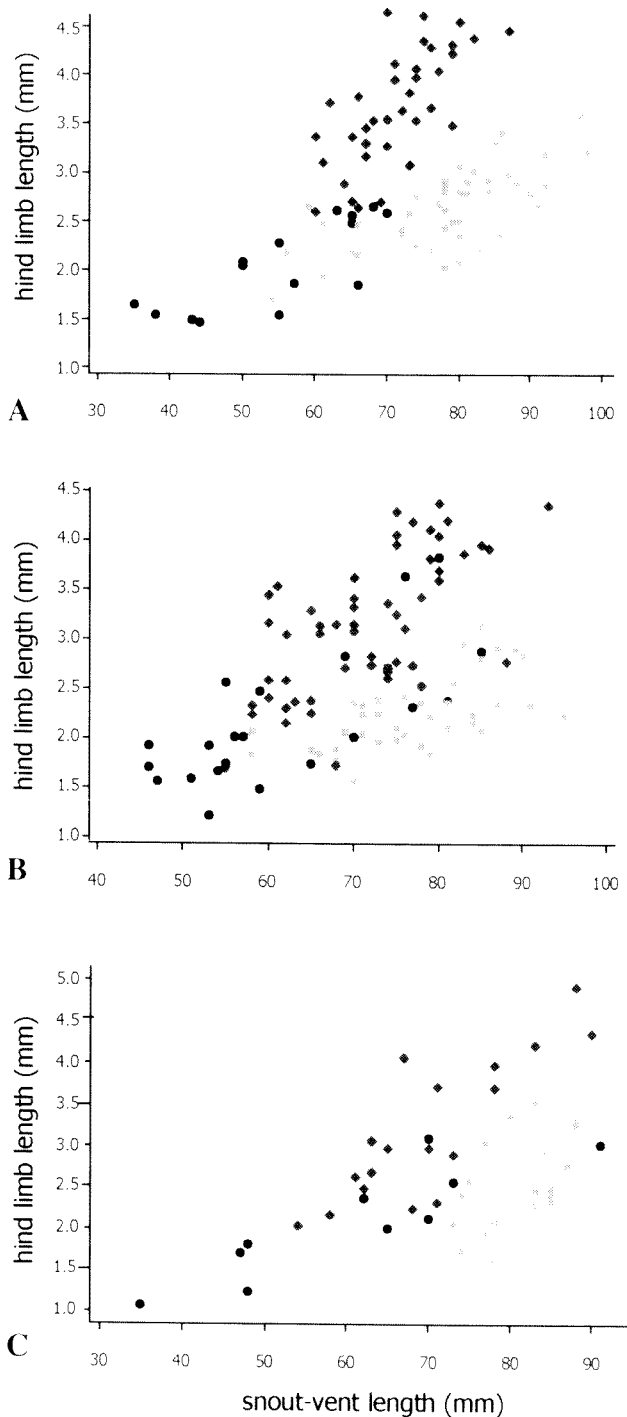


Figure 1 Bivariate plots of Hindlimb L against SVL for each of *D. pax* (A); *D. borea* (B) and the 'desert' morphotype (C). In each plot, males (diamonds) are distinguished from females (squares) and unsexed individuals (circles). The plots demonstrate that male-biased sexual dimorphism in hindlimb length in each species arises through more rapid growth of this appendage in males than in females.

present hindlimb lengths but did report a lack of sexual dimorphism in hindlimb scale counts in all *Delma* species.

For head dimensions, only a few statistically significant or near significant contrasts (Table 2) are observed between the sexes in each of *D. pax* (Head W, Rostral W), *D. borea* (Head W, Snout L), with mean values for females exceeding those of males in all cases. In contrast, the 'desert' morphotype shows female-biased sexual dimorphism in most head dimensions. Examination of bivariate plots of each head dimension against SVL (Figure 2A-C) indicate a clear lack of sexual dimorphism in *D. borea*, with no differences in the slopes or intercepts of regression lines, but a more complex situation in each of *D. pax* and the 'desert' morphotype. In these taxa, regression slopes are slightly higher in males than females, indicating a more rapid growth of the head relative to SVL in males than in females. However, for both taxa ANCOVA-s were not significant for any head dimension against SVL (Table 3). Bivariate plots of all other head dimensions against Head L for each taxon failed to reveal any sexual dimorphism in head proportions (Figure 2D-F for Head W against Head L) and this was also confirmed by non-significant results from ANCOVA (not shown). Males in each of these species of *Delma* thus develop a slightly larger head than females through life, but without any obvious proportional changes.

No sexual dimorphism was observed in loreal counts. This finding is consistent with that of Kluge (1974) for other *Delma* species and for pygopodids generally. Uniquely among pygopodids, *Lialis burtonis* Gray, 1835 is sexually dimorphic in the number of supralabial scales (Kluge 1974: 132).

Table 4 gives a summary of pairwise statistical comparisons among *D. pax*, *D. desmosa* and *D. borea* for various measurements and scale counts, with separate comparisons for each sex. Comments on statistically significant contrasts are provided under the individual species accounts.

For head dimensions, interspecific contrasts were examined separately for each sex by bivariate plots and then by PCA (results not shown). No clear interspecific differences were found. Instead, the head appears to be remarkably conservative in proportions among all of the species examined.

Allozyme analysis

We were able to score a total of 43 presumptive allozyme loci. Nine loci (*Est1*, *Gapd*, *Idh1*, *Lap*, *Ldh1*, *Ldh2*, *Mdh*, *Pk*, and *Tpi*) were invariant and hence uninformative for assessing genetic relationships among individuals. Appendix 2 presents the allozyme profiles of the 41 specimens examined at the 34 variable loci.

The initial PCoA on all specimens revealed the presence of four discrete clusters, labeled A-D on

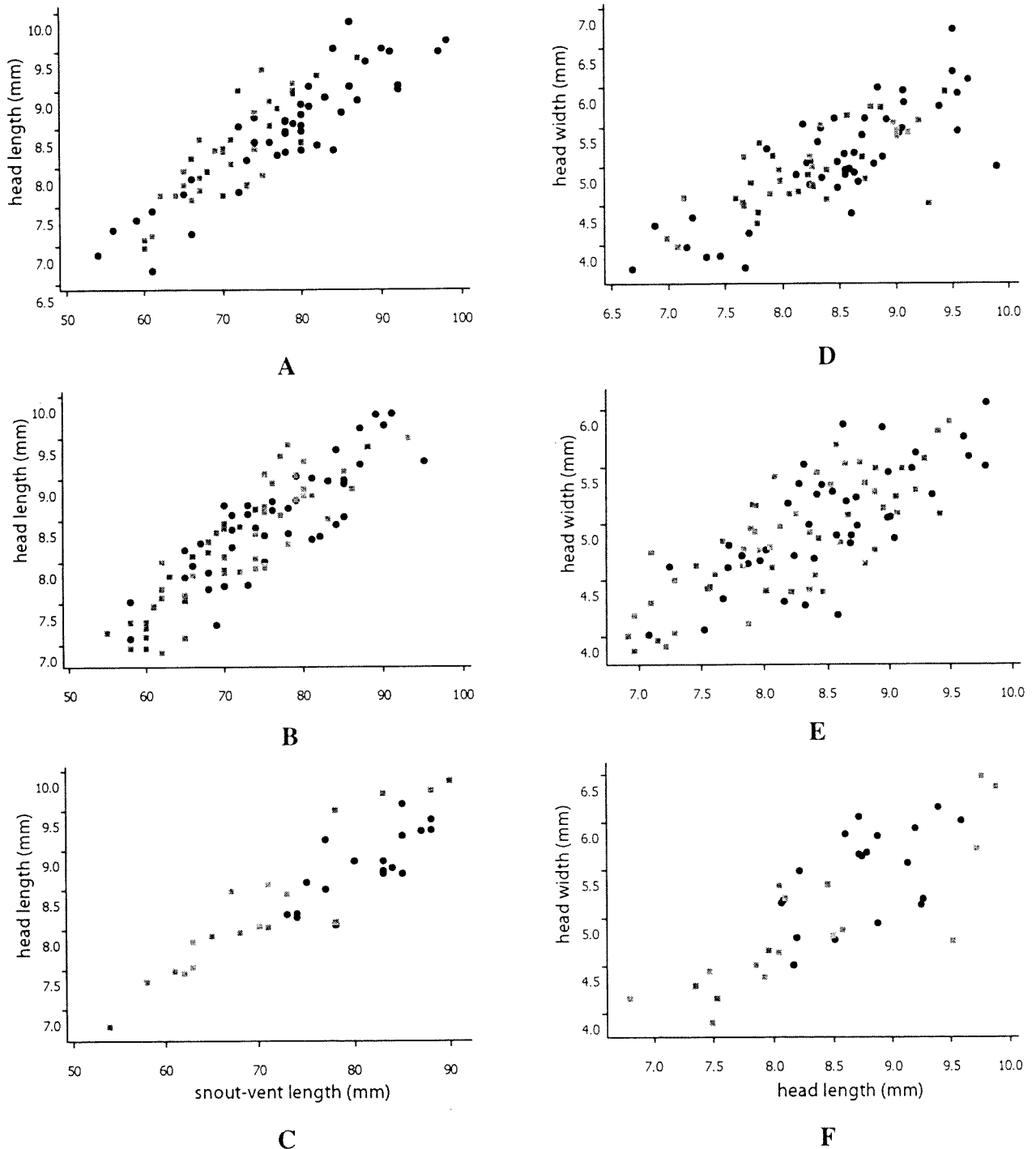


Figure 2 Bivariate plots of Head L against SVL and Head W against Head L for each of *D. pax* (A, D); *D. borea* (B, E) and the 'desert' morphotype (C, F). In each plot, males (squares) are distinguished from females (circles). The plots demonstrate slightly more rapid growth of the head relative to SVL in each of *D. pax* and the 'desert' morphotype, and a lack of differentiation between the sexes in head proportions.

Figure 3. As shown, only group D comprised specimens of a single *a priori* taxon (i.e. *D. tincta*). All other groups were composites: group A comprised specimens displaying either the *pax* or 'desert' morphotype, group B contained specimens referable to the 'Cape Range' morphotype or *D. borea*, and group C was a mix of both *D. butleri* and *D. haroldi*.

In order to determine whether all taxa were

independently diagnosable by their allozyme profiles, a second round of PCoAs was undertaken on individuals within each of the composite groups A, B, and C (Figure 4). Unequivocal discrimination was indeed obtained between *D. pax* and the 'desert' morphotype (Figure 4A) and between *D. borea* and the 'Cape Range' morphotype (Figure 4B). The outcome was more complex for group C, since while *haroldi* was distinguishable from

Table 3 Statistical analysis (ANCOVA) of intraspecific sexual dimorphism for hindlimb and selected head dimensions for each of *D. borea*, *D. desmosa* and *D. pax*. Regression values are slope (a) ± s.e. and intercept (i). All regressions are highly significant and all contrasts passed tests of homogeneity of variance.

Comparison	SEX	Hindlimb L vs SVL		Head L vs SVL		Head L vs Head W	Loreals
<i>D. borea</i>	♂	a = 0.052 ± 0.007 i = 0.590	F = 5.67 d.f. = 1,92	a = 0.073 ± 0.006 i = 2.99	F = 2.06 d.f. = 1,94	a = 0.565 ± 0.065 i = 0.230	F = 0.01 d.f. = 1,94
	♀	a = 0.025 ± 0.009 i = 0.30	P = 0.019	a = 0.061 ± 0.007 i = 3.88	P = 0.155	a = 0.554 ± 0.086 i = 0.310	P = 0.921
<i>D. pax</i>	♂	a = 0.065 ± 0.010 i = -1.15	F = 35.93 d.f. = 1,79	a = 0.082 ± 0.009 i = 2.41	F = 2.44 d.f. = 1,79	a = 0.547 ± 0.103 i = 0.443	F = 2.54 d.f. = 1,80
	♀	a = 0.027 ± 0.005 i = 0.27	P < 0.001	a = 0.066 ± 0.005 i = 3.33	P = 0.123	a = 0.752 ± 0.077 i = -1.297	P = 0.115
<i>D. desmosa</i>	♂	a = 0.072 ± 0.012 i = -1.83	F = 0.24 d.f. = 1,36	a = 0.085 ± 0.008 i = 2.33	F = 0.52 d.f. = 1,36	a = 0.676 ± 0.111 i = -0.699	F = 0.19 d.f. = 1,36
	♀	a = 0.059 ± 0.023 i = -2.20	P = 0.624	a = 0.073 ± 0.015 i = 2.87	P = 0.477	a = 0.572 ± 0.208 i = 0.450	P = 0.662

Table 4 Statistical analysis of pairwise interspecific differences between each of *D. desmosa*, *D. pax*, and *D. borea* for selected mensural and meristic characters. The available sample of *D. tealei* is too small to yield significant results.

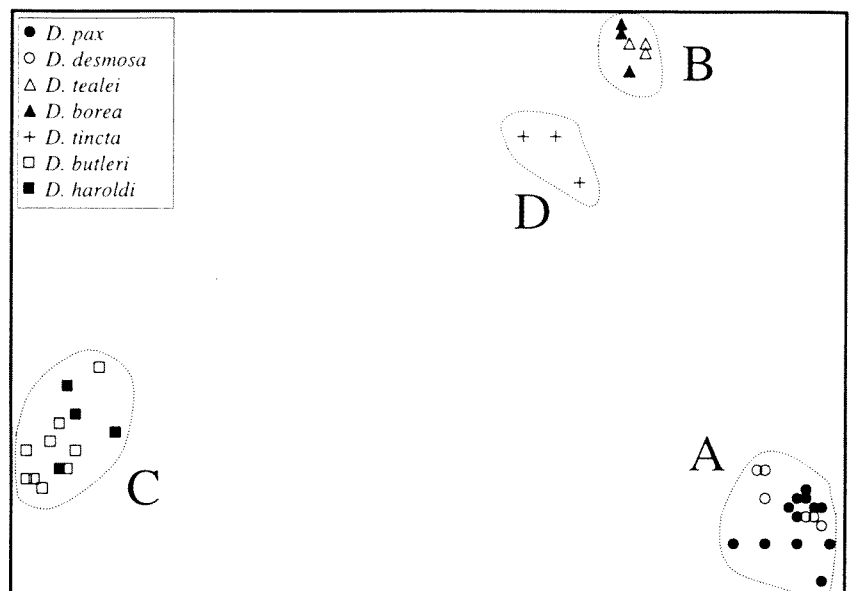
Comparison	SEX	SVL	Ventrals	Head L	Eye W	Hindlimb L	Loreals
<i>pax vs desmosa</i>	♂	F = 3.582 d.f. = 1,65 P = 0.063	F = 27.707 d.f. = 1,66 P < 0.001	F = 7.002 d.f. = 1,66 P = 0.010	F = 5.452 d.f. = 1,65 P = 0.023	F = 0.037 d.f. = 1,66 P = 0.847	F = 3.149 d.f. = 1,66 P = 0.081
	♀	F = 0.817 d.f. = 1,53 P = 0.370	F = 27.178 d.f. = 1,53 P < 0.001	F = 1.113 d.f. = 1,53 P = 0.296	F = 0.318 d.f. = 1,53 P = 0.575	F = 3.936 d.f. = 1,53 P = 0.053	F = 3.560 d.f. = 1,53 P = 0.065
<i>pax vs borea</i>	♂	F = 5.118 d.f. = 1,83 P = 0.026	F = 0.612 d.f. = 1,84 P = 0.436	F = 7.084 d.f. = 1,84 P = 0.009	F = 4.618 d.f. = 1,83 P = 0.035	F = 73.475 d.f. = 1,83 P < 0.001	F = 0.237 d.f. = 1,82 P = 0.628
	♀	F = 11.196 d.f. = 1,88 P = 0.001	F = 12.295 d.f. = 1,88 P = 0.001	F = 6.860 d.f. = 1,88 P = 0.010	F = 6.391 d.f. = 1,88 P = 0.013	F = 45.916 d.f. = 1,87 P < 0.001	F = 1.173 d.f. = 1,88 P = 0.282
<i>desmosa vs borea</i>	♂	F = 1.232 d.f. = 1,107 P = 0.270	F = 16.981 d.f. = 1,108 P < 0.001	F = 3.264 d.f. = 1,108 P = 0.074	F = 1.015 d.f. = 1,65 P = 0.318	F = 10.466 d.f. = 1,107 P = 0.002	F = 4.551 d.f. = 1,63 P = 0.037
	♀	F = 0.131 d.f. = 1,103 P = 0.718	F = 11.240 d.f. = 1,103 P = 0.001	F = 0.004 d.f. = 1,103 P = 0.952	F = 1.385 d.f. = 1,64 P = 0.244	F = 19.146 d.f. = 1,102 P < 0.001	F = 0.931 d.f. = 1,64 P = 0.338

butleri, the latter also displayed considerable heterogeneity which broadly manifested itself as three geographically-based clusters herein referred to as 'western', 'central', and 'eastern' (Figure 4C, Appendix 1). Thus the final outcome of the four PCoAs was the recognition of nine Operational Taxonomic Units (OTUs) among the 41 specimens examined, each diagnosable from all others using stepwise PCoA of the allozyme data. Table 5 compares allele frequencies for each OTU at the 34 informative loci, while Table 6 presents pairwise

genetic distance (Nei D and % fixed difference) values.

In general, each of the OTUs is well-differentiated genetically from all others, with only five of the 36 pairwise comparisons involving fewer than six fixed differences (equivalent to 12%FD). Regarding the five exceptions, all but one occurred among the four OTUs identified within group C (*butleri/haroldi*); indeed, in the case of *D. haroldi* versus 'central' *D. butleri* the two OTUs shared alleles at all loci (0 %FD, Table 6).

Figure 3 Principal Co-ordinates Analysis of the 41 specimens included in the allozyme study. The 'desert' and 'Cape Range' morphotypes are listed in this and all subsequent figures as *D. desmosa* and *D. tealei*, respectively, reflecting the ultimate taxonomic arrangement. The relative PCoA scores have been plotted for the first (X-axis) and second (Y-axis) dimensions, which individually explained 43% and 14% respectively of the total multivariate variation.



The only other pairwise comparison not characterized by multiple fixed differences is that between typical *pax* and the 'desert' morphotype. These OTUs displayed a single fixed difference (= 2%FD) and a modest Nei D of 0.08 (Table 6). In contrast, the 'Cape Range' morphotype shows fixed differences at 21% of loci to each of *D. pax* and the 'desert' morphotype (Nei D = 0.25–0.27) and a closer association with *D. borea* (12%FD and Nei D = 0.16). Pairwise contrasts within the *D. butleri/haroldi* group range from 0–14% for fixed differences and 0.04 to 0.21 for Nei D, with a closer affinity between *D. haroldi* and eastern *D. butleri* on the one hand, and between 'western' and 'central' populations of *D. butleri* on the other.

The Neighbour-Joining tree constructed from pairwise Nei D values (Figure 5) shows a deep division of the OTUs into two groups, one containing *D. butleri* and *D. haroldi*, and the other containing *D. tincta*, *D. pax* and *D. borea* and both the 'desert' and 'Cape Range' morphotypes. Within this latter group, *D. tincta* appears to be the most divergent, with the remaining four OTUs forming a common group made up of two pairs of OTUs: *pax* + 'desert' and *borea* + 'Cape Range'.

Figure 4 Principal Co-ordinates Analyses for each of the three groups identified in the initial PCoA (Figure 3). A) PCoA of group A specimens; the first and second dimensions individually explained 34% and 13% respectively of the total variance. B) PCoA of group B specimens; the first and second dimensions individually explained 75% and 16% respectively of the total variance. C) PCoA of group C specimens; the first and second dimensions individually explained 26% and 15% respectively of the total variance. Codes, legends, and general layout as per Figure 3.

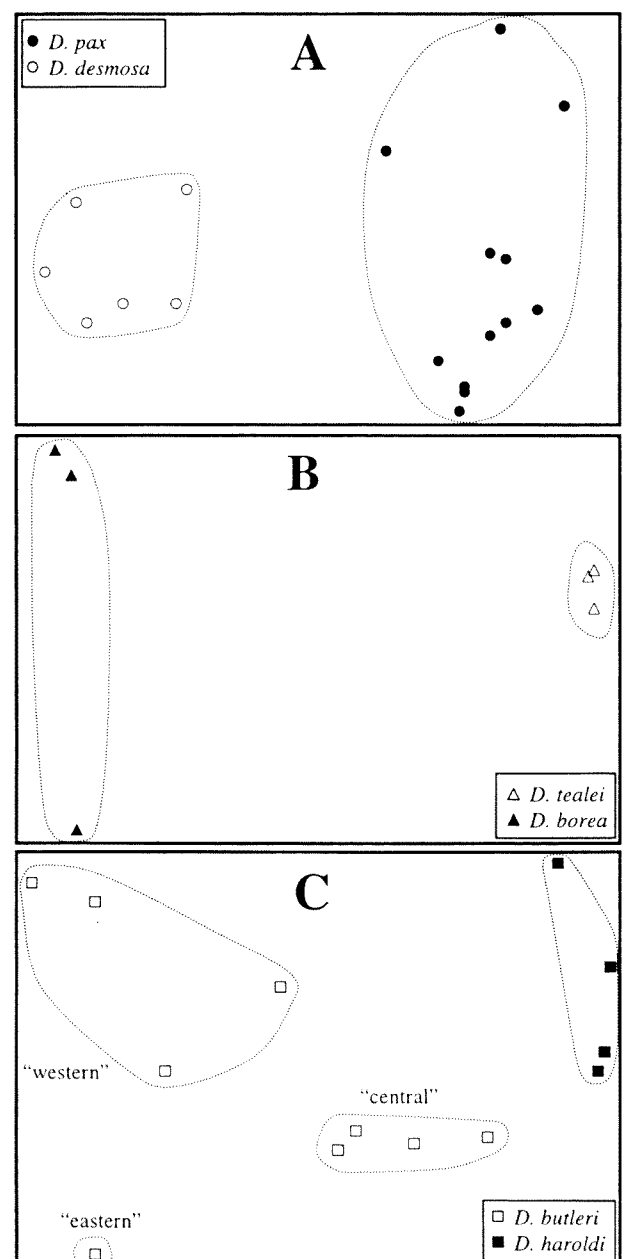


Table 5 Allele frequencies at 34 variable loci for the nine OTUs identified in the allozyme study. For polymorphic loci, the frequencies of all but the rarer/rarest alleles are expressed as percentages and shown as superscripts (allowing the frequency of each rare allele to be calculated by subtraction from 100%). A dash indicates no genotypes assignable at this locus.

Locus	<i>pax</i>	<i>desmosa</i>	<i>tealei</i>	<i>borea</i>	<i>tincta</i>	<i>butleri</i> "western"	<i>butleri</i> "central"	<i>butleri</i> "eastern"	<i>haroldi</i>
<i>Acon1</i>	a	a	a	a	a	b ⁸⁸ ,c	a ⁵⁰ ,b	b	a ⁷⁵ ,b
<i>Acon2</i>	d ⁴⁶ ,b	c ⁶⁷ ,d	c	c ⁸³ ,d	b ⁵⁰ ,c ³³ ,a	a ⁸⁸ ,b	d	d ⁵⁰ ,e	a ³⁸ ,d ³⁷ ,c
<i>Acp1</i>	a	a	a	b	a	a	a	a	a
<i>Acp2</i>	b	b	b	b	a	a	a	a	a
<i>Acyc</i>	b ⁶² ,a	b	a	a	a ⁶⁷ ,b	a	a	a	a ⁷⁵ ,c
<i>Ada</i>	b	b ⁹² ,c	b	b	b ⁶⁷ ,d	b	b	b	b ⁸⁷ ,a
<i>Adh1</i>	b	c ⁷³ ,b	b	b	b	b	b ⁸⁷ ,a	b	b
<i>Adh2</i>	d	a ⁵⁰ ,c	c	c	a	c	b ⁶³ ,c	c	b
<i>Ca</i>	a	a	a	a	a	b	b	b	b
<i>Dia</i>	b ⁷¹ ,e	b ⁷⁰ ,a	h ⁸⁸ ,j	h ⁸⁶ ,g ¹⁷ ,d	g ⁸³ ,h	g ⁷⁵ ,i	c ²⁵ ,f ²⁵ ,g ¹³ ,i ¹³ ,h ¹² ,j	g	–
<i>Enol</i>	c	c	b	c	c	c ⁶² ,b ²⁵ ,a	c	c	c ⁷⁵ ,b
<i>Est2</i>	d ⁶³ ,e	d	b	b ⁶⁷ ,c	b ⁷⁵ ,a	b	b	b	b ⁸⁸ ,c
<i>Fdp</i>	c	c ⁹² ,b	a	a	a	a	a	a	a
<i>Fum</i>	b	b	b	b	b	b ⁸⁸ ,d	b ⁸⁸ ,d	b ⁵⁰ ,c	b ⁷⁵ ,a ¹³ ,d
<i>Gda</i>	c	c	e	d	d	c ⁸⁷ ,a	c	c	c ⁸⁷ ,b
<i>Glo</i>	c ⁴⁶ ,b	c ⁸³ ,a	c	c	c	d	d	d	d
<i>Got1</i>	b ⁴⁶ ,a	b	b	b	b	b	b	c	b
<i>Got2</i>	b ⁸³ ,a	a	b	b	b	c	c	c	c ⁷⁵ ,d
<i>Gpd</i>	b	b	b	b	b ⁶⁷ ,a	b	b	b	b
<i>Gpi</i>	b	b ⁹² ,a	b	b	b	c	c	c	c
<i>Guk</i>	b ⁷⁵ ,a	b	b	a ⁸³ ,b	a	a	a	a	a
<i>Idh2</i>	c	c	c	c	c	b ⁸⁷ ,a	b	b	b ⁷⁵ ,a ¹³ ,d
<i>Me1</i>	c	c ⁶⁷ ,a	c	c	c	b ⁷⁵ ,c	b	b	c ⁸⁷ ,b
<i>Mpi</i>	b	b	b	b	b	a	a	a	a
<i>Ndpk1</i>	a	a	a	a	a	b	b	b	b
<i>Ndpk2</i>	b	b ⁸³ ,c	b	b ⁸³ ,a	b	b	b ⁸⁸ ,d	b	b
<i>PepA</i>	c ⁶² ,b	c	c	c	c	c ⁸⁷ ,a	c	d	c
<i>PepB</i>	f ⁴⁶ ,e	f ² ,d	e	e	e	e ⁷⁵ ,b	e ⁶² ,b	a	b ⁵⁰ ,e ²⁵ ,a ¹³ ,c
<i>PepD</i>	c ⁵⁴ ,d	d ⁵⁸ ,c	c ⁸⁷ ,a	d ⁵⁰ ,c ³³ ,f	d ⁸³ ,b	d ⁶³ ,c ²⁵ ,f	d	c ⁵⁰ ,d	d ⁶³ ,f ¹³ ,e ¹² ,g
<i>6Pg</i>	b ⁸⁸ ,c	b	b ⁸⁷ ,a	b	b ⁶⁷ ,c	d	d	e	d
<i>Pgm1</i>	c	c ⁷⁰ ,b	e	g	d	c ⁶⁷ ,a	e ⁸⁸ ,f	f	e ⁸⁸ ,f
<i>Pgm2</i>	a	a	a	a ⁸³ ,b	a	a	a	a	a
<i>Sod</i>	d ⁴⁶ ,g	d	d	c	d	d	d ⁷⁵ ,a	d	a ⁵⁰ ,b ²⁵ ,e ¹³ ,f
<i>Srdh</i>	b ⁹² ,a	b	b	b	d ⁶⁷ ,b	b ⁵⁰ ,c	c	c	c

Table 6 Genetic distance matrices for the nine OTUs of *Delma* identified by the Principal Co-ordinates Analyses. Lower triangle = %FDs; upper triangle = Nei Ds

OTU	<i>pax</i>	<i>desmosa</i>	<i>tealei</i>	<i>borea</i>	<i>tincta</i>	<i>butleri</i> "western"	<i>butleri</i> "central"	<i>butleri</i> "eastern"	<i>haroldi</i>
<i>pax</i>	–	0.08	0.25	0.27	0.27	0.55	0.55	0.68	0.53
<i>desmosa</i>	2	–	0.27	0.30	0.31	0.58	0.61	0.74	0.59
<i>tealei</i>	21	21	–	0.16	0.27	0.48	0.53	0.68	0.49
<i>borea</i>	21	23	12	–	0.17	0.50	0.54	0.67	0.49
<i>tincta</i>	21	21	16	12	–	0.40	0.43	0.56	0.40
<i>butleri</i> 'western'	37	40	35	35	28	–	0.07	0.13	0.10
<i>butleri</i> 'central'	40	42	37	35	33	5	–	0.15	0.04
<i>butleri</i> 'eastern'	47	49	49	44	42	14	9	–	0.21
<i>haroldi</i>	38	43	36	36	31	7	0	12	–

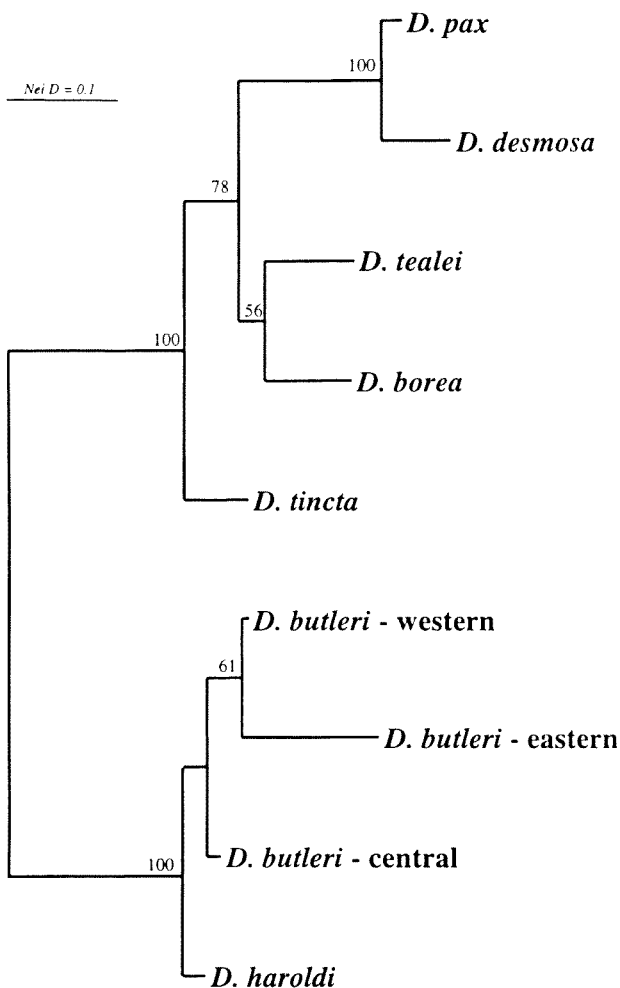


Figure 5 Neighbor-joining tree depicting the phylogenetic affinities of nine OTUs of *Delma*, based on Nei distances and rooted at the midpoint of the longest branch. Bootstrap proportions of 50% or greater from 100 pseudo-replications are indicated for all nodes. Scale represents a Nei D of 0.1.

The case for recognition of the 'Cape Range' morphotype as a distinct species is strongly supported by the genetic evidence. Although this population was historically associated first with *D. pax* and then with *D. tincta*, its genetic affinities clearly lie with *D. borea*. Nevertheless, the 'Cape Range' morphotype and *D. borea* are well-differentiated genetically, with a total of six fixed differences and a Nei D of 0.16 between them. This is equivalent to the observed genetic differentiation between *D. borea* and *D. tincta* (12%FD and Nei D of 0.17), two species that are broadly sympatric (but rarely syntopic; Shea 1991) across northern Australia. Furthermore, the 'Cape Range' morphotype is readily distinguished on several morphological criteria from *D. borea* (see below).

In contrast, the 'desert' morphotype is weakly differentiated from typical *D. pax*, with only a single observed fixed difference in their allozyme profiles. Despite this, there remains a strong case

for treating these morphologically distinct populations as discrete evolutionary lineages. First, in addition to their single fixed difference at the *Adh2* locus, they also displayed major differences in allele frequency at a further three loci (*Acon2^d* DP = 63%, *Adh1^b* DP = 75%, *Got2^e* DP = 83%; Table 5). Second, the spatial distribution of variation in each of the 'near fixed' loci within each taxon is not clustered in specific localities around the periphery of the Pilbara, as might be expected if regular gene flow was occurring between the two morphotypes, nor is it arranged in any geographic pattern that might be identified as a genetic cline. Last, each of the *D. pax* and the 'desert' morphotypes have quite large geographic distributions (see below), which nevertheless appear to abut around the perimeter of the Pilbara uplands, involving a total distance of many hundreds of kilometres. Such a geographic arrangement ought to facilitate gene flow between the two forms, yet they appear to maintain their morphological distinctiveness across their ranges.

In the following section we diagnose two new species of *Delma*, redefine *D. pax* as a taxon restricted to the Pilbara uplands, and comment on the distribution and morphology of *D. borea* populations in Western Australia.

SYSTEMATICS

Delma tealei sp. nov.

Figures 6–7

Material examined

Holotype

153811 in the Western Australian Museum, an adult female collected on 12 September 2003 by B. Maryan and D. Algaba on Charles Knife Road, Cape Range, Western Australia (22°07'08"S 114°03'44"E). Liver sample preserved in -75°C ultrafreeze at W.A. Museum.

Paratypes

Sex indicated in brackets.

Western Australia: 52934-35 (both F) Shothole Canyon (22°03'S 114°02'E); 82532 (M) 6 km W Exmouth (21°56'S 114°04'E); 88548 (F) 2 km E Yardie Creek mouth (22°20'S 113°49'E); 102837 (M) Cape Range National Park (22°09'01"S 113°59'52"E); 153813 (M) 2 km S Yardie Homestead Caravan Park (21°53'37"S 114°00'34"E); 153819 (M) Shothole Canyon (22°03'49"S 114°00'42"E).

Diagnosis

A moderately small species of *Delma* (SVL up to 88mm) with modally 14 midbody scales, two pairs of supranasals and relatively plain colouration apart from variegated ventrolateral scales on forebody.



Figure 6 Holotype (153811) of *Delma tealei*, photographed in life (B. Maryan).

Adults lack any trace of dark markings on head or neck. Differs from the otherwise similar *D. borea* in lower modal midbody scale count, typically the third supralabial positioned below the eye, absence of pattern on head and neck in adults and longer hindlimb flaps in both sexes.

Description

Rostral with obtuse apex, penetrating between rostral supranasals; two pairs of supranasals, caudal pair much larger; rostral supranasals in moderate contact with first supralabial; caudal supranasals in point to moderate contact with nostril; postnasal single; loreals 5–9, subequal; suboculars 3–4; supraciliaries 5, fifth much larger; supraoculars 2, second wider than first; supralabials 5, third elongate and positioned below eye, fifth much smaller; infralabials 4, third elongate; occipital scale present; upper temporals 2. General form of head and details of scalation illustrated in Figure 7. Midbody scale rows 14; transversely enlarged ventral scales 50–52; hindlimb scales 8.

Morphological Variation: 82532 has a small scale partly wedged between second and third supralabial on left side; 52934 has upper temporals divided on both sides.

Colouration and patterning

In preservative, upper and lateral surfaces light grey or light to dark brown, head slightly darker. Supralabials pale to dark brown and infralabials pale with brownish vertical streaks or blotches mostly centered on first and third sutures along series. Lateral scales on forebody typically variegated, bases greyish white to white, centres blackish (mostly a dark smudge) and apices greyish

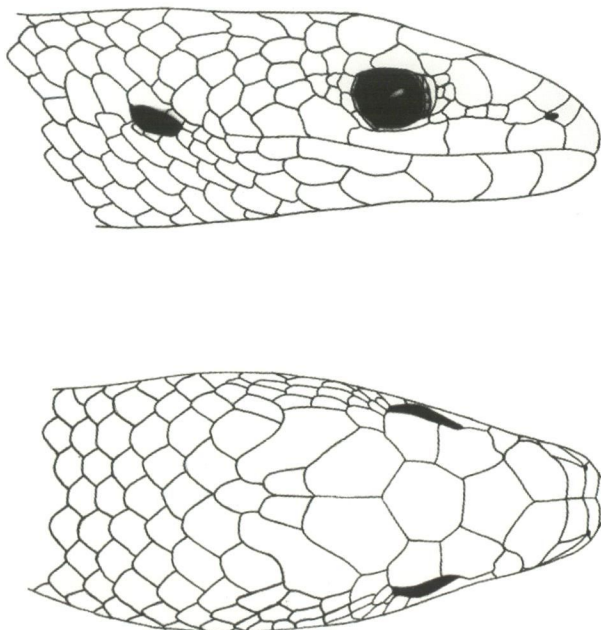


Figure 7 Head scalation of *Delma tealei* holotype (153811) in lateral (top) and dorsal (bottom) views.

to brownish grey. Variation includes individuals (e.g., 102837) with barely discernible variegation; and others (e.g., 52934) with distinct white-centred scales bordered by black smudging and with light brown apices. Lower surface greyish white or white with diffuse dark smudging on posterior edges of some scales.

In life, a subtle pinkish flush is noticeable on the dorsal and lateral scales immediately forward of and behind vent (e.g., 153811, 153813, 153819); this colour is lost in preservative.

No immature specimens are available for this

species. Accordingly, it is not known whether or not it displays the ontogenetic fading of head and neck patterning displayed by *D. pax* and some *D. borea* (see below for details).

Details of Holotype

Snout-vent length (mm) 79; tail 210; loreals 8; midbody scale rows 14; ventrals 52; hindlimb scales 8. Light grey upper and lateral surface, supralabials smudged grey aligned with dark vertical streaks on infralabial sutures 1–3, variegated lateral scales on forebody bases greyish white, apices greyish and some scales with blackish centres. Lower surface white and unpatterned.

Etymology

Named for zoologist Mr Roy Teale, in recognition of his contribution to Western Australian natural history and the collections of the Western Australian Museum, and his active support of numerous taxonomic research projects.

Distribution and sympatry

Apparently restricted to the Cape Range Peninsula of North West Cape in Western Australia

(Figure 8), a heavily dissected limestone plateau, sparsely vegetated with *Triodia*, shrubs and low eucalypts; gorges within the range are more heavily vegetated (Storr and Hanlon 1980).

Three other species of *Delma* are recorded on the Cape Range Peninsula. *Delma nasuta* Kluge, 1974 and *D. tincta* De Vis, 1888 are known from multiple localities and the regional sample is consistent with other populations of these widespread taxon. A third taxon, currently associated with *D. australis* Kluge, 1974 of southern Australia, is known from a single specimen (132470) collected at Shothole Canyon. Specimens of *D. tincta* were collected on the same occasion as *D. tealei* at four localities (Shothole Canyon, 52933; Cape Range National Park, 102838; 2 km S Yardie Homestead Caravan Park, 153814; Charles Knife Road, 153820).

Comparison with other species

Delma tealei will be compared first with *D. borea* and *D. tincta*, the two species with which it is most similar to, then with each of the regionally sympatric *D. nasuta* and *D. australis*, and finally with geographically distant congeners with which it shares important characters.

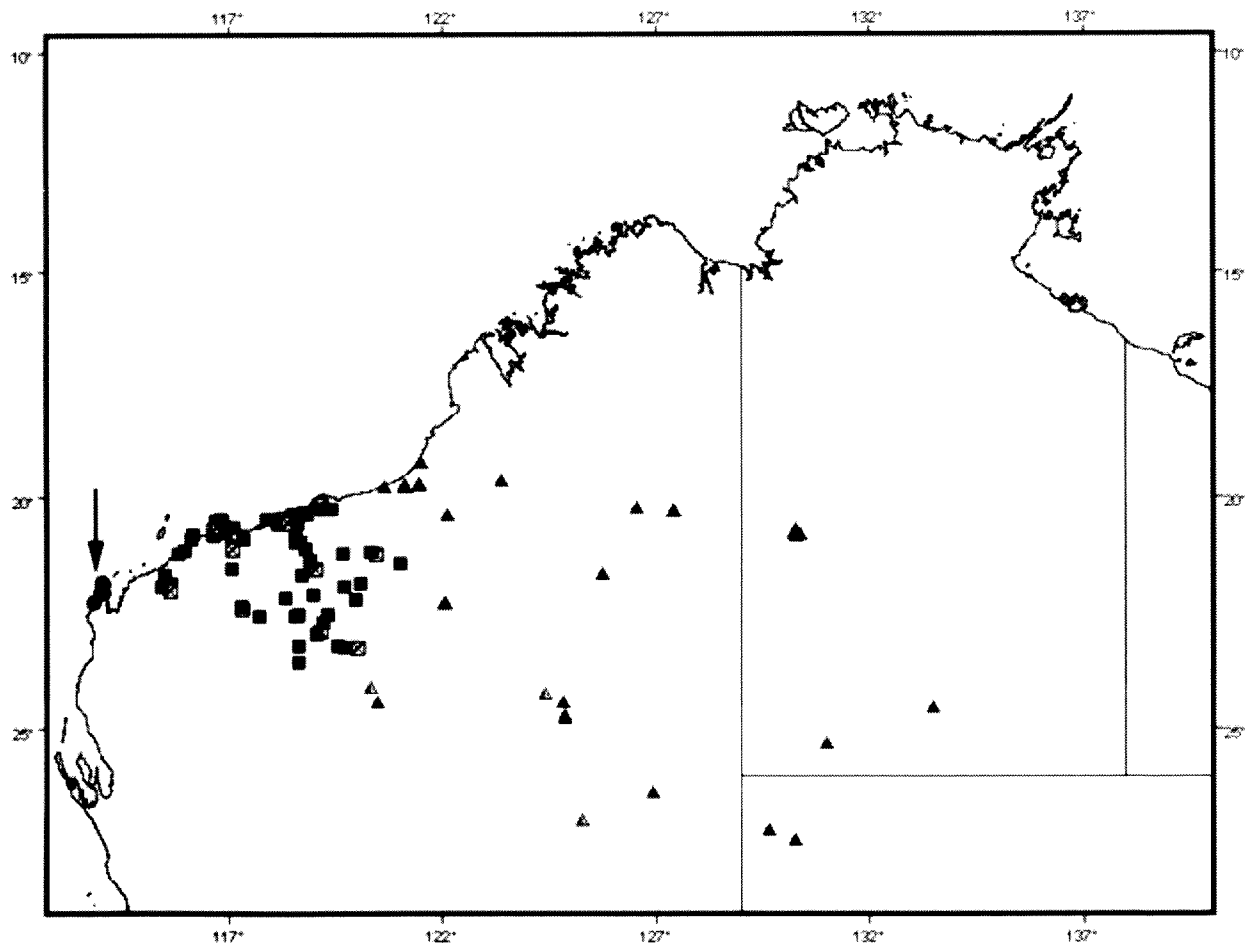


Figure 8 Map of northwestern Australia showing location of specimens examined in this study of *Delma tealei* (circles with arrow), *Delma desmosa* (triangles) and *Delma pax* (squares). Open symbols with cross indicate specimens examined in allozyme analysis.

Delma tealei is morphologically most similar to populations of *D. borea* on the western Pilbara islands (e.g., 28656, 37371, 37406, 48559). These taxa are similar in body size and share two pairs of supranasals and some indication of variegated ventrolateral scales on the forebody. However, all populations of *D. borea* have higher midbody scale row counts (modally 16 versus 14), some indication in adults of pale brown bands on the head and neck, and typically the fourth supralabial positioned below the eye (typically the third in *D. tealei*).

Delma tealei and *D. tincta* share modally 14 midbody scales and indication of variegated ventrolateral scales on the forebody. *Delma tincta* has one pair of supranasals (two pairs in *D. tealei*) and dark dorsal head markings that are especially distinctive on immature specimens but remain visible on most adult specimens (Storr *et al.* 1990) including individuals (e.g., 52933, 102838, 153814) from some of the same localities as the new species. *Delma tincta* also has smaller hindlimb flaps than *D. tealei* (Table 1). The hindlimb scale counts are correspondingly lower in *D. tincta* (5 versus 8).

Delma nasuta from Cape Range Peninsula and elsewhere grows to larger size (SVL up to 112mm versus 88mm) and has a more elongate snout, higher midbody scale row counts (modally 16 or 18 versus 14), more loreals (6–23 versus 5–9) and a reticulated or spotted body pattern formed by a dark spot or emargination on numerous body scales.

The Cape Range Peninsula specimen of *D.*

'*australis*' is smaller than *D. tealei* (SVL 57mm versus up to 88mm) and further differs in having one pair of supranasals (versus two), more midbody scale rows (modally 18 versus 14), and very different patterning that includes fine black lateral bars on the neck and throat. It also shares an unusual arrangement of the loreal scales with typical *D. australis* (loreal row is broken by prefrontal-supralabial contact versus continuous in *D. tealei*).

Delma pax and *D. desmosa* are both allopatric to *D. tealei* (Figure 8). They are distinguished by higher midbody scale row counts (modally 16 versus 14) and uniformly coloured ventrolateral scales on the forebody. Adult *D. desmosa* differ further by the ontogenetic retention of dark dorsal head markings.

Habitat

The holotype was raked (using a 3-prong cultivator) from dead *Triodia* clumps on a low hill vegetated with *Triodia* and sparse shrubs on brown stony loam (Figure 9). The paratypes were collected in the same manner except for 88548 that was found beneath an exfoliated limestone slab on heavy *Eucalyptus* leaf litter, and 102837 that was pit-trapped in a valley floor surrounded by low limestone breakaways (P. Kendrick, *pers. comm.*). All collection sites for this species combine hummock grass and limestone, an association that is overwhelmingly dominant on the Cape Range Peninsula.



Figure 9 Low stony hills covered with dense *Triodia* at the Charles Knife Road, Cape Range WA, the type locality for *Delma tealei* (B. Maryan).

Remarks

Delma tealei was originally thought to represent a southern outlier population of *D. pax* when first collected during herpetofaunal surveys (Storr and Hanlon 1980). The combination of two pairs of supranasals and third upper labial in subocular position probably influenced this decision. However, in preparation for publication of a handbook to the gekkonoid lizards of Western Australia (Storr *et al.* 1990), fresh examination resulted in the transfer of this population to *D. tincta*. This action probably reflected the shared condition of 14 midbody scale rows in each of *D. tealei* and *D. tincta*.

In Storr *et al.* (1990) the species account for *D. tincta* (incorporating *D. tealei*) included the statement 'usually one (occasionally two) pairs of supranasals' but without reference to a specific population. We consulted Kluge (1974) and also examined all Western Australian Museum holdings of *D. tincta* (see Appendix 1) to ascertain whether this statement holds true following exclusion of *D. tealei*. Kluge (1974) examined 168 specimens and encountered a single individual (22323) with unilateral division (left side) of the supranasals. Similarly, in a total of 163 specimens examined by us, we found only one example (104426) with bilateral division into two pairs of asymmetrically shaped supranasals, and another (85190) with unilateral division (right side). Both of these examinations suggest that any individual variation away from the conditional state of undivided supranasals in *D. tincta* is extremely rare. Accordingly, we believe that the reference by Storr *et al.* (1990) to supranasal multiplication in *D. tincta* was in specific reference to specimens from the Cape Range Peninsula referred herein to *D. tealei*. *Delma inornata* from eastern Australia appears to be the only species of *Delma* that exhibits regular intraspecific variation (around 10%) in having either 1 or 2 pairs of supranasals (Kluge 1974: 103). Among Western Australian *Delma* the combination of 14 midbody scale rows and 2 pairs of supranasals is unique to *D. tealei*.

Delma tealei would probably receive an IUCN conservation rating of 'Least Concern' on account of the lack of evidence for any population decline and most of its geographic range being protected within the Cape Range National Park. However, in many areas on the Cape Range Peninsula, introduced Buffel Grass (*Cenchrus ciliaris*), has virtually replaced the original ground cover (Aplin 1998) and there is an identified priority to monitor and manage its spread (Keighery and Gibson 1993). Particular attention should be given to the impact on species such as *Delma tealei* that are probably dependent on *Triodia* and other hummock grasses for their survival.

Delma desmosa sp. nov.

Figures 10–12

Material examined

Holotype

102657 in the Western Australian Museum, an adult female collected on 10 October 1996 by S. van Leeuwen at Site Cooma 4, Little Sandy Desert, Western Australia (24°06'17"S 120°19'30"E). Liver sample preserved in -75°C ultrafreeze at W.A. Museum.

Paratypes

Sex indicated in brackets.

Western Australia: NTM 17987 (M) Sandfire Flat (19°47'S 121°09'E); 45809-10 (both M) Wallal Downs Homestead (19°47'S 120°38'E); 63313 (M) Djaluwon Creek (20°20'S 127°26'E); 64001 (M) Anketell Ridge (20°24'S 122°07'E); 64097 (F) Staffords Bore (20°21'S 127°24'E); 64143 (F) Breaden Pool (20°15'S 126°34'E); 64186 (F) 1 km S Waddawalla Well (21°41'S 125°46'E); 75798 (F) Dragon Tree Soak (19°39'S 123°23'E); 75830 (M) Anna Plains Homestead (19°15'S 121°29'E); 87007 (F) Sandfire Roadhouse (19°46'S 121°06'E); 87353 (M) 3 km SE Wallal Downs Homestead (19°47'S 120°40'E); 88535-41 (M, F, F, F, M, F, F) 55 km S Anna Plains Homestead (19°44'S 121°28'E); 94757, 94776-77 (F, M) 80 km S Telfer Mine (22°20'12"S 122°02'26"E); AM 100853, 101548 (both M) 6.6 km N Sandfire Roadhouse (19°19'S 121°16'E); 102650 (M) Cooma 5, Little Sandy Desert (24°06'41"S 120°19'10"E); 108477 (M) 18 km S Lake Hancock (24°27'S 124°50'E); 114555 (F) Sandfire Roadhouse (19°46'S 121°06'E); 126496 (M), 126498 (M) Gibson Desert Nature Reserve (24°43'S 124°52'E); 132802 Warri Airstrip (24°15'S 124°24'E); 139089 (M) Mandora Station (19°45'16"S 121°26'59"E); 140442 (M) Yanneri Lake (24°27'08"S 120°29'02"E); 145073 (M) Officer Basin area (26°55'58"S 125°16'44"E); 151252 (F) Townsend Ridges (26°20'25"S 126°56'26"E). **Northern Territory:** NTM 14901 (F) 12 km SW Sangsters Bore (20°52'S 130°16'E); NTM 15038 (M) Uluru National Park (25°21'S 131°01'E); NTM R15138 (M), NTM 15144 (M), NTM 15146 (F), NTM 15151 (M) 12 km SW Sangsters Bore (20°52'S 130°16'E); NTM 15230 (M) 17 km W Sangsters Bore (20°48'S 130°14'E); NTM 15501 (M) Uluru National Park (25°21'S 131°01'E); NTM 20250 (M) Sangsters Bore (20°51'09"S 130°23'09"E); NTM 26789 Henbury (24°34'S 133°30'E); NTM 32301 (M) 10 km WSW Sangsters Bore (20°44'S 130°16'E); NTM 34489 (F) Ayers Rock (25°20'S 131°01'E). **South Australia:** SAM 48671 (M) 9.3 km NNW Cheeseman Peak (27°19'46"S 130°17'36"E); SAM 59561 (F) 3.3 km W Mount Holder, Birksgate Range (27°08'43"S 129°39'51"E).



Figure 10 Holotype (102657) of *Delma desmosa*, photographed in life (B. Maryan).

Diagnosis

A moderately small, stout species of *Delma* (SVL up to 90mm) with modally 16 midbody scales, two pairs of supranasals and distinctive dark dorsal head markings present throughout life (any ontogenetic fading is restricted to markings forward of the eyes).

Description

Rostral with obtuse apex, penetrating between rostral supranasals; two pairs of supranasals, caudal pair much larger; rostral supranasals in moderate contact with first supralabial and caudal supranasals in point contact or only narrowly separated from the nostril; postnasal single; loreals 3–9, subequal; suboculars 3–4; supraciliaries 5, fifth much larger; supraoculars 2, second wider than first; supralabials 5–6, third typically elongate and positioned below eye (rarely, fourth is below eye); posteriormost supralabial much smaller; infralabials 4 (rarely 5), third elongate; occipital present; upper temporals 2.

General form of head and details of scalation illustrated in Figure 11. Midbody scale rows 16; transversely enlarged ventral scales 48–59; hindlimb scales 8–10.

Morphological Variation: 75798 and 132802 have third supralabial divided on left side; 94757 has this scale divided on both sides. The location of accessory supralabial suture (e.g., anterior, centre

or posterior) determines whether it is the third or fourth that is positioned below the eye.

64186 has third infralabial divided on right side; 114555 has this scale divided on both sides.

64097 has second supraocular fused with fourth supraciliary on both sides.

63313 has an upper loreal that is interposed between first and second loreals and contacts second supralabial on both sides.

88539 has supraoculars fused into one scale on right side.

NTM 15146 has a small scale interposed between caudal pair of supranasals and rostral supranasals divided into two scales on right side.

AM 100583 has first supraciliary fused with an upper loreal on right side.

AM 101548 has three small scales interposed between third and fourth supraciliary on right side.

Colouration and patterning

In preservative, upper and lateral surface grey to greyish brown merging with light brown on tail (particularly regenerated portion). Irregular black smudging on dorsal scales in some individuals (e.g., 64186, 88537, 15038, 15151, 15501). Lateral scales on forebody are plain. Lower surface immaculate white.

Head of juveniles and adults typically with three to four dark brown to black dorsal to lateral bands, that narrow as they descend and terminate obtusely

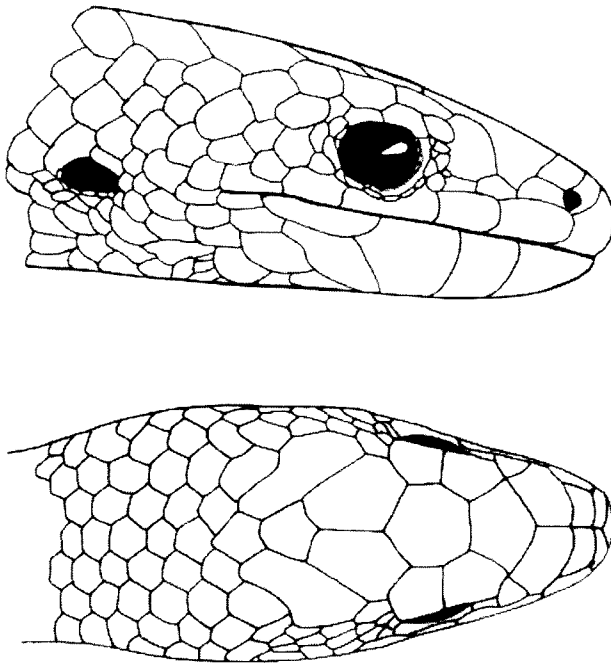


Figure 11 Head scalation of *Delma desmosa* holotype (102657) in lateral (top) and dorsal (bottom) views.

on mental scale, on infralabials and behind the ear. Dark head bands are most intense on immature specimens (Figure 12A) but remain well-defined in most adults (Figure 12C; ontogenetic fading is a common occurrence in other *Delma* spp.). Interspaces between dark bands light brown, greyish to white and usually widest on back of head through ear and neck. Supralabials and infralabials whitish in between dark bands. Below the mouth, bands are typically centred on suture between mental and first infralabial, and on suture between second and third infralabials; suture between first and second infralabials is invariably clear; occasionally, the first dark head band completely covers the first infralabial but not its anterior suture (e.g., 140442).

In adults that show signs of ontogenetic fading of the head pattern (Figure 12B), the first band (on snout and lores) and second band (over eyes) typically become diffuse and merge to form a cream to light brown colour forward of eyes. The broader third and fourth dark bands (forward of and behind ears, respectively) are persistent in adults and are rarely diffuse or broken. In some individuals (e.g., 15038, 34489, 88537) coalescent dark smudges positioned transversely across forebody are suggestive of a fifth dark band. Adult specimens of *D. desmosa* with pronounced ontogenetic fading come from localities spread across the western half of the range of the species, including localities in the Great Sandy Desert (e.g., 64097, 64143, 75830) that are remote from the range of *D. pax* in the Pilbara region. The wide geographic distribution of

these individuals make it unlikely that they are the product of introgression between *D. pax* and *D. desmosa*.

In life, some adults have pale orange-brown interspaces between the dark bands; this pigment is lost in preservative.

Details of Holotype

Snout-vent length (mm) 87; tail 163; loreals 8 on left side, 9 on right; midbody scale rows 16; ventrals 59; hindlimb scales 9. Greyish brown upper and lateral surface.

Indication of four dark brown head bands as follows: first on lores is diffuse and terminates as smudge on first infralabial; second terminates on suture between second and third infralabial, leaving preceding suture clear white; third and fourth bands are dark brown and well-defined.

Etymology

From the Greek *desmos*, a chain, tie, or band, in specific reference to the distinctive and persistent dorsal head bands of this species.

Distribution and sympatry

Widespread in arid desert regions of western and central Australia (Figure 8) extending west to the vicinity of the 80 mile beach (Anna Plains and Wallal Downs Stations), south to the Little Sandy Desert and Officer Basin area and east through the Great Sandy, Tanami and Great Victoria Deserts into central Northern Territory (Sangsters Bore, Uluru National Park and Henbury) and northwestern South Australia (Cheeseman Peak).

The geographic distributions of *D. desmosa* and *D. pax* appear to be allopatric (Figure 8). Currently the two species are known to occur within 90 km of each other (e.g., 102650, 102657 from Little Sandy Desert versus 125452 from 30 km E Newman, respectively). Specimens from these proximate localities do not show any admixture of characters as might be expected if significant levels of gene flow were occurring across a contact zone or step cline.

Five *Delma* species have geographic distributions that overlap that of *D. desmosa*: *D. borea*, *D. butleri*, *D. haroldi*, *D. nasuta* and *D. tincta*. Among these species, the greatest morphological similarity occurs between *D. desmosa* and *D. borea* (see below). The distributions of *D. borea* and *D. desmosa* are broadly overlapping in the south Kimberley, southern Northern Territory and northwestern South Australia (Figures 8, 15) but there are few known instances of actual sympatry. Recent collections by P. Kendrick of the Department of Environment and Conservation have extended the mainland W.A. range of *D. borea* south to the vicinity of Mandora (e.g., 112725-26, 139058,

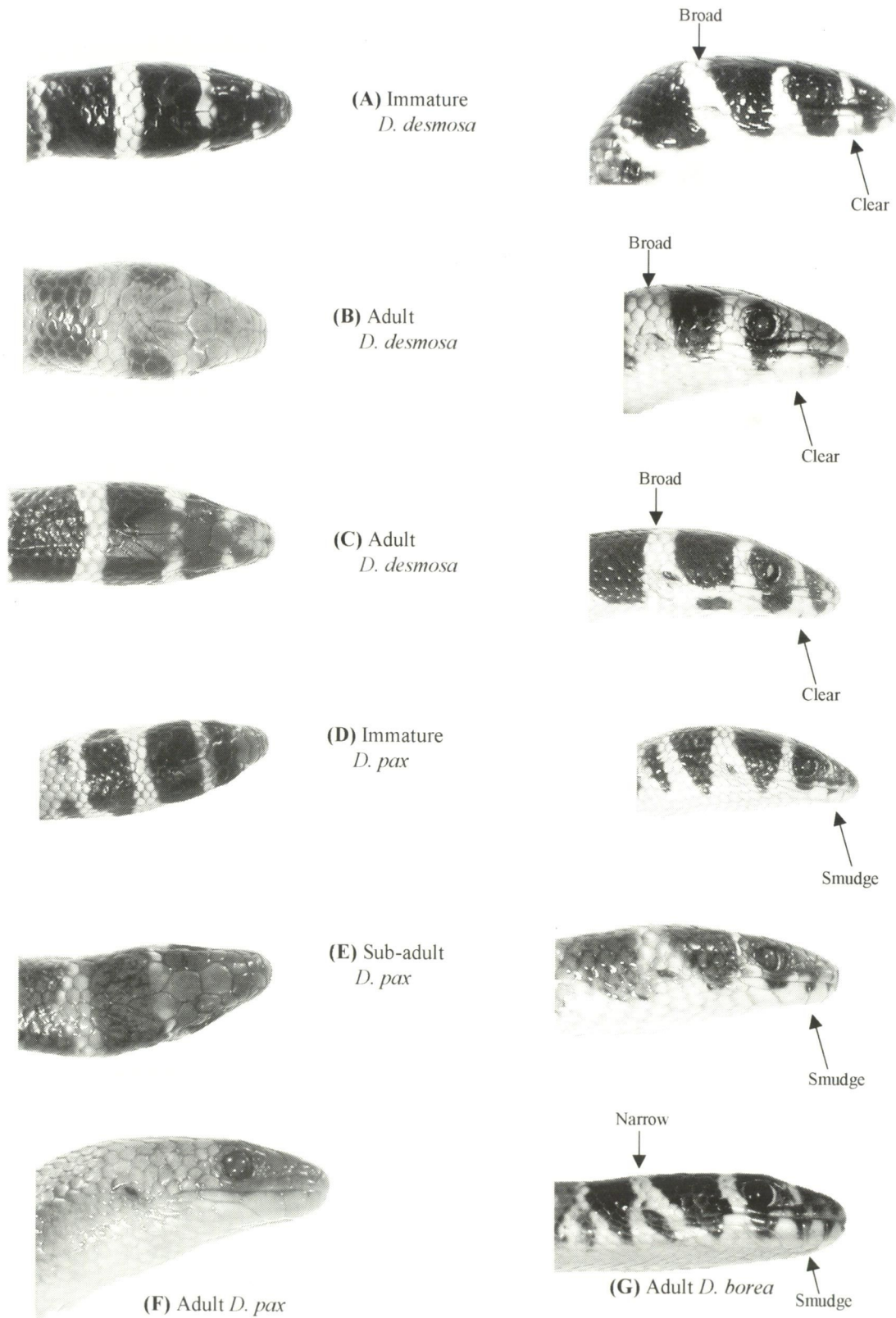


Figure 12 Head patterning of A, *D. desmosa*, immature from Townsend Ridges (151252), B, *D. desmosa* adult with weak bands forward of eyes from Staffords Bore (64097), C, *D. desmosa* adult with strong bands from Ayers Rock, Northern Territory (NTM 34489), D, *D. pax* immature from 82km E Port Hedland (140396), E, *D. pax* sub-adult with fading bands from DeGrey River Station (132549) and arrows indicating clear or pigmented suture and broad auricular band in *D. desmosa*, all shown in dorsal and lateral views and F, *D. pax* adult from Potter Island (139353) showing complete lack of head patterning, G, *D. borea* adult with strong bands from Mitchell Plateau (77201) and arrows indicating pigmented suture and narrow auricular band, shown in lateral views.

139062-63) where *D. desmosa* (e.g., 139089) is also recorded. Currently this represents the only known instance of sympatry for these two species in Western Australia. However, the single specimen of *D. desmosa* was obtained on the crest of a *Triodia*-covered sandridge, while specimens of *D. borea* came from the edge of a spring with *Melaleuca leucadendra* on clayey soil. Records of *D. desmosa* and *D. borea* from the arid southern Northern Territory and northwestern South Australia also tend to come from different localities. Systematic faunal surveys have only recently recorded *D. borea* from northwestern South Australia (Robinson *et al.* 2003) and the Uluru National Park (McAlpin 2005). Generally, *D. borea* prefers areas of stony or heavy soils with *Triodia* and tussock grasses or savanna woodland with grass/leaf litter (B. Maryan, *personal observation*) and appears to not occupy *Triodia* on sandplains (Kluge 1974: 82), the preferred habitat of *D. desmosa*. The available information thus suggests a degree of habitat partitioning between *D. desmosa* and *D. borea* in areas where their ranges interdigitate.

In Western Australia, other recorded instances of sympatry involving *D. desmosa* include *D. haroldi* and *D. nasuta* in the Little Sandy Desert and Central Ranges (B. Maryan and P. Doughty, *personal observation*) and *D. butleri* has been collected from the Officer Basin area, where *D. desmosa* (e.g., 145073) is also recorded. In the Northern Territory, Reid *et al.* (1993) records both *D. butleri* and *D. nasuta* from the same survey site as '*D. pax*' (= *D. desmosa*) in Uluru National Park.

Comparison with other species

Delma desmosa will be compared first with *D. pax* and *D. borea*, two species with which it has previously been confused, and then with other regionally sympatric *Delma* spp.

Delma pax and *D. desmosa* are similar in body proportions (Table 1) and agree in most details of head and body scalation. The head pattern of juveniles is also similar, consisting of four 'opalescent' black bands and pale interspaces (Figure 12A, D), but the fate of this pattern is very different. In *D. desmosa* the bands are retained through to adult life (Figures 10, 12C) while in *D. pax* they undergo pronounced ontogenetic fading (Figure 12E) such that adults typically lack any head pattern (Figures 12F, 14). Another difference in head pattern concerns the ventral extent of the anterior dark head bands; in *D. pax* the first (on snout) and second (through eyes) bands typically terminate on the infralabials, while in *D. desmosa* they extend onto the mental scale and below the infralabials, and are visible in ventral view. In addition, the first dark head band on the snout in *D. pax* is regularly weak or absent and usually distinct in *D. desmosa*. Immature specimens of *D. pax*

typically have three dark brown smudges on the lower lip, situated over the sutures between the mental and anterior two infralabial scales (Figure 12D–E). In *D. desmosa* the suture between the first and second infralabial typically is unpigmented (Figure 12A–C).

On meristic and mensural data, *D. desmosa* averages slightly smaller than *D. pax* for most measurements (Table 1). This contrast is particularly striking for males, reflecting more pronounced sexual dimorphism in *D. pax* than *D. desmosa* (Table 1). In both sexes the mean ventral scale count is significantly lower in *D. desmosa* than in *D. pax* (Table 4).

Delma borea is similar to *D. desmosa* in overall body size but has shorter hindlimb flaps and a significantly higher average number of ventral scales in both sexes (Tables 1, 4). The two species are readily distinguished by head pattern. *Delma borea* has a pale inter-band on the back of head which narrows dorsally but broadens or 'forks' at the ear aperture (Figure 12G). In *D. desmosa* the auricular inter-band typically is of even width or only slightly broader laterally (Figure 12A–C). Most *D. borea* also have some variegated ventrolateral scales on the forebody. These scales are unpatterned in *D. desmosa*. *Delma borea* typically have the fourth supralabial positioned below the eye (typically the third in *D. desmosa*).

Delma borea and *D. pax* both have three dark brown smudges situated between the nostril and the eye, and positioned over the mental and infralabial scale sutures (Figure 12D–E, G). These smudges are absent only in some adults devoid of any head pattern (Figure 12F). In contrast, the suture between the first and second infralabial typically is clear in *D. desmosa*; in occasional specimens (e.g., 140442) the first head band completely covers the upper portion of the first infralabial scale.

Apart from *D. borea*, the only *Delma* species with distributions overlapping that of *D. desmosa* are *D. butleri*, *D. haroldi*, *D. nasuta* and *D. tincta*. *D. desmosa* is easily distinguished from the first three by having dark dorsal head markings and from *D. tincta* by the presence of two pairs of supranasal scales (one pair in *D. tincta*), a higher midbody scale row count (modally 16 versus 14) and unpatterned ventrolateral scales on the forebody.

Habitat

The holotype was raked (using a 3-prong cultivator) from *Eucalyptus chippendalei* leaf litter in dune swale on red sand with groundcover of *Thryptomene* and *Triodia* (Figure 13). Notes accompanying some Western Australian paratypes include "raked from dead *Triodia* clumps and shrubs on crest of sandridges" (e.g., 88535-41); "pit-trapped on claypan with *Acacia* over mixed grasses



Figure 13 *Triodia* sandplain in swale with red sand dune covered with *Eucalyptus chippendalei*, *Acacia* and *Triodia* at the Little Sandy Desert WA, the habitat for *Delma desmosa* (B. Maryan).

and samphire" (e.g., 75798); "along minor drainage lines with fringing *Eucalyptus*" (e.g., 63313, 94776-77) and "active at night on road in sandplain with sparse *Acacia* over *Triodia*" (e.g., 114555). Habitat details for paratypes from Northern Territory and northwestern South Australia are "pit-trapped in *Triodia* grassland" (e.g., 14901, 15038, 15138, 15144, 15146, 15151, 15230, 15501, 20250); "mulga woodland over bluebush and tussock grasses on sandplain" (e.g., 48671) and "under loose stones on rocky hillside" (e.g., 59561).

Remarks

The specific characteristics of *D. desmosa* have created prior confusion between *D. borea* and *D. pax*. Shea (1991) drew attention to this problem by mentioning a specimen from Ayers Rock (NTM 1319; renumbered 34489) that shares *D. borea* and *D. pax* scalation characters. This specimen is herein referred to *D. desmosa* (Figure 12C). Systematic faunal surveys by Reid *et al.* (1993) and McAlpin (2005) also mentioned problems with identification and variously assigning a *Delma* sp. to *D. borea* or *D. tincta* in previous reports, but identified by them as '*D. pax*'. Their accounts of '*D. pax*' from Uluru National Park are most likely based on individuals of *D. desmosa*.

Ehmann (1992: 94) and Reid *et al.* (1993: 49) illustrate *D. desmosa* from the Great Sandy Desert, Western Australia and from Uluru National Park, Northern Territory respectively; in both publications the specimens are identified as *D. pax*.

Delma pax Kluge, 1974

Figure 14

Delma pax Kluge (1974: 113–117). 14804 in the Western Australian Museum, an adult female collected on 21 May 1961 by G.M. Storr at Jones River, Western Australia (20°58'S, 117°23'E).

Revised diagnosis

A moderately small, stout species of *Delma* (SVL up to 98mm) with modally 16 midbody scales, two pairs of supranasals, and a plain adult colouration due to pronounced ontogenetic fading of dorsal head markings (markings prominent in juveniles).

Description

Rostral with obtuse apex, penetrating between rostral supranasals; two pairs of supranasals, caudal pair much larger; rostral supranasals in moderate contact with first supralabial and caudal supranasals in point contact or only narrowly separated from the nostril; postnasal single; loreals 4–10, subequal; suboculars 2–4; supraciliaries 5 (rarely 4), fifth much larger; supraoculars 2, second wider than first; supralabials 5–6, third typically elongate and positioned below eye (occasionally, fourth is below eye), posteriormost supralabial much smaller; infralabials 4, third elongate; occipital present; upper temporals 2. Midbody scale rows usually 16 [14 in 12.4 % of specimens; 18 in one specimen (119045; from Port Hedland)]; specimens with 14 midbody scale rows are Bohemia



Figure 14 Adult *Delma pax* from Meentheena, photographed in life (B. Maryan).

scattered throughout the range of *D. pax* and often come from the same localities as specimens with 16 midbody scale rows. Storr *et al.* (1990) state that *D. pax* has 'rarely 17' midbody scale rows but without citing specimen details. Transversely enlarged ventral scales 50–60; hindlimb scales 8–10.

Morphological Variation: Kluge (1974) examined 16 *D. pax* and recorded only a single specimen with the fourth supralabial below the eye on one side only (SAM 3445 from Pilgangoora Well). Our examination of a further 97 specimens found this condition in unilateral or bilateral states in 20% of individuals, as follows: fourth supralabial below eye on both sides in 73146, 102137, 113387, 119045-046, 129930, 132657, 135919, 139294, 140396, 145680 and 146649; fourth supralabial below eye on right side only in 127829, 135320, 139353 and 146591; on left side only in 9943, 73841 and 129658.

Other variants are:

9946 has fusion of second and third supraciliaries (total 4) on both sides; 132606 has same condition on right side only.

81390 has rostral contacting caudal supranasals and thus separating rostral supranasals; 129930 has small scale interposed between rostral supranasals.

119045 has two upper loreal scales on right side.

145748 has rostral and caudal supranasals fused on right side.

Colouration and patterning

In preservative, upper and lateral surface brown to reddish brown merging into pale grey on lower

lateral surfaces. Lateral scales on forebody are plain. Lower surface white and unpatterned.

Head of juveniles typically with strong pattern of transverse bands (Figure 12D). Intensity of bands diminishes with increasing body size (= age) such that head and neck of large adults are typically light to reddish brown and unpatterned (Figures 12F, 14). Where traces of pattern are retained (e.g., 129658, 132548, 139170, 140021), this consists of very diffuse pale brown spaces ('ghosting' of bands) between the ears and behind the eyes.

Head pattern of immature specimens consists of three to four brown to blackish brown bands that narrow as they descend and terminate obtusely on the infralabials and behind the ear. The first band (on snout) is variably developed and may be absent, even on juveniles. The bands crossing the back of the head and the neck are broader and more distinct and the pale interbands are typically of even width, without any lateral widening. The interband spaces are pale reddish brown in life but this typically fades to a lighter brown or a greyish-white (e.g., 140396) in preservative. A narrow and faint pale band is usually present on the neck behind the posteriormost dark band; this is, occasionally followed on the side of the neck by a narrow dark band (e.g., 140396).

Supralabials and infralabials of juveniles whitish in between dark bands. Dark bands extend below mouth and terminate on suture lines between mental and first infralabial scales, between second and third infralabials, and between third and fourth

infralabials. These suture line smudges undergo ontogenetic fading in concert with the general head pattern.

Distribution and sympatry

Widespread throughout Pilbara region of Western Australia (Figure 8) with southerly extension to northern Gascoyne at Turee Creek, extending north to DeGrey River Station, east to Carawine Gorge and 30km east of Newman and southwest to Mount Minnie and Cane River Stations. Also occurs on Potter Island off Pilbara coast. Endemic to Western Australia.

As noted earlier, *D. pax* appears to be allopatric with respect to the closely related *D. desmosa* (Figure 8). However, *D. pax* is regionally sympatric in the Pilbara region with *D. butleri*, *D. haroldi*, *D. elegans* Kluge, 1974, *D. nasuta* and *D. tincta*. Recorded instances of sympatry involving *D. pax* include *D. haroldi*, *D. nasuta* and *D. tincta* from multiple localities throughout the Pilbara region. For instance, in the vicinity of Port Hedland, *D. pax*, *D. haroldi* and *D. tincta* have all been observed crossing the same section of sealed road at night. *Delma pax* and *D. nasuta* were observed together in the same context in the vicinity of Newman (B. Maryan and B. Bush, *personal observation*). *Delma pax* also has been recorded with *D. elegans* from several localities including Meentheena and Pannawonica.

Comparison with other species

Delma pax will be compared first with *D. borea*, and then with other regionally sympatric *Delma* spp. For comparison with *D. desmosa* see the preceding account.

Both sexes of *D. pax* average larger than *D. borea* in almost all linear measurements (Tables 1, 4), while average ventral scale counts are significantly higher in female *D. pax* than female *D. borea* but not in males. Body pattern in *D. pax* features plain ventrolateral scales on the forebody, whereas *D. borea* typically has variegated scales in this area. Specimens of *D. pax* that retain traces of the immature head pattern (Figure 12E) are distinguished from *D. borea* by having a band on back of head that is slightly broader and of more even width (in *D. borea* the auricular band is narrower mid-dorsally but broadens laterally, often 'forking' at the ear aperture; Figure 12G). *Delma pax* typically have the third supralabial positioned below the eye (typically the fourth in *D. borea*).

As indicated above, five other *Delma* species occur in regional sympatry with *D. pax* (*D. butleri*, *D. haroldi*, *D. elegans*, *D. nasuta* and *D. tincta*). The relatively inornate *D. butleri* bears a superficial resemblance to adult *D. pax* but differs in having more complex patterning on the lips, side of head and neck (variably marked with brown and white

spots, blotches or vertical streaks). *Delma haroldi* is more distinct with narrow wavy pale bands (but no dark bands) across the head and neck. *Delma elegans* has five or six dark head bands that descend obliquely forward and also has higher midbody scale row counts (modally 18 versus 16). *Delma nasuta* has a longer, sharper snout with a spotted or reticulated pattern on the dorsal and ventral surfaces. Finally, *D. tincta* has one pair of supranasals (versus two in *D. pax*), lower midbody scale row counts (modally 14 versus 16), fewer loreal scales on average (Table 1) and variegated scales on the lateral forebody (versus plain scales in *D. pax*). *Delma tincta* generally averages smaller than *D. pax* in linear dimensions (Table 1).

Habitat

Delma pax occupies a variety of habitats in the Pilbara region including sandy riverside flats and stony slopes with heavy soils. It is most frequently obtained from *Triodia* clumps but also shelters in flood debris along dry watercourses. The species is often observed at night active on sealed roads (B. Maryan, *personal observation*).

Remarks

Kluge (1974: 116–117) illustrates the head region of both immature and adult *D. pax*. Adult *D. pax* is illustrated by Wilson and Knowles (1988: 249), Storr *et al.* (1990: Plate 17.3), Cogger (2000: 290) and Wilson and Swan (2003: 117). Wilson and Swan (2003: 111) illustrate an immature *D. pax* (140396) from the Port Hedland district, mislabeled as *D. borea*.

Remarks on the distribution of *Delma borea*

The taxonomic changes proposed above also help clarify the species limits and geographic distribution of *D. borea*. As delimited here, *D. borea* in Western Australia is a moderately small, stout species of *Delma* (SVL up to 98mm) with modally 16 (rarely 17) midbody scales, two pairs of supranasals, the fourth supralabial scale positioned below the eye (unilaterally third supralabial below eye in two out of 114 specimens), and variegated ventrolateral scales on forebody. Juveniles possess well-defined dark head bands. Adults undergo ontogenetic fading to varying degree and usually possess indistinct pale brown bands on the head and neck. These morphological characteristics are consistent with previous accounts of *D. borea* in the more easterly parts of its range (Kluge 1974).

Figure 15 shows the distribution of *D. borea* in Australia, based on our reassessment of specimens in the collection of the Western Australian, Northern Territory and South Australian Museums. In Western Australia, this species ranges from the Kimberley southwest to Mandora inland of the 80 mile beach, and south to the Edgar Ranges, 25 km E

Downs and Denison Range. It is present on numerous islands off the Kimberley coast (Troughton, Naturalist, Coronation, Heywood, Sunday, Augustus, King Hall, Cockatoo and Koolan) and at least three islands off the Pilbara coast (Barrow, Hermite and Rosemary). It also occurs in the Northern Territory, western Queensland and northwestern South Australia (Kluge 1974; Shea 1987, 1991; Ingram and Raven 1991; Ehmann 2005). In the Northern Territory, *D. borea* is most common in the Top End, with the southernmost records at Wave Hill, Helen Springs and 50 km S MacArthur River camp (Shea 1991); it appears to be sparsely distributed south of the 20° parallel that includes its occurrence in northwestern South Australia on Aboriginal Lands (Ehmann 2005). Kluge's (1974: Figure 47) map for this species shows a record in northwestern South Australia but without an equivalent specimen listed under Paratypes; we assume that the map is in error.

Three specimens included by Kluge (1974: 192) within *D. borea* warrant special mention. Specimen 25201 from 32 km E Jiggalong was also mapped as *D. borea* by Storr *et al.* (1990) and further cited by

Shea (1991) as representing this taxon. This specimen is confirmed here as a member of the *D. tincta* group due to the presence of an enlarged upper temporal scale bordering each parietal. It differs from each of *D. borea* and from *D. desmosa* in being more slender bodied, and differs from *D. desmosa* in having more pronounced variegation of the ventrolateral scales on the forebody. In both of these respects, the specimen resembles *D. tincta*. However, it differs from *D. tincta* in having paired supranasals and 16 midbody scale rows, and in these respects, more closely resembles *D. borea* and *D. desmosa*. This specimen might represent an outlier of *D. borea*, a somewhat aberrant *D. desmosa*, or another, as yet unrecognized taxon.

Specimen SAM 5058 referred to *D. borea* also by Shea (1991) from the Warburton Range is similar in most respects to specimen 25201. The colour pattern is similar to both *D. borea* and *D. tincta*, most notably in the presence of variegated ventrolateral scales on the forebody. The specimen has two pairs of supranasal scales and the fourth supralabial positioned bilaterally below the eye, both features shared with typical *D. borea*. However, it is slender

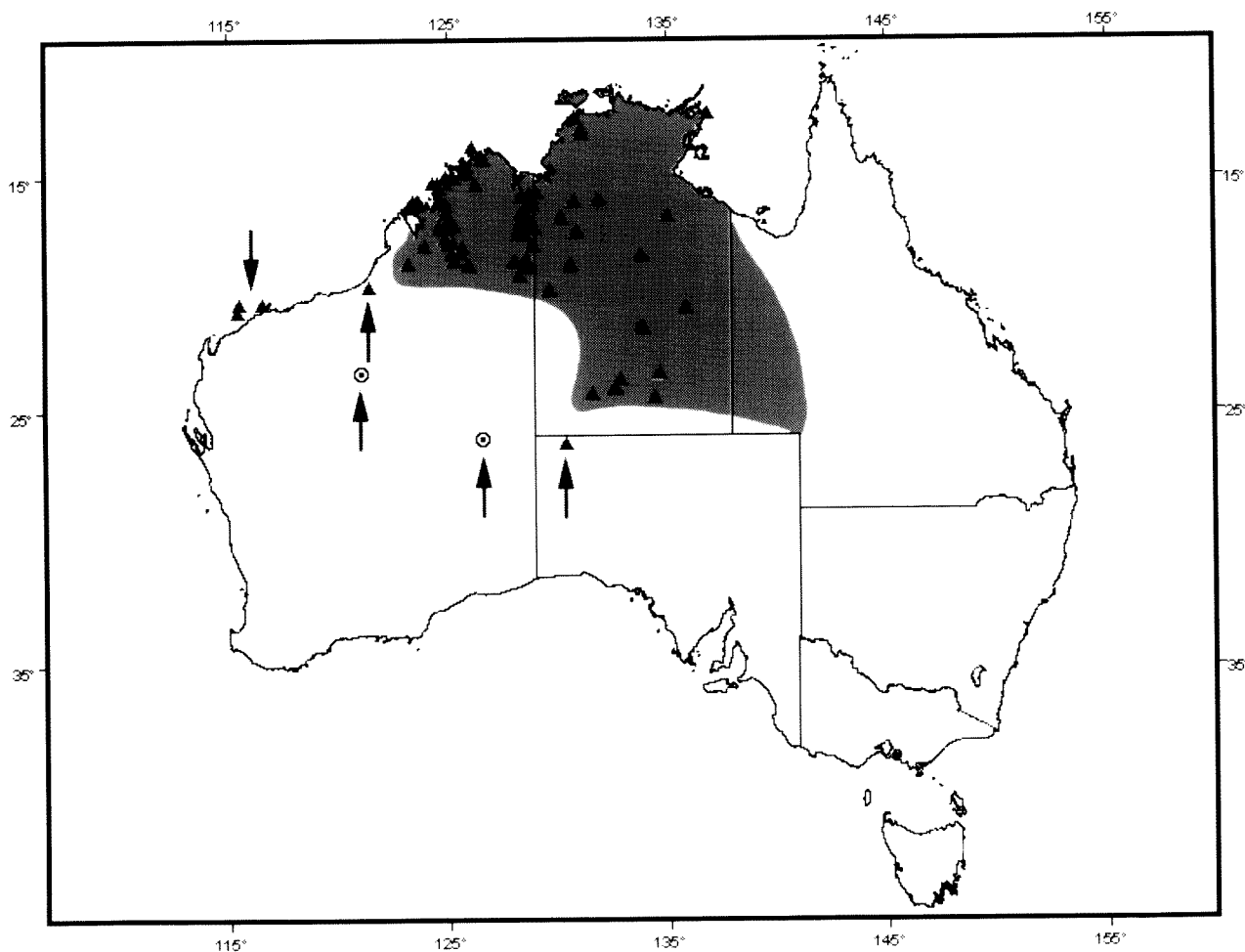


Figure 15 Map of Australia showing distribution of *D. borea* (shading) and location of specimens examined in this study (triangles). Arrows indicate outlier populations at Mandora, western Pilbara islands and northwestern South Australia and the two specimens (circles with cross) from 32 km E Jiggalong and Warburton Range that are regarded as *D. sp. incertae sedis* pending further field survey and analysis.

bodied and has 14 midbody scales, more typical of *D. tincta*. The presence of variegated ventrolateral scales on the forebody and the absence of strong head patterning distinguish the specimen from regionally sympatric *D. desmosa*. The desert regions are poorly sampled for herpetofauna (How and Cowan 2006) and until further material is available, we recommend that the Warburton Range and Jiggalong populations be treated as *Delma* sp. *incertae sedis*.

Specimen SAM 4475 from Tambrey is listed twice by Kluge (1974: 192), once as a paratype of *D. borea* and again as a paratype of *D. elegans*. Advice from the South Australian Museum indicates that there have been no changes made in relation to this registration number which is currently attached to a paratype of *D. elegans* (M. Hutchinson, *personal communication*); the duplicate listing under *D. borea* is assumed to be an editorial error.

DISCUSSION

Taxonomic diversity of the *Delma tincta* group

The present study has identified two additional members of the *Delma tincta* group as defined by Shea (1991). *Delma desmosa* from the arid sand deserts of western and central Australia is a close relative of *D. pax* which is now recognized as endemic to the Pilbara region. The ranges of *D. pax* and *D. desmosa* appear to be allopatric or parapatric (current records suggest a gap of no more than 90 km between populations). These species are weakly differentiated genetically and they differ morphologically mainly in features of colouration (most notably the degree of ontogenetic fading of the juvenile head markings), and in the degree to which sexual dimorphism is expressed. However, the fact that an abrupt boundary is maintained between the two taxa over a very large distance around the periphery of the Pilbara uplands indicates that they represent discrete evolutionary lineages, each with its own set of ecophysiological requirements, and thus warrant specific recognition. Gene flow between the populations, if it occurs at all, is clearly limited and insufficient to influence the genetic or morphological characteristics of the spatially adjacent populations. Nevertheless, contact zones between *D. pax* and *D. desmosa* should be sought in which to investigate the nature and extent of genetic interactions between these taxa. Furthermore, ecological and behavioural comparisons of these closely related species might yield valuable insights into the adaptive significance of head patterning in *Delma*.

Delma tealei, an endemic of the Cape Range Peninsula, is most similar morphologically to *D. borea* and to a lesser extent, to *D. tincta*, all three

taxa sharing the unusual characteristic of variegated scales on the ventrolateral forebody. The allozyme data suggest a possible sibling relationship between *D. borea* and *D. tealei*, and a more remote association with *D. tincta*. However, the level of divergence is much greater than that observed between *D. pax* and *D. desmosa*, and identifies *D. tealei* as a well established lineage within the *D. tincta* group.

Biogeography of the *Delma tincta* group

The *D. tincta* group as a whole has a 'Torresian' distribution (sensu Cogger and Heatwole 1981). This appears to be unique within the genus *Delma*, since other species groups recognized on morphological (Kluge 1974; Shea 1991) or molecular criteria (Jennings *et al.* 2003) have geographic distributions that either range across southern Australia (*D. australis* + *D. torquata* Kluge, 1974; *D. fraseri* + *D. grayii*; *D. petersoni* + *D. inornata*), are confined to eastern Australia (*D. impar* + *D. mollerii* + *D. mitella* Shea, 1987), or are centred on the arid inland region (*D. butleri*/*D. haroldi* + *D. nasuta*). With a total of five species, the *D. tincta* group is also the most speciose of the major intrageneric lineages identified to date. However, as noted above, this may reflect a lack of complete taxonomic discrimination in some other groups, most notably in the *D. butleri*/*D. haroldi* complex and in the *D. australis* group (Aplin and Smith 2001).

Within the *Delma tincta* group, the widely distributed *D. tincta* appears to be broadly sympatric with each of *D. borea*, *D. pax* and the two additional members described in this paper. Whether this entails instances of true syntopy is not known. However, in our view the likelihood of syntopy is enhanced by the unusual morphological characteristics of *D. tincta* within this group, in particular its relatively small adult size and slender build (as reflected by a reduced number of midbody scale rows). *Delma tealei*, which is at least regionally sympatric with *D. tincta* on the Cape Range Peninsula, shares several of these characteristics and it would be of great interest to know more about the ecological interaction between these species.

Delma pax and *D. desmosa* have allopatric or parapatric distributions, the former confined to the Pilbara region, and the latter found in the surrounding sandy deserts and extending east into the central Australian deserts. Along its northern margin, the range of *D. desmosa* appears to interdigitate with that of *D. borea* but with no records of syntopy. These taxa differ in relatively subtle aspects of body colouration, meristics and in relative hindlimb flap length, and they may be weakly differentiated ecologically and subjected to mutual competitive exclusion. Somewhat surprisingly, given the high degree of

morphological similarity, *D. desmosa* and *D. borea* are well-differentiated genetically.

The ranges of *D. borea* and *D. pax* approach regional sympatry in northwestern Australia. *Delma pax* is restricted to the mainland Pilbara region where it occupies a variety of local habitat types being only recently recorded on Potter Island off the Pilbara coast. *Delma borea*, in contrast, is present on several of the western Pilbara islands. On Barrow Island it is found together with *D. nasuta* and *D. tincta* and on Hermite Island it is recorded with *D. nasuta* (Burbidge *et al.* 2000).

The disjunct occurrence of *D. borea* in northwestern Australia begs explanation. The flora and fauna of Barrow and Hermite Islands off the Pilbara coast are closely allied with those of the Cape Range Peninsula (Keighery and Gibson 1993; Baynes and Jones 1993; Kendrick 1993), reflecting not only the geological similarity between the two areas (both are anticlinal structures comprised of Miocene limestones) but also that during periods of lowered sea level through the late Pliocene and Pleistocene, both formed rocky plateaux on a sandy, emergent continental shelf. Despite this overall similarity, the Pilbara islands host a number of 'northern monsoonal' faunal elements that are absent from the Cape Range Peninsula. One of these is *D. borea*, perhaps replaced on the peninsula by the morphologically similar *D. tealei*. Others include a murid rodent *Pseudomys nanus* (Gould, 1858) and a skink *Ctenotus angusticeps* Storr, 1988. Another 'northern monsoonal' mammal species, the Northern Nailtail Wallaby *Onychogalea unguifera* (Gould, 1841), is represented in an early Holocene subfossil assemblage from the Montebello islands (Veth 1993). These taxa are typically associated either with grassland communities on coastal plains (*P. nanus* and *O. unguifera*) or with coastal samphire communities (*C. angusticeps*), vegetation types that were most likely broadly continuous along the emergent northwestern continental shelf during periods of lower sea level. The present distribution of *D. borea* suggests that it, too, was a member of this now emergent continental shelf community that survives in relictual form only on the Pilbara islands.

Molecular clock estimates suggest a staggered origin of the major species group lineages within *Delma* during the early to mid-Miocene, around 20–28 million years ago (Jennings *et al.* 2003). The *Delma tincta* group probably arose during the latter part of this radiation. Divergence of the modern species lineages (*D. pax*, *D. tincta*, *D. borea*) probably occurred during the late Miocene (ca. 8–9 million years ago). Other speciation events in *Delma* typically are of similar or even greater antiquity, if the molecular clock estimates are accepted as valid (Jennings *et al.* 2003).

Delma tealei shows a similar level of genetic differentiation to the other previously recognized members of the *D. tincta* group and thus may also have originated during the late Miocene. This corresponds closely to the time of emergence of the Cape Range (Wyrwoll *et al.* 1993) and it is tempting to link the two events via a dispersal or vicariance event. However, the probable great antiquity of the *D. tealei* lineage (as indicated by its genetic distinctiveness) leaves open the possibility that *D. tealei* was formerly more widespread under the very different bioclimatic regime of the late Tertiary period and is relictual on Cape Range Peninsula. *Delma desmosa*, in contrast, is genetically close to its sibling *D. pax* and these taxa probably diverged during the late Pliocene or Pleistocene (i.e., within the last 2–3 million years). In broad terms, this corresponds to the period of progressive desertification of Australia (White 1994; Fujioka *et al.* 2005) and it seems likely that this later period of diversification within the *D. tincta* group occurred in response to the emergence of new kinds of arid zone habitats.

Species identification in *Delma* and a new dichotomous key

As noted in the Introduction, this study was initiated in response to seemingly anomalous identifications of Pilbara *Delma* specimens obtained through application of the key published in Storr *et al.* (1990: 114). In most cases, this confusion involved individuals of *D. pax* or *D. desmosa* in which the third supralabial scale is divided unilaterally or bilaterally, thereby leading to ambiguity at the second key couplet in which the relationship of supralabial scales to the eye is used. Similar difficulties were also encountered as a consequence of intraspecific variation in other 'diagnostic' characters within the genus *Delma*, including the condition of the supranasal scales, the number of midbody scale rows and aspects of head patterning. Fundamentally, these difficulties reflect the fact that the genus *Delma* is speciose yet morphologically conservative. Moreover, problems of identification are compounded by marked ontogenetic transformations in head pattern that occur in some species of *Delma* but not in others.

In conclusion, we offer a revised dichotomous key to the *Delma* species of Western Australia. Given the difficulties in accurate identification of this group, we suggest that the key be used only as a first step towards taxonomic identification of adult specimens, which should then be confirmed by direct comparison with voucher material or through genetic analysis. Moreover, if possible, we recommend that the following conditions be met prior to application of the key: 1) that the stage of sexual maturity of individual animals is determined; 2) that 'typical' scalation characters are determined

through examination of locally obtained series rather than individual specimens; and 3) that close attention is paid not only to the small number of standard diagnostic features employed in the key but also to subtleties of head and body scale patterning within regional *Delma* assemblages.

Key to Western Australian *Delma*

1. Typically one pair of supranasals 2
Typically two pairs of supranasals 3
2. Smaller (SVL up to 57mm); typically 18 midbody scale rows; side of neck and forebody usually finely barred with black; no broad dark bands across head and neck
..... *australis*
Longer (SVL up to 92mm); typically 14 midbody scale rows; side of forebody usually with variably coloured scales; broad dark bands across head and neck (often fade with age) *tincta*
3. Typically third supralabial below the eye; typically 14 midbody scale rows; Cape Range Peninsula *tealei*
Either third or fourth supralabial below the eye; between 16–20 midbody scale rows 4
4. Typically third (occasionally fourth) supralabial below the eye 5
Typically fourth supralabial below the eye 6
5. Dark bands across head and neck persistent at all ages; two dark smudges on infralabials below lores; deserts *desmosa*
Dark bands across head and neck absent in adults; three dark smudges on infralabials below lores; Pilbara *pax*
6. Typically 16 midbody scale rows 7
Typically 18 midbody scale rows 8
7. Throat white; Kimberley and some Pilbara islands *borea*
Throat with fine dark variegations; southwest of WA *fraseri*
8. Dark bands across head and neck descend obliquely forwards, terminating acutely; Pilbara *elegans*
Dark bands run straight across head and neck and meet to form black bands across the chin and throat; southern Great Victoria Desert ...
..... *petersoni*
9. Narrow, wavy pale bands across head and neck *haroldi*
No pale bands across head and neck 10
10. Side of forebody with numerous pale vertical streaks or bars; lower surface yellow ... *grayii*

Side of forebody without numerous pale vertical streaks or bars; lower surface white with or without dark markings 11

11. Snout long; dorsal scales spotted and flecked with dark brown; ventral scales usually dark-edged *nasuta*

Snout short; dorsal scales finely dark-edged; ventral scales without dark edges *butleri*

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APPENDIX 1

Lists of Specimens examined

Legend for Museum registration numbers: WAM = Western Australian Museum; NTM = Northern Territory Museum; SAM = South Australian Museum.

Delma borea Kluge 1974

SAM: 42018-20, 42046, 42189 2 km W Hanging Knoll (26°19'23"S 130°23'36"E).
 NTM: 1317 Barrow Creek (21°31'S 133°53'E); 1574 Tanami Bore (19°58'S 129°40'E); 5371 Barrow Creek (21°31'S 133°53'E); 5824-25, 6516-6517, 6610 Wave Hill (17°29'S 130°57'E); 6594 70 km N Top Springs (16°00'S 131°56'E); 9133 Keep River National Park (15°45'S 129°05'E); 12727 George Gill Ranges (24°19'S 131°35'E); 13047 Ord River (16°10'S 128°44'E); 15414 Chewings Range (23°40'S 132°54'E); 16473 Sambo Bore, Wave Hill Station (18°53'S 130°40'E); 18042 Alyawarre Desert Area (20°44'S 135°50'E); 20644 Finke Gorge National Park (24°04'30"S 132°40'39"E); 20660 Finke Gorge National Park (24°04'02"S 132°37'36"E); 21128 Carpentaria Highway (16°44'S 135°02'E); 22702 Macdonnell Ranges (24°27'13"S 134°24'59"E); 23764 Gregory National Park (16°49'43"S 130°11'01"E); 23765 Gregory National Park (16°50'20"S 130°10'58"E); 23807 Gregory National Park (16°47'50"S 130°09'15"E); 25495 Jasper Gorge (16°05'50"S 130°45'18"E); 34524-25 Arltunga Ruins (23°26'S 134°42'E).
 WAM: 13496 Yirrkala (12°15'S 136°53'E); 21852 8 km N Kalumburu (14°14'S 126°37'E); 21980 Darwin (12°27'S 130°50'E); 23480 Nightcliff (12°23'S 130°52'E); 24001 11 km N Adelaide River (13°08'S 131°08'E); 24198 Helen Springs (18°26'S 133°52'E); 26224 Parap (12°25'S 130°52'E); 28656 Barrow Island (20°50'S 115°25'E); 34331-32 Yirrkala (12°15'S 136°53'E); 37371 Rosemary Island (20°29'S 116°35'E); 37406 Hermite Island (20°29'S 115°31'E); 40296, 40835 Darwin (12°27'S 130°50'E); 41271 Augustus Island (15°19'S 124°32'E); 41370 Heywood Island (15°20'S 124°20'E); 41409 Coronation Island (15°00'S 124°56'E); 43071-75 Crystal Creek (14°31'S 125°48'E); 43119 Port Warrender (14°34'S 125°51'E); 43151, 43185, 43204, 43211, 43341-42 Mitchell Plateau (14°52'S 125°50'E); 44278 Geikie Gorge (18°05'S 125°43'E); 44566-71 Behn River Mouth, Lake Argyle (16°15'S 128°45'E); 44572-75 Ord River (16°17'S 128°47'E); 45066 Napier Range (17°13'S 124°38'E); 48559 Shark Point, Barrow Island (20°52'S 115°25'E); 51277 East Palm Spring, Denison Range (19°20'S 128°20'E); 52670 Lake Argyle (16°07'S 128°44'E); 54141 Edgar Ranges (18°50'S 123°15'E); 56208-09 Crystal Creek (14°30'S 125°47'E); 57039 Doongan Homestead (15°23'S 126°18'E); 60352 3 km E Nicholson (18°03'S 128°55'E); 69845 Koolan Island (16°09'S 123°45'E); 70365 12.5 km 309°New Lissadell Homestead (16°36'12"S 128°27'34"E); 70385 10.5 km 249°New Lissadell Homestead (16°43'S 128°27'E); 70564 5.2 km 202°Mount Percy (17°39'37"S 124°54'24"E); 70582 6.3 km 172°Mount Percy (17°40'23"S 124°56'03"E); 70625 5.2 km 202°Mount Percy (17°39'37"S 124°54'24"E); 75376, 75398 12 km NW New Lissadell Homestead (16°37'S 128°28'E); 75533 11 km WNW New Lissadell Homestead (16°39'S 128°28'E); 77201 Mitchell Plateau (14°44'30"S 125°47'00"E); 77472 Camp Creek (14°53'30"S 125°45'00"E); 79063 Brooking Springs Station (17°54'S 125°16'E); 80028 Sunday Island (16°25'S 123°11'E); 81286 Koolan Island (16°09'S 123°45'E); 94881 Lake Argyle (16°07'S 128°42'E); 96784 Sale River (16°05'S 124°40'E); 96828 Camden Head (15°30'S 124°37'E); 96944 The Dromedaries (16°34'20"S 124°56'40"E); 97091 3.7 km NW Mount Darglish (16°15'05"S 124°56'00"E); 99774, 99776 10

km SW Silent Grove (17°06'55"S 125°10'30"E); 101335 30 km ENE Calwinyardah Homestead (17°57'S 125°02'E); 103120, 103129 Purnululu National Park (17°26'S 128°24'E); 103151 Purnululu National Park (17°33'S 128°15'E); 103207 Purnululu National Park (17°10'S 128°44'E); 103384, 103395 Purnululu National Park (17°15'S 128°18'E); 103483 Purnululu National Park (17°32'S 128°21'E); 103489-90 Purnululu National Park (17°29'S 128°22'E); 103733 Koolan Island (16°09'S 123°45'E); 106284 Augustus Island (15°26'S 124°36'E); 108737 10 km N Gordon Downs Homestead (18°40'S 128°35'E); 108815 30 km SE Gordon Downs Homestead (18°56'S 128°47'E); 112725-26 Mandora Station (19°47'52"S 121°26'53"E); 114462 King Hall Island (16°05'S 123°25'E); 138149 Napier Range (17°13'S 124°38'E); 139058, 139062-63 Mandora Station (19°47'52"S 121°26'53"E); 141530 Quanbun Downs Station (18°21'27"S 125°13'10"E).

Delma pax Kluge 1974

NTM: 9939 24 km N Port Hedland (20°23'S 118°48'E); 9943 13 km N Port Hedland (20°25'S 118°42'E); 9945 15 km N Port Hedland (20°25'S 118°42'E); 9946 22 km N Port Hedland (20°23'S 118°47'E).
 WAM: 14803 19 km W Mundabullangana (20°30'S 117°53'E); 51620 10 km NE Mount Newman (23°17'S 119°45'E); 58965 Marble Bar Pool (21°16'S 119°42'E); 64701 Nullagine (21°54'S 120°06'E); 64986 Dampier (20°40'S 116°42'E); 68370-71 Between Nullagine and Roy Hill (22°15'S 120°00'E); 70103 Between Dampier and Karratha (20°45'S 116°45'E); 73144, 73146 24.2 km 234°Marillana Homestead (22°46'00"S 119°13'08"E); 73542-43 Dampier (20°40'S 116°42'E); 73604 24.2 km 234°Marillana Homestead (22°46'00"S 119°13'08"E); 73841 22 km S Roebourne (21°06'S 117°05'E); 76469 10 km SSW Cooya Pooya Homestead (21°07'S 117°07'E); 80379 Carrawella Well (21°43'S 115°31'E); 80599 8 km SE Peedamulla Homestead (21°55'S 115°40'E); 80995-96 South Hedland (20°24'S 118°36'E); 81387-91 Miaree Pool (20°51'S 116°37'E); 82605 Carawine Gorge (21°29'S 121°01'E); 83153 Karratha (20°44'S 116°51'E); 84982 Dampier Archipelago (20°33'S 116°42'E); 87854 Wickham (20°40'S 117°07'E); 90886 Woodstock (21°37'01"S 118°57'13"E); 94660-61 Crossing Pool (21°35'S 117°06'E); 94882 Mardie Station (21°15'S 115°50'E); 102046 2 km N Crossing Pool (20°53'S 116°40'E); 102066 Karratha (20°53'S 116°40'E); 102091 Dampier (20°40'S 116°42'E); 102115 7 km NE Mount Windell (22°37'28"S 118°36'26"E); 102137 5 km NNE Mount Windell (22°36'16"S 118°34'01"E); 102149 10 km ENE Mount Windell (22°35'58"S 118°38'20"E); 104176 Woodstock (21°36'34"S 119°01'17"E); 104297 Woodstock (21°36'25"S 119°02'23"E); 106257, 106278-79, 108711, 108791, 113387 South Hedland (20°24'S 118°36'E); 114437 Wittenoom (22°14'S 118°20'E); 116300 King Bay (20°38'S 116°45'E); 119045-46 South Hedland (20°24'S 118°36'E); 120021 3.5 km NE Mount Brockman (22°28'S 117°18'E); 120030 Hope Downs (22°58'00"S 119°09'45"E); 120735 Boodarie Hill (20°24'S 118°31'E); 125023 Yandicoogina (22°43'S 119°01'E); 125452 30 km E Newman (23°19'S 120°02'E); 127829 Mount Brockman (22°25'05"S 117°18'03"E); 129658 120 km NW Newman (22°59'45"S 119°18'30"E); 129930 West Angelas (23°15'S 118°40'E); 132548 DeGrey River Station

(20°13'14"S 119°09'58"E); 132549 DeGrey River Station (20°17'16"S 119°12'36"E); 132593, 132596 Burrup Peninsula (20°36'45"S 116°47'37"E); 132606 Burrup Peninsula (20°40'49"S 116°44'37"E); 132657 Burrup Peninsula (20°31'40"S 116°49'11"E); 135320, 135336-37 Cape Lambert (20°48'36"S 116°56'31"E); 135632 Bea Bea Creek (21°43'S 118°44'E); 135919-20 32 km SW South Hedland (20°36'S 118°22'E); 137857 Munjina Roadhouse (21°59'S 119°45'E); 139170-71 Cane River Homestead (22°05'19"S 115°37'31"E); 139294 Meentheena (21°17'13"S 120°27'34"E); 139352-53 Potter Island (20°57'S 116°08'E); 139369 Meentheena (21°13'56"S 120°19'40"E); 139457 Mount Minnie Homestead (21°58'23"S 115°25'51"E); 140021 Millstream-Chichester National Park (21°10'53"S 117°03'28"E); 140396 82 km E Port Hedland (20°18'53"S 119°24'41"E); 141269-70 24 km ESE Port Hedland (20°23'S 118°48'E); 141311 Cape Preston area (20°50'00"S 116°09'47"E); 145512 98 km S Port Hedland (21°09'36"S 118°48'36"E); 145544 80 km S Port Hedland (21°00'36"S 118°42'00"E); 145569 34 km S Port Hedland (20°36'36"S 118°36'36"E); 145614 18 km S Port Hedland (20°28'12"S 118°35'24"E); 145680 Abydos Station (21°25'S 118°55'E); 145748 Chichester Range (22°04'44"S 118°58'40"E); 145753 Chichester Range (22°01'01"S 118°58'55"E); 146591 124 km S Port Hedland (21°26'53"S 118°55'24"E); 146649 80 km S Port Hedland (21°00'36"S 118°42'00"E); 151161 Tom Price area (22°37'13"S 117°44'37"E).

Delma tincta De Vis 1888

WAM: 3440 La Grange (18°40'S 122°01'E); 4511 East Chapman (28°40'S 114°50'E); 8109 Wandagee Station (23°49'S 114°27'E); 9782-84 Carnarvon (24°53'S 113°40'E); 10615 Minilya (23°51'S 113°58'E); 11494 Learmonth district (22°15'S 114°05'E); 12114 Kimberley Research Station (15°39'S 128°42'E); 13653 Wyndham (15°29'S 128°07'E); 13838 Kalumburu (14°18'S 126°38'E); 13933 Mount Pleasant * (32°02'S 115°51'E); 14791-95 Northampton (28°21'S 114°38'E); 14801 Mundabullangana (20°31'S 118°03'E); 17683 Turee Creek Station (23°37'S 118°39'E); 22323 Nabawa (28°30'S 114°47'E); 22366 Kimberley Research Station (15°39'S 128°42'E); 24812 Binu (28°02'S 114°40'E); 25221 Murchison House (27°39'S 114°14'E); 28370 Coordewandy (25°36'S 115°58'E); 28391 Murchison House (27°39'S 114°14'E); 28454 Barrow Island (20°48'S 115°24'E); 30259 Carnarvon (24°53'S 113°40'E); 31397 35 km NE Mingenew (29°03'S 115°37'E); 31487 Eradu (28°42'S 115°02'E); 44555-65 Lake Argyle (16°10'S 128°44'E); 47854 Barrow Island (20°52'S 115°22'E); 48560-62 Barrow Island (20°52'S 115°25'E); 50091 Yalgoo (28°21'S 116°41'E); 51003-04 Exmouth (21°56'S 114°07'E); 51641 Marandoo (22°38'S 118°08'E); 52933 Shothole Canyon (22°03'S 114°02'E); 53791-93 Gascoyne Junction area (25°06'S 115°13'E); 54606 Wooramel Homestead (25°44'S 114°17'E); 55019 Hamelin Homestead (26°26'S 114°12'E); 55094 Wooramel Homestead (25°44'S 114°17'E); 55406-07, 55440 71 km W Barry Caves (19°52'S 136°03'E); 58413 5 km N Coulomb Point (17°19'S 122°10'E); 59687, 59689 Meeberrie Homestead (26°58'S 115°58'E); 62208 Mingenew (29°12'S 115°26'E); 62416 5 km W Williambury Homestead (23°54'S 115°10'E); 63678 25 km NNW Winning Homestead (22°56'S 114°27'E); 66313 36 km 137°Mount Meharry (23°12'30"S 118°49'30"E); 66314 34 km 136°Mount Meharry (23°11'40"S 118°49'30"E); 66327 36 km 137°Mount Meharry (23°12'30"S 118°49'30"E); 67606-09 Marble Bar (21°10'S 119°44'E); 67806 Hamelin Pool (26°24'S 114°10'E);

67905 36 km 137°Mount Meharry (23°12'30"S 118°49'30"E); 69779 Mount Bruce (22°35'S 118°10'E); 70757, 70761, 70764 30.2 km 238°Marillana Homestead (22°46'55"S 119°09'35"E); 71059 Hamelin Homestead (26°26'S 114°12'E); 73138 30.2 km 238°Marillana Homestead (22°46'58"S 119°09'35"E); 73897 Pender Bay area (16°45'S 122°49'E); 78239 70 km W Barry Caves (19°51'S 136°02'E); 81330 57 km NNE Nanutarra Roadhouse (22°01'S 115°36'E); 83152 Karratha (20°44'S 116°51'E); 83210 Carnarvon (24°53'S 113°40'E); 84150-52 Yalgoo (28°21'S 116°41'E); 85190 8 km ESE Kununurra (15°49'S 128°48'E); 86429 Hamelin Homestead (26°26'S 114°12'E); 88547 Carnarvon (24°53'S 113°40'E); 91132 10 km NE Paynes Find (29°11'S 117°42'E); 92727 Hamelin Homestead (26°26'S 114°12'E); 93701 53 km NNE Broome (17°32'S 122°25'E); 95291-93 Walga Rock (27°24'S 117°28'E); 99180 Woodstock Station (21°36'35"S 118°57'44"E); 101246 Galena (27°50'S 114°41'E); 101278 Barrow Island (20°48'S 115°24'E); 102154 10 km ENE Mount Windell (22°35'58"S 118°38'20"E); 102401 Barlee Range Nature Reserve (23°04'47"S 115°47'14"E); 102815 Burrup Peninsula (20°40'39"S 116°45'11"E); 102838 Cape Range National Park (22°09'01"S 113°59'52"E); 102852 Meentheena (21°14'16"S 120°23'31"E); 139140 Meentheena (21°25'18"S 120°25'36"E); 104426, 105987 Carnarvon (24°53'S 113°40'E); 112511 Urala Station (21°47'04"S 114°52'07"E); 112689 10 km SSW Onslow (21°43'51"S 115°05'49"E); 112690 5.5 km SE Onslow (21°40'33"S 115°08'42"E); 112691 11 km S Onslow (21°44'27"S 115°06'46"E); 112715 5.5 km SE Onslow (21°40'33"S 115°08'42"E); 112716 12 km SE Onslow (21°42'39"S 115°11'49"E); 112747 Bibawarra Crossing (24°53'S 113°42'E); 113012, 113030 Lesley Salt Works (20°14'50"S 118°50'50"E); 114101-02 Carnarvon Airport (24°54'S 113°39'E); 114391-92 9 km NE Broome (17°55'S 122°15'E); 114490 Wicherina Dam (28°44'S 115°00'E); 115018 Spalding Park (28°39'S 114°38'E); 116439 15 km NNW Carleton Hill Homestead (15°23'39"S 128°28'13"E); 116545 Depot Hill (29°08'S 115°21'E); 117215 Narnagulu (28°49'S 114°41'E); 117342 Hope Downs (22°56'45"S 119°07'30"E); 120020 3.5 km NE Mount Brockman (22°28'S 117°18'E); 125032 Yandicoogina (22°43'14"S 118°59'26"E); 127718, 127768, 127792 5 km S Mount Tom Price Mine (22°47'55"S 117°46'10"E); 129587, 129623 120 km NW Newman (22°55'S 118°54'E); 131752 Mount Robinson (22°57'19"S 118°46'14"E); 132209 Urala Station (21°47'09"S 114°51'58"E); 135322 Cape Lambert (20°45'16"S 117°04'52"E); 135422 Mount Brockman (22°18'38"S 117°15'08"E); 135487 Urala Station (21°46'58"S 114°52'11"E); 137953 35 km NNE Kununurra (15°35'20"S 128°59'00"E); 138222 Karijini National Park (22°37'S 118°17'E); 138226 Karijini National Park (23°01'S 118°43'E); 138243 Karijini National Park (22°59'S 118°44'E); 139140 Meentheena (21°25'18"S 120°25'36"E); 139282 Meentheena (21°17'07"S 120°24'55"E); 139308 Meentheena (21°14'41"S 120°19'20"E); 139314 Meentheena (21°13'04"S 120°27'20"E); 139321 Meentheena (21°15'20"S 120°27'18"E); 139328 Meentheena (21°16'54"S 120°27'58"E); 141273 22 km ESE Port Hedland (20°23'S 118°47'E); 141584 1 km N Quobba Homestead (24°22'24"S 113°24'19"E); 141585-86 Quobba Station (24°27'42"S 113°24'28"E); 145250 5 km S Mount Tom Price Mine (22°48'31"S 117°47'09"E); 145650 235 km SSW Port Hedland (22°23'24"S 118°58'48"E); 146589, 146645 228 km SSW Port Hedland (22°20'24"S 119°00'00"E); 146890 Mirima National Park (15°47'S 128°44'E); 146957 Kalumburu (14°18'S 126°38'E); 151059-60 10 km E

Carnarvon (24°53'S 113°46'E); 153814 2 km S Yardie Homestead Caravan Park (21°53'37"S 114°00'34"E); 153820 Charles Knife Road (22°07'08"S 114°03'44"E); 153821 Bullara Station (22°48'33"S 113°56'39"E).

*As noted by Kluge (1974), this locality record is considered erroneous.

Delma sp. incertae sedis

SAM: 5058 Warburton Range (26°06'S 126°39'E); WAM: 25201 32 km E Jiggalong (23°22'S 121°05'E).

Specimens examined in allozyme analysis

Delma pax

WAM: 104297 Woodstock Station; 120021 3.5 km NE Mount Brockman; 120030 Hope Downs; 125452 30 km E Newman; 132548 De Grey River Station; 132596, 132606 Burrup Peninsula; 135920 South Hedland; 139171 Cane River Homestead; 139294 Meentheena; 140021 Millsteam-Chichester National Park; 141270 24 km ESE Port Hedland.

Delma desmosa sp nov.

WAM: 102650, 102657 Little Sandy Desert; 114555 Sandfire Roadhouse; 132802 Warri Airstrip; 139089 Mandora; 145073 Officer Basin area.

Delma tealei sp nov.

WAM: 102837 Cape Range National Park; 153811 Charles Knife Road; 153813 2 km S Yardie Homestead Caravan Park; 153819 Shothole Canyon.

Delma borea

WAM: 139058, 139063 Mandora; 141530 Quanbun Downs Station.

Delma tincta

WAM: 102401 Barlee Range Nature Reserve; 102838 Cape Range National Park; 114391 9 km NE Broome.

Delma butleri

"western"

WAM: 120819 Peron Peninsula (26° 00'S 113° 30'E); 141590 Boolathana Station (24° 39'S 113° 42'E); 127461 East Yuna Nature Reserve (28° 20'S 115° 00'E); 144711 Bungalbin Hill (30° 24'S 119° 38'E).

"central"

WAM: 106163 Mount Frazer (25° 38'S 118° 23'E); 135249 Wiluna (26° 35'S 120° 14'E); 145072 Officer Basin (29° 58'S 123° 46'E).

SAM: 35027 Bloodweed Bore (26° 57'S 140° 57'E).

"eastern"

SAM: 45210 Peebinga Conservation Park (34° 58'S 140° 50'E).

Delma haroldi

WAM: 102123 Mount Windell (22° 39'S 118° 33'E); 135924 Sandfire Roadhouse (19° 46'S 121° 05'E); 145653 Port Hedland (20° 18'S 118° 35'E); NTM: 16484 Wave Hill Station (17° 29'S 130° 57'E).

APPENDIX 2

Allozyme profiles for 41 specimens at 34 variable loci

Legend for Museum registration numbers: WAM = Western Australian Museum; NTM = Northern Territory Museum; SAM = South Australian Museum; (c) = "central"; (w) = "western"; (e) = "eastern". A dash indicates the enzyme lacked sufficient activity to determine a profile.

Species	Accession Number	Acon1	Acon2	Acp1	Acp2	Acy1	Ada	Adh1	Adh2	Ca	Dia	Enol	Est2	Fdp	Fum	Gda	Glo	Got1	Got2	Gpd	Gpi	Guk	Idh2	Me1	Mpi	Ndpk1	Ndpk2	PepA	PepB	PepD	6Pgd	Pgm1	Pgm2	Sod	Srdh
<i>pax</i>	WAM104297	a	d	a	b	ab	b	b	d	a	b	c	d	c	b	c	c	b	b	b	b	b	c	c	b	a	b	c	ef	cd	b	c	a	d	b
<i>pax</i>	WAM120021	a	d	a	b	b	b	b	d	a	be	c	de	c	b	c	c	b	b	b	b	ab	c	c	b	a	b	b	f	c	bc	c	a	d	ab
<i>pax</i>	WAM120030	a	d	a	b	b	b	b	d	a	e	c	d	c	b	c	c	b	a	b	b	b	c	c	b	a	b	b	f	cd	b	c	a	d	b
<i>pax</i>	WAM125452	a	d	a	b	a	b	b	d	a	be	c	de	c	b	c	c	b	a	b	b	ab	c	c	b	a	b	b	f	d	bc	c	a	dg	ab
<i>pax</i>	WAM132548	a	d	a	b	a	b	b	d	a	b	c	d	c	b	c	c	b	b	b	b	b	c	c	b	a	b	c	f	cd	b	c	a	d	b
<i>pax</i>	WAM132596	a	bd	a	b	ab	b	b	d	a	b	c	de	c	b	c	c	b	b	b	b	b	c	c	b	a	b	bc	f	cd	b	c	a	d	b
<i>pax</i>	WAM132606	a	d	a	b	ab	b	b	d	a	b	c	de	c	b	c	c	b	b	b	b	ab	c	c	b	a	b	c	f	c	bc	c	a	d	b
<i>pax</i>	WAM135920	a	d	a	b	ab	b	b	d	a	b	c	d	c	b	c	c	b	b	b	b	b	c	c	b	a	b	c	f	c	b	c	a	d	b
<i>pax</i>	WAM139171	a	d	a	b	b	b	b	d	a	b	c	e	c	b	c	c	b	b	b	b	b	c	c	b	a	b	b	f	cd	b	c	a	d	b
<i>pax</i>	WAM139294	a	d	a	b	b	b	b	d	a	e	c	de	c	b	c	c	b	b	b	b	ab	c	c	b	a	b	c	f	cd	b	c	a	d	b
<i>pax</i>	WAM140021	a	d	a	b	ab	b	b	d	a	be	c	e	c	b	c	c	b	b	b	b	b	c	c	b	a	b	c	f	cd	b	c	a	d	b
<i>pax</i>	WAM141270	a	d	a	b	b	b	b	d	a	b	c	d	c	b	c	bc	ab	b	b	b	a	c	c	b	a	b	c	f	d	b	c	a	d	b
<i>desmosa</i>	WAM102650	a	c	a	b	b	b	c	a	a	ab	c	d	c	b	c	ac	b	a	b	b	b	c	c	b	a	b	c	df	d	b	b	a	d	b
<i>desmosa</i>	WAM102657	a	cd	a	b	b	b	c	ac	a	b	c	d	c	b	c	c	b	a	b	b	b	c	c	b	a	b	c	f	cd	b	bc	a	d	b
<i>desmosa</i>	WAM114555	a	cd	a	b	b	b	c	a	-	c	-	c	b	c	c	b	a	-	ab	b	b	c	a	b	a	b	c	f	cd	b	-	a	d	-
<i>desmosa</i>	WAM132802	a	cd	a	b	b	b	bc	ac	a	b	c	d	c	b	c	c	b	a	-	b	b	c	c	b	a	b	c	f	cd	b	c	a	d	b
<i>desmosa</i>	WAM139089	a	cd	a	b	b	b	c	c	a	a	c	d	bc	b	c	ac	b	a	b	b	b	c	a	b	a	b	c	f	c	b	c	a	d	b
<i>desmosa</i>	WAM145073	a	c	a	b	b	bc	c	a	a	b	c	d	c	b	c	c	b	a	b	b	b	c	c	b	a	c	c	f	d	b	c	a	d	b

Species	Accession Number	Acon1	Acon2	Acp1	Acp2	AcyC	Ada	Adh1	Adh2	Ca	Dia	Enol	Est2	Fdp	Fum	Gda	Glo	Got1	Got2	Gpd	Gpi	Guk	Idh2	Me1	Mpi	Ndpk1	Ndpk2	PepA	PepB	PepD	6Pgd	Pgm1	Pgm2	Sod	Srdh
<i>tealei</i>	WAM102837	a	c	a	b	a	b	b	c	a	hj	b	b	a	b	e	c	b	b	b	b	b	c	c	b	a	b	c	e	c	b	e	a	d	b
<i>tealei</i>	WAM153811	a	c	a	b	a	b	b	c	a	h	b	b	a	b	e	c	b	b	b	b	b	c	c	b	a	b	c	e	c	b	e	a	d	b
<i>tealei</i>	WAM153813	a	c	a	b	a	b	b	c	a	h	b	b	a	b	e	c	b	b	b	b	b	c	c	b	a	b	c	e	c	b	e	a	d	b
<i>tealei</i>	WAM153819	a	c	a	b	a	b	b	c	a	h	b	b	a	b	e	c	b	b	b	b	b	c	c	b	a	b	c	e	ac	ab	e	a	d	b
<i>borea</i>	WAM139058	a	c	b	b	a	b	b	c	a	h	c	bc	a	b	d	c	b	b	b	b	a	c	c	b	a	b	c	e	cd	b	g	a	c	b
<i>borea</i>	WAM139063	a	c	b	b	a	b	b	c	a	h	c	bc	a	b	d	c	b	b	b	b	a	c	c	b	a	b	c	e	cd	b	g	ab	c	b
<i>borea</i>	WAM141530	a	cd	b	b	a	b	b	c	a	dg	c	b	a	b	d	c	b	b	b	b	ab	c	c	b	a	ab	c	e	df	b	g	a	c	b
<i>tincta</i>	WAM102401	a	ac	a	a	a	bd	b	a	a	gh	c	-	a	b	d	c	b	b	b	b	a	c	c	b	a	b	c	e	d	b	d	a	d	d
<i>tincta</i>	WAM102838	a	bc	a	a	a	bd	b	a	a	g	c	ab	a	b	d	c	b	b	a	b	a	c	c	b	a	b	c	e	bd	c	d	a	d	d
<i>tincta</i>	WAM114391	a	b	a	a	b	b	b	a	a	g	c	b	a	b	d	c	b	b	b	b	a	c	c	b	a	b	c	e	d	b	d	a	d	b
<i>butleri</i> (c)	WAM106163	b	d	a	a	a	b	b	bc	b	fi	c	b	a	bd	c	d	b	c	b	c	a	b	b	a	b	b	c	be	d	d	e	a	d	c
<i>butleri</i> (w)	WAM120819	b	a	a	a	a	b	-	c	b	-	ac	-	-	b	c	d	b	c	-	c	a	ab	b	a	b	b	ac	e	d	d	-	a	-	b
<i>butleri</i> (w)	WAM127461	bc	a	a	a	a	b	-	c	b	g	c	b	a	bd	c	d	b	c	b	c	a	b	c	a	b	b	c	be	cd	d	a	a	d	c
<i>butleri</i> (c)	WAM135249	b	d	a	a	a	b	b	b	b	fh	c	b	a	b	c	d	b	c	-	c	a	b	b	a	b	b	c	e	d	d	e	a	d	c
<i>butleri</i> (w)	WAM141590	b	a	a	a	a	b	b	c	b	-	b	b	a	b	ac	d	b	c	b	c	a	b	b	a	b	b	c	e	cd	d	c	a	d	b
<i>butleri</i> (w)	WAM144711	b	ab	a	a	a	b	-	c	b	gi	c	b	a	b	c	d	b	c	-	c	a	b	b	a	b	b	c	be	df	d	c	a	d	c
<i>butleri</i> (c)	WAM145072	a	d	a	a	a	b	b	c	b	gj	c	b	a	b	c	d	b	c	b	c	a	b	b	a	b	bd	c	be	d	d	e	a	ad	c
<i>butleri</i> (e)	SAM45210	b	de	a	a	a	b	b	c	b	g	c	b	a	bc	c	d	c	c	b	c	a	b	b	a	b	b	d	a	cd	e	f	a	d	c
<i>butleri</i> (c)	SAM35027	a	d	a	a	a	b	ab	b	b	c	c	b	a	b	c	d	b	c	b	c	a	b	b	a	b	b	c	be	d	d	ef	a	ad	c
<i>haroldi</i>	WAM102123	a	a	a	a	a	b	b	b	b	-	b	b	a	bd	c	d	b	c	b	c	a	ab	c	a	b	b	c	ac	dg	d	e	a	a	c
<i>haroldi</i>	WAM135924	ab	d	a	a	a	b	b	b	b	-	c	b	a	ab	c	d	b	c	b	c	a	b	c	a	b	b	c	b	df	d	e	a	a	c
<i>haroldi</i>	WAM145653	a	c	a	a	ac	ab	b	b	b	-	c	b	a	b	c	d	b	c	b	c	a	b	bc	a	b	b	c	be	de	d	e	a	bf	c
<i>haroldi</i>	NTM16484	ab	ad	a	a	ac	b	b	b	b	-	c	bc	a	b	bc	d	b	d	b	c	a	bd	c	a	b	b	c	be	d	d	ef	a	be	c