Morphological and genetic discrimination of new species and subspecies of gekkonid and scincid lizards (Squamata: Lacertilia) from the Carnarvon Basin region of Western Australia

K P Aplin[1] & M Adams[2]

[1] Department of Terrestrial Vertebrates,Western Australian Museum, Francis St, Perth, WA 6000
email: aplink@museum.wa.gov.au
[2] Evolutionary Biology Unit, South Australian Museum, North Terrace, Adelaide, SA 5000 email: markadam@senet.com.au

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Abstract

Two new species and one new subspecies of lizards are described under the gekkonid genus *Diplodactylus* and the scincid genera *Ctenotus* and *Menetia*. The gecko *Diplodactylus klugei* sp nov and the skink *Ctenotus maryani* sp nov both qualify as 'cryptic species' in the sense that they are morphologically similar but genetically distinct from sympatric congeners. The skink *Menetia surda cresswelli* subsp nov is morphologically distinct from the typical race but shows only a minimal level of genetic divergence in allopatry. The three taxa clearly illustrate the frequent lack of congruence between morphological and genetic differentiation among squamates. A plea is made for more routine use of allozyme analysis to detect 'cryptic' species within regional vertebrate faunas.

Introduction

The Carnarvon Basin region of northwest Western Australia is an area of exceptional reptile diversity with more than 120 species recorded as a consequence of herpetological surveys conducted during the mid 1970s to early 1980s (Storr & Hanlon 1980; Storr & Harold 1978, 1980, 1984; Storr *et al.* 1983). In 1995–97 the area was resampled as part of the southern Carnarvon Basin Biological Survey, a joint project of the Western Australian Department of Conservation and Land Management and the Western Australian Museum. Close study of the combined regional collections, now totalling over 11000 specimens, has led to the recognition of new species within the genera *Ramphotyphlops* (Typhlopidae), *Crenadactylus* and *Diplodactylus* (Gekkonidae), *Delma* (Pygopodidae), and *Ctenotus, Cryptoblepharus, Lerista* and *Menetia* (Scincidae). In most cases, clarification of formal taxonomy will require large scale revisionary studies, several of which are currently in progress. However, in a few cases the taxonomic issues were largely confined to the Carnarvon Basin or adjacent regions and thus could be resolved without major revisionary work.

In this paper we describe two new species and one new subspecies of lizards belonging to the genera *Diplodactylus, Ctenotus* and *Menetia* respectively. Allozyme electrophoresis has been used to demonstrate reproductive isolation between sympatric congenors and/or to determine the level of genetic differentiation between allopatric populations.

Materials and Methods

Species detection and morphometric analysis

The new taxa were initially detected by careful examination of voucher specimens obtained from the Biological Survey sampling quadrats (each with an area of 16 ha). In the case of the new *Ctenotus* and *Diplodactylus* species, material provisionally identified as *C. iapetus* Storr and *D. pulcher* (Steindachner) showed subtle but consistent patterns of variation which led to suspicions that the samples might each contain more than one biological species. Material of each potential species-composite was initially divided up according to quadrat and sex. Starting with one of the more peripheral localities (*e.g.* most easterly), the material of each sex was examined in turn, paying close attention to the nature of any variation within and between each quadrat sample. By working systematically through the voucher material in this way, it was possible to detect subtle but systematic shifts in character states which might otherwise be overlooked as intrapopulational variation. Each of "*C. iapetus*" and "*D. pulcher*" were divided into two putative species.

Allozyme electrophoresis was then used to test for the presence of more than one biological species in each case. The 'null hypothesis', that all of the individuals are drawn from a single, freely interbreeding population, would be supported by random allelic variation between the two putative taxa. Rejection of the null hypothesis (*i.e.* recognition of discrete, reproductively isolated populations) would be indicated where significant non-random patterns of allelic variation are observed. In the case of sympatric populations, a lack of interbreeding constitutes strong grounds for recognition of distinct species, irrespective of which of the various contemporary species concepts is followed (see Baum (1992) for an introduction to this literature; and Frost & Hillis (1990) for some herptological examples).

Once the existence of an additional taxon was confirmed by allozyme electrophoresis, all available voucher specimens from the wider study area were examined. This phase of the analysis allowed for a wider

assessment of the degree of congruence among the various 'diagnostic' morphological features and provided an indication of the wider distribution of each taxon.

In the case of *Menetia surda*, the majority of Carnarvon Basin specimens conformed to a single 'morph', but this differed from 'typical' *M. surda* from the northwest of Western Australia. Specimens from a geographically intermediate population on Mardathuna appeared morphologically distinct from both northwestern and southern populations. In this case, allozyme electrophoresis was used to estimate the level of genetic differentiation between the various allopatric (and thus, by definition, reproductively isolated) populations.

The following measurements were taken with vernier calipers for all taxa: SVL (snout-vent length); Tail (tail length); and ForelimbL (length of forelimb including manus). The hindlimb was measured as HindlimbL (length of hindlimb including pes) for skinks but as TibialL (length of lower hindlimb, from upper surface of knee to plantar surface of pes) and BifemoralW (combined upper hindlimb width, measured across the knees with femora in horizontal plane) for *Diplodactylus*; this reflects differences in the most frequent preservational posture, namely hindlimbs extended in the skinks but flexed in the gekkos. Two measurments were taken of the head in *Diplodactylus*, namely; HeadL (measured from tip of snout to anterior margin of auricular fossa); and HeadW (maximum width of head).

Except where noted, head scale terminology follows Taylor (1935) for skinks and Kluge (1967) for *Diplodactylus*. Paravertebral scales (PV) in skinks were counted from immediately behind the parietal scales down to a point opposite the vent. Subdigital lamellae (SDL) were counted on the longest finger (3rd; SDLM3) and longest toe (4th; SDLP4), from the point of divergence of the digit up to, but not including, the claw-sheath. For purposes of pattern description of skinks, longitudinal scale rows are numbered outward from the paravertebral series (SR-1) around to the ventral midline (*e.g.* SR-13). Midbody scales rows (MBS) were counted midway between the axilla and groin in skinks.

Statistical analyses of individual measurements and scale counts were performed by analysis of variance. Before performing interspecific analyses, each sample was examined for intraspecific sexual dimorphism. In all cases, this was found to be non-significant (*i.e.* $P > 0.05$) for the measured variables. Relative limb lengths were examined by ratios calculated against SVL; these values are not directly amenable to statistical analysis (Atchley *et al*. 1976) but provide a useful guide to interspecific differences in shape.

Unless otherwise indicated, specimen registration numbers refer to the herpetological collection of the Western Australian Museum. The sex of voucher specimens was determined by dissection and inspection of gonads.

Allozyme electrophoresis

Liver samples suitable for allozyme electrophoresis were removed from freshly-killed lizards in the field or at the WA Museum. Samples were frozen in liquid nitrogen immediately after removal and stored at -80 ºC.

Allozyme electrophoresis of liver homogenates was conducted on cellulose acetate gels ('Cellogel', MALTA) according to the methods of Richardson *et al.* (1986). The following enzymes or non-enzymatic proteins exhibited zygograms of sufficient activity to proceed for at least one species-group: aconitate hydratase (*Acon*, EC 4.2.1.3), acid phosphotase (ACP, EC 3.1.3.2), aminoacyclase (*Acyc*, EC 3.5.1.14), alcohol dehydrogenase (*Adh*, EC 1.1.1.1), adenlyate kinase (*Ak*, EC 2.7.4.3), albumin (*Alb*), carbonate dehydratase (*Ca*, EC 4.2.1.1), diaphorase (*Dia*, EC 1.6.99), enolase (*Enol*, EC 4.2.1.11), esterase (*Esi*, 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), glutamate dehydrogenase (*Gdh*, EC 1.4.1.13), lactoyl-glutathione lyase (*Glo*, EC 4.4.1.5), aspartate aminotransferase (*Got*, EC 2.6.1.1), glucose-6-phosphate dehydrogenase (*G6pd*, EC 1.1.1.49), glycerol-3-phosphate dehydrogenase (*Gpd*, EC 1.1.1.8), glucose-6-phosphate isomerase (*Gpi*, EC 5.3.1.9), alanine aminotransferase (*Gpt*, EC 2.6.1.2), glutathione peroxidase (*Gpx*, EC 1.11.1.9), glutathione reductase (*Gsr*, EC 1.6.4.2), 3-hydoxybutyrate dehydrogenase (*Hbdh*, EC 1.1.1.30), 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), purine-nucleoside phosphorylase (*Np*, EC 2.4.2.1), dipeptidase (*PepA*, EC 3.4.13), tripeptide aminopeptidase (*PepB*, EC 3.4.11), proline dipeptidase (*PepD*, EC 3.4.13), phosphoglycerate mutase (*Pgam*, EC 5.2.4.1), phosphogluconate dehydrogenase (*6pgd*, EC 1.1.1.44), phosphoglycerate kinase (*Pgk*, EC 2.7.2.3), phosphoglucomutase (*Pgm*, EC 5.4.2.2), pyruvate kinase (*Pk*, EC 2.7.1.40), superoxide dismutase (*Sod*, EC 1.15.1.1), L-iditol dehydrogenase (*Sordh*, EC 1.1.1.14), and triose-phosphate isomerase (*Tpi*, EC 5.3.1.1). The nomenclature for identifying loci and allozymes is outlined by Adams *et al.* (1987).

Genetic distances were expressed as percentage fixed differences (% FD, Richardson *et al.* 1986) and Nei's unbiased genetic distance (Nei D; Nei 1978). Heterozygosity values for each taxon were calculated as the proportion of all genotypes observed to be heterozygotes, averaged over all loci.

Systematics

Family Gekkonidae

Diplodactylus klugei sp nov

(Fig 1A)

Holotype

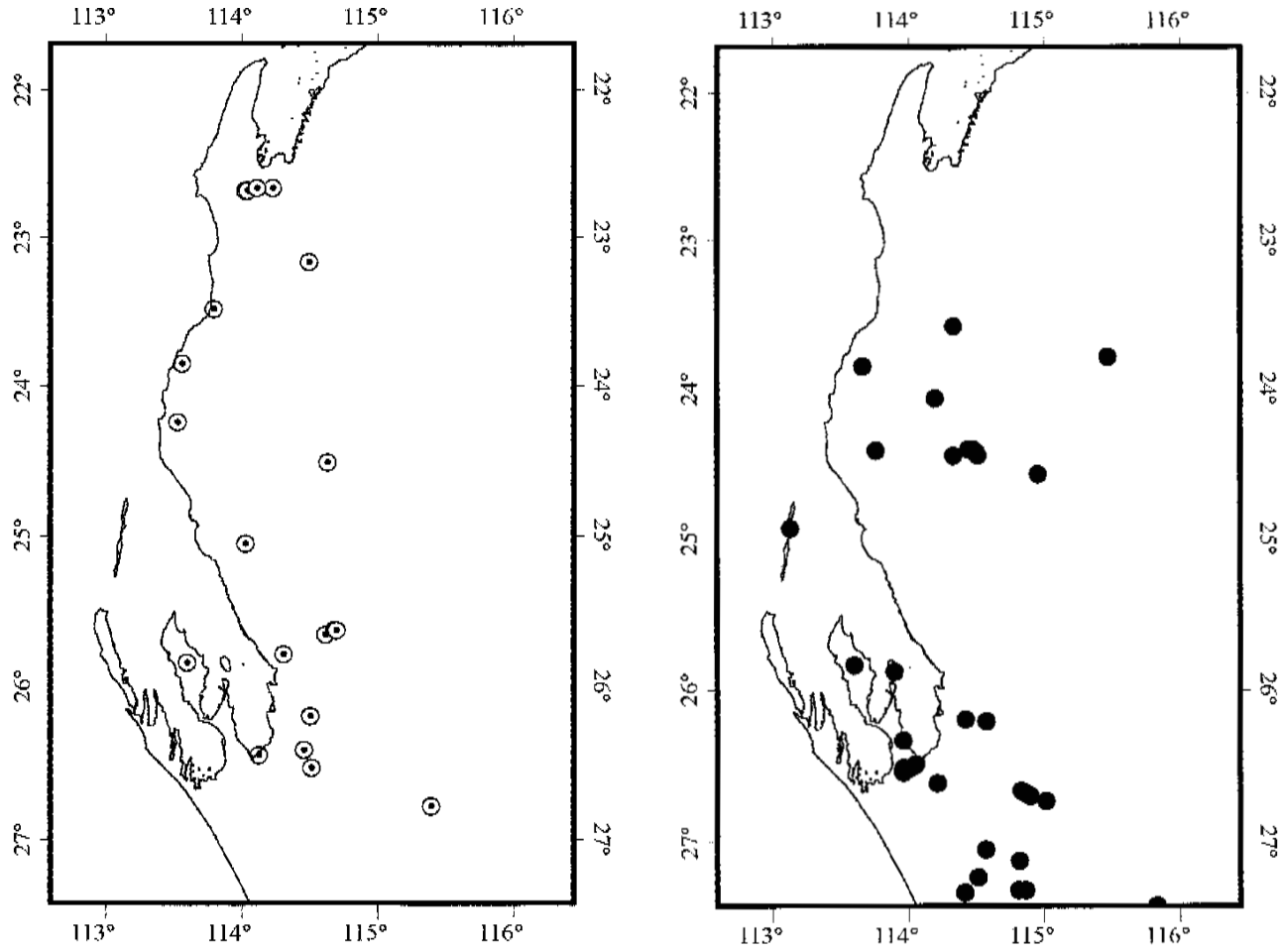
R120941 in the collection of the Western Australian Museum, an adult female collected on 11/10/1994 at Biological Survey quadrat WO4, 7 km SE of Woodleigh Outstation in 26º 11' 30" S, 114º 30' 34" E (Fig 2).

Paratypes (Biological Survey quadrats in boldtype)

14 km W Giralia HS (2-2º 40' S, 114º 14' E): 61089; 26

A. *Diplodactylus klugei* B. *Diplodactylus pulcher*

Figure 1. Individuals of *Diplodactylus klugei* sp nov. and *D. pulcher* (Steindachner), illustrating the close similarity of these probable sibling species. Details of specimens as follows; *D. klugei*, WAM R131016, an adult male from 11 km WNW Woodleigh Outstation, photographed by B Maryan; *D. pulcher*, an adult female from Kambalda East, photographed by B Maryan. Note the relatively larger head and eye of *D. pulcher*.



D. klugei *D. pulcher*

Figure 2. Distribution of *Diplodactylus klugei* sp nov and *D. pulcher* in the Carnarvon Basin area of Western Australia where they occur in regional sympatry. *Diplodactylus pulcher* is widely distributed outside of the study area.

km W Giralia HS (22° 40' S, 114° 07' E): 61265-66; Bullara (22° 41' S, 114° 02' E): 60412-13; 2 km E Bullara HS (22° 41' S, 114° 03' E): 61129-32; 3 km W Winning HS (23° 10' S, 114° 30' E): 71308; Warroora (23° 29' S, 113° 48' E): 8159-60; 5 km SE Gnaraloo HS (23° 51' S, 113° 34' E): 71572; **CU1**, 14 km E Cape Cuvier (24° 14' 41" S, 113° 32' 07" E): 126905; **MR1**, 9.8 km E Mardathuna HS (24° 30' 41" S, 114° 38' 13" E): 120715, 123460, 126758; Callagiddy HS (25° 03' S, 114° 02' E): 36748, 40669, 41589; **MD2**, 9.7 km NE Meedo HS (25° 37' 23" S, 114° 41' 39" E): 120982, 121013, 122579, 122658, 122666, 124989; **MD1**, 10.9 km NE Meedo HS (25° 37' 31" S, 114° 42' 16" E): 121050, 122527, 122550-51, 122560, 122650, 126691; **MD3**, 1.25 km NE Meedo HS (25° 39' 14" S, 114° 37' 33" E): 121610; 18.4 km N Yaringa HS (25° 47' S, 114° 19' E): 71110; 11 km WNW Woodleigh OS (26° 09' S, 114° 26' E): 131016; **WO4**, 7 km SE Woodleigh OS (26° 11' 30" S, 114° 30' 34" E): 120872, 120884, 120925, 120939, 122961, 125075; **WO5**, 13.5 km SE Woodleigh OS (26° 11' 44" S, 114° 25' 24" E): 120870, 120881; Overlander Roadhouse (26° 25' S, 114° 28' E): 15278, 55189; 7 km W Hamelin HS (26° 27' S, 114° 08' E): 54843; 10 M S Shark Bay turnoff, Northwestern Highway (26° 32' S, 114° 31' E): 28654; 6 km NE Mungawolagudi (26° 47' S, 115° 24' E): 60618.

Diagnosis

A moderate-sized member of subgenus *Diplodactylus* with rostral and first supralabial both entering nostril; posterior supralabials not much larger than general head scales; mental in long contact with first infralabial; digits with single pair of enlarged apical plates, claws project well forward of plates; other subdigital scales small, rounded, arranged in transverse rows; dorsal pattern usually a series of 4-5 large, dark-rimmed pale blotches on red-brown ground colour (blotches are occasionally united into broad, dark-edged vertebral stripe).

Description

A slender-bodied, moderately long-limbed terrestrial *Diplodactylus*. Tail shorter than head + body, round in cross-section, widening slightly from base and tapering gradually to tip. Head relatively long and narrow, with distinctly 'beaked' snout. SVL to 58 mm; Tail to 33 mm; HeadL to 11.1 mm; HeadW to 9.0 mm; TibialL to 9.0 mm; BifemoralW to 20.5 mm. Other statistical data are given in Table 1. Males have higher mean values than females for every dimension but none of the contrasts is statistically significant.

General head and body scalation finely granular, granules slightly larger on dorsum and forward onto head. No tubercles or spines present on body or tail. Dorsal and lateral surfaces of tail covered in regular rows of small triangular scales (apices directed posteriorly). Ventral surface with smaller, non-aligned rounded scales. Postcloacal sac (housing hemipenes in males) covered in larger rounded scales; sac relatively smaller in females. Cloacal spine cluster of males consists of 6-10 small, conical scales arranged in 2-3 transverse rows; cluster present in females but scales smaller, rounded rather than conical. Preanal region without enlarged scale series or associated pores.

Plantar surface of manus and pes finely granular. Digits moderately elongate, narrowing at level of terminal phalanx, terminating in paired, ovate apical plates. Fine claws project well past end of apical plates, visible to naked eye. Undersurface of digits with small, rounded scales in transverse rows, 2-4 per row.

Head elongate, narrow and moderately deep. Snout distinctly 'beaked', weakly grooved between nostrils. Eye moderately large; supraciliary scales small, triangular except for 2-3 small conical scales at posterior corner of eye. Ear aperture small, horizontally ovate.

Rostral scale high, rectangular, forming anterior border of nostril (Fig 3). Well-defined rostral crease extends $^{1}/_{3}$ - $^{2}/_{3}$ way towards lip. First supralabial high, forming inferior rim of nostril. Enlarged supranasal scale forms upper rim of nostril, opposing scales usually in broad midline contact but occasionally separated by small internasal scale (*e.g.* R122961). Series of 2-4 small scales complete posterior rim of nostril. Variable number of enlarged scales (0-2) located immediately behind supranasals. Second supralabial about $^{1}/_{3}$ height of first. All successive supralabials much smaller, decreasing in size towards oral rictus. Supralabial tally 13-17. First row of loreal scales only slightly smaller than supralabials.

Mental elongate, triangular. First infralabial large, in broad contact with mental and succeeded by 12-13 additional infralabials in decreasing series.

Dorsal pattern variable. Most specimens with 4-5

Table 1

Mensural and meristic data for *Diplodactylus klugei* sp nov and a sample of *D. pulcher* from the southern Carnarvon Basin region. All summary values are mean ± standard deviation. Sexual dimorphism was not present in any dimension so data are pooled for both sexes. *Diplodactylus klugei* is smaller than *D. pulcher* in all dimensions except tail length which is approximately equal in the two species. The ratio data indicate that *D. klugei* is similar in body shape except for having relatively shorter legs. *Diplodactylus klugei* has a significantly higher number of supralabial scales. Values are mean ± standard error with range and/or sample size (n), and with significance of interspecific difference by ANOVA with F-value and probability (P; NS indicates no significance).

	***D. klugei* sp nov**	***D. pulcher***	**ANOVA**
SVL	44.1 ± 6.95 22-55 (n = 49)	50.10 ± 5.81 32-59 (n = 21)	$F_{1,69}$ = 11.83 (P < 0.01)
Tail	30.13 ± 3.23 23-33 (n = 18)	31.25 ± 6.29 22-36 (n = 4)	$F_{1,21}$ = 0.18 (NS)
HeadL	9.51 ± 1.15 6.3-11.3 (n = 48)	10.36 ± 6.71 8.8-11.4 (n = 19)	$F_{1,67}$ = 8.31 (P < 0.01)
HeadW	7.43 ± 1.03 4.7-9.0 (n = 48)	8.27 ± 0.85 7.1-9.7 (n = 18)	$F_{1,65}$ = 9.62 (P < 0.01)
TibialL	7.70 ± 1.00 4.5-9.0 (n = 48)	8.70 ± 0.77 6.2-9.6 (n = 21)	$F_{1,69}$ = 16.58 (P < 0.001)
BifemoralW	17.91 ± 2.01 11.4-20.4 (n = 41)	19.9 ± 2.12 13.9-23.3 (n = 21)	$F_{1,62}$ = 13.46 (P < 0.001)
Tibial / SVL as %	14.2-19.0 % (n = 7)	15.4-19.4 % (n = 4)	
BifemoralW/SVL as %	34.2-43.9 % (n = 40)	35.9-44.4 % (n = 21)	
Supralabials	14.54 ± 1.18 13-17 (n = 24)	13.10 ± 1.33 11-16 (n = 19)	$F_{1,42}$ = 14.07 (P < 0.01)

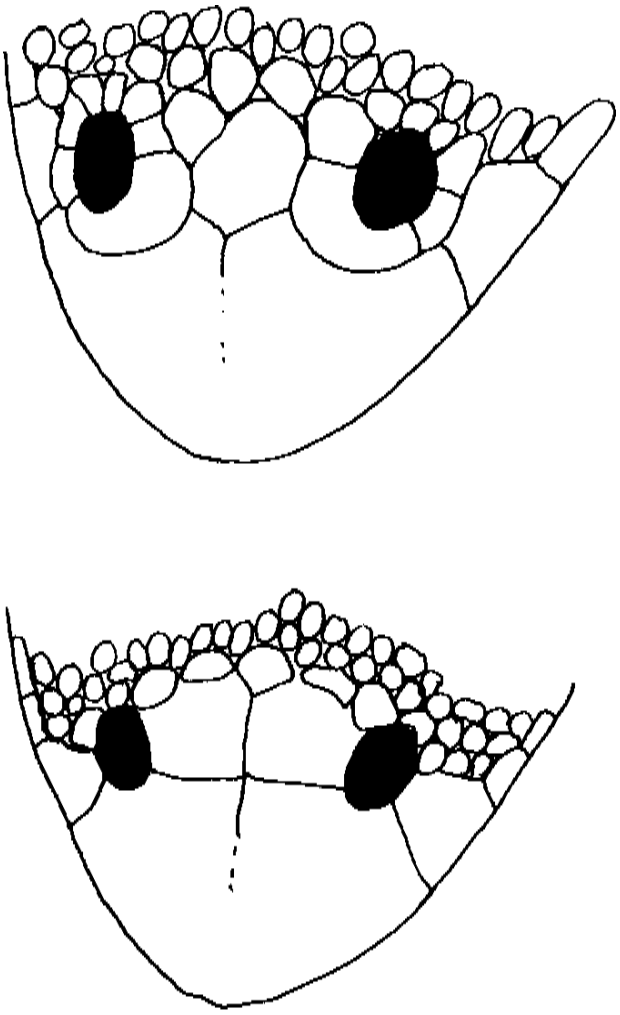


Figure 3. Rostral scalation of *Diplodactylus klugei* sp nov (bottom; WAM R120925) compared with that of *D. pulcher* (top; WAM R126707). Note the diagnostic fusion of prenasal and rostral scales and the absence of an internasal scale in *D. klugei*.

large, pale dark-edged blotches on brown to reddish-brown ground colour (80 % of total sample), but occasional specimens with longitudinal anastomoses between adjacent blotches (8 %; *e.g.* R120925) or with continuous dark-bordered vertebral stripe (12 %; *e.g.* R120884). Flanks pale brown to reddish-brown with irregular pale spots, occasionally interspersed with dark spots (*e.g.* R120941). Tail with 4-5 irregular blotches. Regrown tails lack blotches, usually have irregular dark spotting. Limbs with indistinct pale spotting. Lower flanks and venter immaculate.

Dorsum of head pale brown to reddish-brown, occasionally with darker central spot (*e.g.* R120941). Side of head with broad, pale temporal band which passes through eye to terminate at nostril. Posterior to eye, temporal band bordered below by dark brown to black line or diffuse band which terminates below eye.

Details of holotype

SVL 51mm; Tail 29 mm; HeadL 10.0 mm; HeadW 7.1 mm; TibialL 8.1 mm; BifemoralW 19.3 mm; supralabials 14; supranasals in medial contact. Dorsal pattern a series of irregular, dark-edged blotches. Flanks marked with interspersed pale and dark spots. Single yolked follicle (diameter 7.1 mm) present on each ovary.

Etymology

Named for Professor Arnold Kluge in specific recognition of his contribution to the systematics of the genus *Diplodactylus.*

Distribution

Diplodactylus klugei appears to be confined to the Carnarvon Basin but has a moderately wide distribution within this region (Fig 2). It is recorded from immediately south of Shark Bay north to Giralia and from near coastal localities inland to Mardathuna, Meedo and Woodleigh. It is present on Peron Peninsula but has not been recorded from Edel Land or any of the Shark Bay Islands. Further north, it is present in near coastal habitats on the western margin of Lake Macleod.

Genetic discrimination

Allozyme electrophoresis was conducted with liver samples from five specimens of *D. pulcher* and seven of *D. klugei*. The material selected for analysis comes from two areas where the two taxa were obtained in regional sympatry, *viz*. the Woodleigh and Mardathuna Biological Survey sites. Nine specimens were screened for 41 presumptive loci, with three others scored only for the 13 most informative loci. The individual allele scores for 20 variable loci are shown in Table 2. The following loci were invariant within the initial sample of nine specimens: *Acp1, Acp2, Adh1, Ak1, Alb, Dia, Gapd, Gda, Glo, Got1, Gpi, Gsr, Idh1, Ldh2, Mdh1, Mdh2, Me2, Pgam6, Pk1, Sod* and *Tpi.*

The two taxa show fixed allelic differences at *Acon1, Acyc, PepA* and *Pgm2* and display major differences in allele frequency at six other loci; *Acon2, Est, Gpt, Ihd2, Np* and *Pgm1*. This equates to a genetic distance of 10 % FD or a Nei D of 0.258. Even based solely on the four fixed differences, the odds against the subsamples being drawn at random from a single, freely interbreeding population are exceedingly high (the probability of obtaining no heterozygotes at four loci in a sample of 12 animals drawn at random from a "population" in which each locus has allele frequencies of $p = {}^{5}/_{12}$ and $q = {}^{7}/_{12}$ is $((1\text{-}2pq)^{12})^4$ or $1.3\ 10^{-14}$). Thus the genetic data strongly support recognition of two distinct biological species within this sample.

Given the broad distributional overlap and high degree of morphological similarity between the two taxa, it is of interest to explore the possibility of hybridization between them. The presence of correlated, fixed allelic differences at four loci makes it quite certain that none of the tested individuals represent F1 hybrids. However, examination of the pattern of heterozygosity between the two taxa does show some interesting features suggestive of possible genetic interaction. In both taxa, the overall level of heterozygosity is very similar ($H_o = 0.120 \pm 0.033$ for *D. pulcher*; $H_o = 0.100 \pm 0.027$ for *D. klugei*), but the distribution of heterozygotes at those loci showing major gene frequency differences between the two taxa is somewhat biased towards *D. klugei* ($H_o = 0.376 \pm 0.079$ *vs*

Table 2

Allozyme profiles of *Diplodactylus pulcher* and *D. klugei* sp nov at 20 variable loci. Code for Carnarvon Basin survey sites; MA = Mardathuna Station, WO = Woodleigh. A dash indicates that the genotype was not determined for this locus.

Specimen Number	Site	*Acon1*	*Acon2*	*Acyc*	*Enol*	*Est*	*Fdp*	*Fum*	*Got2*	*Gpt*	*Idh2*	*Ldh1*	*Mpi*	*Np*	*PepA*	*PepD*	*6Pgd*	*Pgk*	*Pgm1*	*Pgm2*	*Sordh*
D. pulcher																					
R120668	MR3	a	c	cd	b	ac	a	a	a	b	ab	ab	b	b	b	ab	b	a	c	a	b
R120676	MR5	a	cd	d	b	a	a	a	a	b	b	a	b	b	b	ab	b	a	c	a	a
R122756	MR5	a	ce	cd	a	a	-	-	-	-	b	-	b	b	b	-	bc	-	c	a	ab
R120958	WO2	a	cd	cd	ab	a	a	a	ab	b	b	a	bc	b	b	ab	bc	a	c	a	a
R121065	WO2	a	c	d	ab	a	a	a	a	bc	b	a	bc	b	b	b	ab	a	c	a	ab
D. klugei																					
R120715	MR1	b	ab	b	a	b	ab	ab	ab	a	a	a	b	a	a	b	b	a	ab	b	b
R120925	WO4	b	b	b	a	b	a	a	a	ab	a	a	b	a	a	a	b	a	ab	b	b
R120941	WO4	b	bc	b	a	ab	a	ab	a	a	a	a	ab	a	a	a	b	ab	b	b	ac
R120939	WO4	b	bc	b	a	ab	-	-	-	-	a	-	ab	ab	a	-	b	-	b	b	a
R120884	WO4	b	b	ab	a	b	-	-	-	-	a	-	b	ab	a	-	b	-	ac	b	ab
R120881	WO5	b	b	b	a	ab	a	a	a	ab	a	a	b	ab	a	a	b	a	a	b	b
R120870	WO5	b	bc	b	a	b	a	a	a	a	a	a	ab	a	a	a	b	a	b	b	b

H_o = 0.209 ± 0.090 for the loci *Acon2, Est, Gpt, Idh2, Np* and *Pgm1*; Table 2). Because overall levels of heterozygosity do not differ between the taxa, this bias is probably not a product of bottle-necking in *D. pulcher*. Instead, it more likely reflects either chance genetic drift operating on loci which were polymorphic in the ancestral taxon, strong selection operating on certain loci only (either for homozygotes in *pulcher* or for heterozygotes in *klugei*), or a predominantly one-way introgression of *pulcher* alleles into the *klugei* genotype. This issue cannot be resolved with allelic data and will require analysis of mitochondrial genotypes for any further clarification.

Comparison with other species

Diplodactylus klugei is remarkably similar to *D. pulcher* in general morphology (Fig 1A,B). Indeed, were it not for the strong evidence of reproductive isolation provided by the genetic data, the morphological differences might well have been ascribed to polymorphism and local phenotypic variation.

For statistical comparison, the type series of *D. klugei* was compared with a regionally sympatric sample of *D. pulcher* (Table 1). This analysis shows that *D. klugei* is significantly smaller than regionally sympatric *D. pulcher* in all dimensions, and further that it has proportionally shorter limbs. *Diplodactylus pulcher* further differs from regionally sympatric *D. klugei* in the presence of a prenasal scale which excludes both the rostral and the first labial from entering the nostril (Fig 3); a flatter internasal region with the supranasals separated by one or more internasal scales; a slightly lower number of supralabial scales (Table 1); a shorter mental scale in narrower contact with the first infralabial; longer digits with wider apical plates and shorter, nearly-concealed claws; and relatively larger eyes. Although *D. klugei* and *D. pulcher* both occur in blotched and lined pattern morphs, the relative frequency of each within the two taxa is very different. In *D. klugei* only 6 out of 51 specimens bear a simple pattern of parallel longitudinal lines, contrasting with 18 out of 23 specimens of the regionally sympatric sample of *D. pulcher*. Four other specimens of *D. klugei* show an intermediate pattern where the more characteristic blotches are united by a verterbal stripe.

Diplodactylus pulcher has an extensive distribution outside of the Carnarvon Basin, covering much of Western Australia except for the southern and the north-eastern regions (Fig 4). The WA Museum holds a total of 430 specimens of *D. pulcher*, which have been examined as part of an ongoing study of geographic variation in this species. In the present context, the most important finding is that *D. pulcher* consistently has separate prenasal scales throughout its range and almost always has one or more internasal scales. In contrast, the frequency of blotched *vs* lined pattern variants shows significant geographic variation, with a higher frequency of blotched individuals in southern populations of *D. pulcher*. Likewise, digit lengths and terminal pad size and relative limb lengths are subject to significant geographic variation in *D. pulcher*. *Diplodactylus klugei* is thus reliably distinguished from *D. pulcher* as a whole only on the basis of rostral scalation features, although dorsal pattern and limb

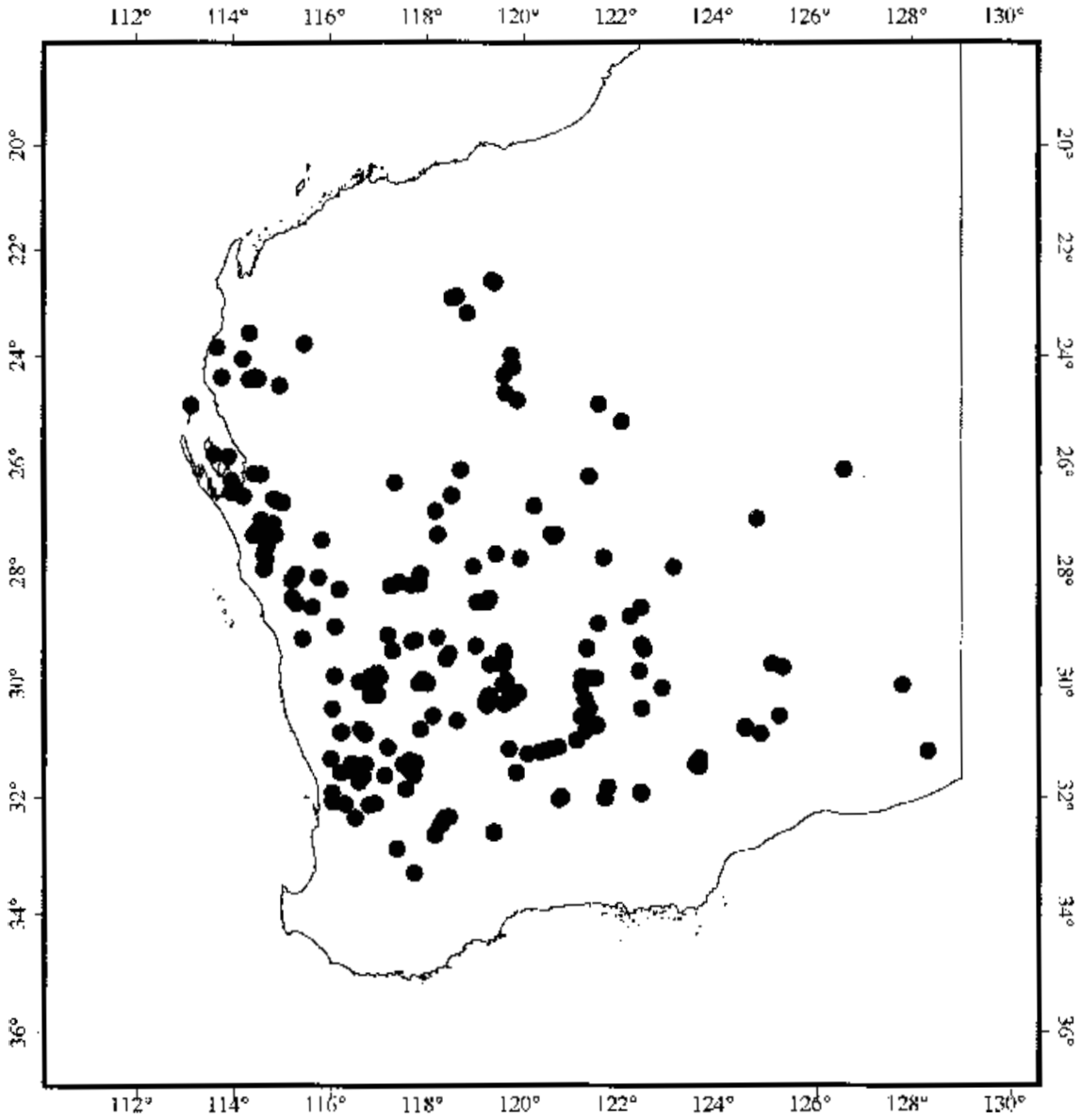


Figure 4. Distribution of *Diplodactylus pulcher* in Western Australia.

proportions provide a supplementary guide to identity in the case of Carnarvon Basin specimens.

Kluge (1967) regarded *D. pulcher* to be an isolated species without close relatives. He included it within his *vittatus* group but noted that it might also have links to the *conspicillatus* group based on the shared reduction of the labial scales. Both *Diplodactylus klugei* and *D. pulcher* show a superficial similarity in body patterning to *D. galeatus* Kluge of the Central Australian highlands and *D. steindachneri* Boulenger of Eastern Australia, but they differ from these species in various features including the greater degree of reduction of the labial scales. To date, there has been no comprehensive phylogenetic analysis of the genus *Diplodactylus* and very little comparative genetic analysis against which to evaluate the results of the present investigation.

Taxonomic remarks

Cogger *et al.* (1993) list three taxa as synonyms of *D. pulcher*. The most important of these in the present context is *Diplodactylus lucasi* Fry (a replacement name for *Diplodactylus bilineatus* Lucas and Frost). The holotype of *Diplodactylus bilineatus* Lucas and Frost (MOV D7570) is accompanied by a label with the following information: Minilya, 80 miles inland from Carnarvon Well, 9.5.1903, D.T. Wall / "TYPE" on rear. The specimen is of adult size and appears to be a female based on the size of the postcloacal spines and sac. According to Kluge (personal communication, 1997), the specimen was in a reasonable condition when he examined it in the mid-1960s; he reported that the rostral and first supralabial scales of MOV D7570 were both excluded from the nostril (Kluge 1963), a character of *D. pulcher* as restricted

here. Unfortunately, the holotype is now very dehydrated and brittle and the critical scale boundaries are no longer visible on the rostrum. As suggested by the original specific epithet, MOV D7570 has the strongly lined dorsal pattern seen in the majority of Carnarvon Basin *D. pulcher*, but a comparable condition is also present in a minority of *D. klugei*. Features more reminiscent of *D. klugei* include an elongate mental in extensive contact with the first infralabial and long claws which protrude beyond the apical plates on all digits (the latter character might reflect shrinkage of the apical pads). Minilya is on the eastern side of Lake Macleod, and both *D. pulcher* and *D. klugei* could be expected to occur in the general vicinity.

The apparent admixture of both *pulcher* and *klugei* characters in the holotype of *bilineatus* is perhaps what might be expected of a hybrid individual. If this is indeed so, *D. bilineatus* Lucas and Frost would be unavailable under the terms of Article 23h of the International Code for Zoological Nomenclature (Anon 1985) which disallows individuals of hybrid origin as holotypes of species-level taxa. However, for the present, we are inclined to treat *D. lucasi* Fry as a junior subjective synonom of *D. pulcher*, based principally on Kluge's record of the rostral scalation at a time when the specimen was in better condition.

The lectotype of *Stenodactylopsis pulcher* Steindachner (from ' Swan River, WA' = hinterland of Perth) and holotypes of *Diplodactylus pulcher dorsotaeniata* Pellegrin (from 'Birrigrin, WA' = 50 km NE of Sandstone) and *Diplodactlyus pulcher dorsalis* Werner (from Eradu, WA) have not been examined during this study. However, we have examined near-topotypic specimens for each of these forms and believe in each case that they can be accomodated within a single, geographically variable species. On present evidence, we thus find no grounds to support Wells & Wellington's (1983, 1985) otherwise unsubstantiated resurrection of *D. lucasi* and *D. dorsalis* from synonymy of *D. pulcher*.

Habitat and sympatry

Diplodactylus klugei clearly occupies a variety of different habitats. Specimens collected during the Biological Survey were obtained from samphire on the edge of Lake Macleod, from the floodplain of the Wooramel river, from the margin of a claypan on Meedo and from *Acacia grasbyi* shrubland on calcareous soils on Woodleigh. A common factor among these localities appears to be the presence of relatively hard, loamy soils rather than looser sands. In contrast, Biological Survey capture records of *D. pulcher* indicate a preference for sandier substrates either on dunes or in sandplain habitats. However, certain of the earlier records of *D. klugei* come from areas of predominantly sandy rather than loamy substrates (*e.g.* 5 km SE of Gnaraloo, Warroora, Giralia) and *D. pulcher* is known to occupy a wide variety of habitat types across its extensive geographic range.

Although *D. klugei* and *D. pulcher* are regionally sympatric over quite a large area, the two species were not found to co-occur on any of the Biological Survey quadrats. On Mardathuna, for example, *D. pulcher* was captured on quadrats MR2-5 while *D. klugei* was obtained exclusively on MR1. Similarly on Woodleigh, *D. pulcher* was obtained on quadrat WO2, and *D. klugei* on quadrats WO4-5. Further, more specific field studies are required to determine the extent and basis of any habitat partitioning between these morphologically similar geckos in the southern Carnarvon Basin.

During the Biological Survey, *Diplodactylus klugei* was obtained from the same quadrats as *D. squarrosus*, *D. stenodactylus*, *D. conspicillatus* and *D. strophurus*. *Diplodactylus pulcher* was found together with this same suite of congenors and additionally with *D. alboguttatus*.

Family Scincidae

Ctenotus maryani sp nov

(Fig 5A)

Holotype

R126761 in the Western Australian Museum, an adult male collected on 18/3/96 at Biological Survey Quadrat MR2, 5.6 km W of Mardathuna Homestead, WA, in 24° 26' 36" S 114° 30' 43" E (Fig 6).

Paratypes

15 km NE Giralia HS (22° 22' S, 114° 29' E): 61185; 3 km E Giralia HS (22° 41' S, 114° 24' E): 61121-2, 61147; 14 km N Marrilla HS (22° 51' S, 114° 27' E): 61255; 4 km W Barradale Roadhouse (22° 51' S, 114° 55' E): 80299; 0.5 km SE Merlinleigh HS (24° 19' S, 115° 11' E): 99636; **MR4**, 11.8 km W Mardathuna HS (24° 24' 26" S, 114° 28' 24" E): 120802, 122777, 126774; **MR3**, 7.7 km W Mardathuna HS (24° 25' 44" S, 114° 29' 60" E): 121555, 122735, 125364; **MR2**, 5.6 km W Mardathuna HS (24° 26' 36" S, 114° 30' 43" E): 120685; **KE1**, 41 km from Binthalya HS (24° 29' 36" S, 115° 01' 51" E): 120530; 9 km NNW Carey Downs HS (25° 32' S, 115° 26' E): 114313.

Diagnosis

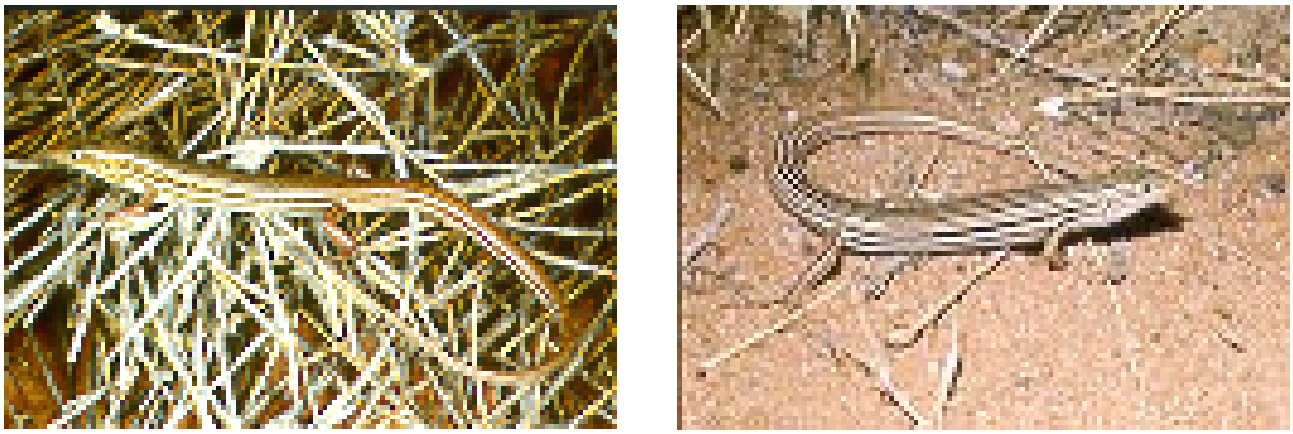
A medium-sized *Ctenotus* with pattern 'simple', comprising eight to ten pale stripes on a dark-brown to reddish-brown ground colour; body with 26-28 midbody scale rows; digits of manus and pes with keeled and weakly mucronate subdigital lamellae, 14-17 on manal digit III and 24-26 on pedal digit IV; ear lobules triangular, numerous and subequal; dorsal and lateral pattern terminating on neck, dorsum and temporal region of head with indistinct, irregular mottling only; legs with irregular and poorly-developed reticulum.

Description

A relatively slender-bodied, long-limbed *Ctenotus* with a predominantly 'simple' pattern of alternating pale and dark stripes. No sexual dimorphism in body size, proportions or colouration. SVL to 54 mm; Tail to 119 mm; ForelimbL to 14.9 mm; HindlimbL to 23.9 mm.

Paravertebral scales 51-62, mean. = 55.8 ± 3.3 (sd); scales in 26-29 rows at midbody, modal count 28 (41% of sample). Other mensural and meristic data are given in Table 3.

Plantar surface of manus and pes spinose, unpigmented. Digits slender, relatively elongate,



A. *Ctenotus maryani* B. *Ctenotus iapetus*

Figure 5. Individuals of *Ctenotus maryani* sp nov. and *C. iapetus* Storr, illustrating the remarkable similarity of these genetically quite distinct species. Details of specimens as follows; *Ctenotus maryani* sp nov, WAM R114313, an adult male from 9 km NNW Carey Downs Homestead, photographed by B Maryan; *C. iapetus*, WAM R51018, an adult female from 3 km NW Bullara Homestead, photographed by R E Johnstone.

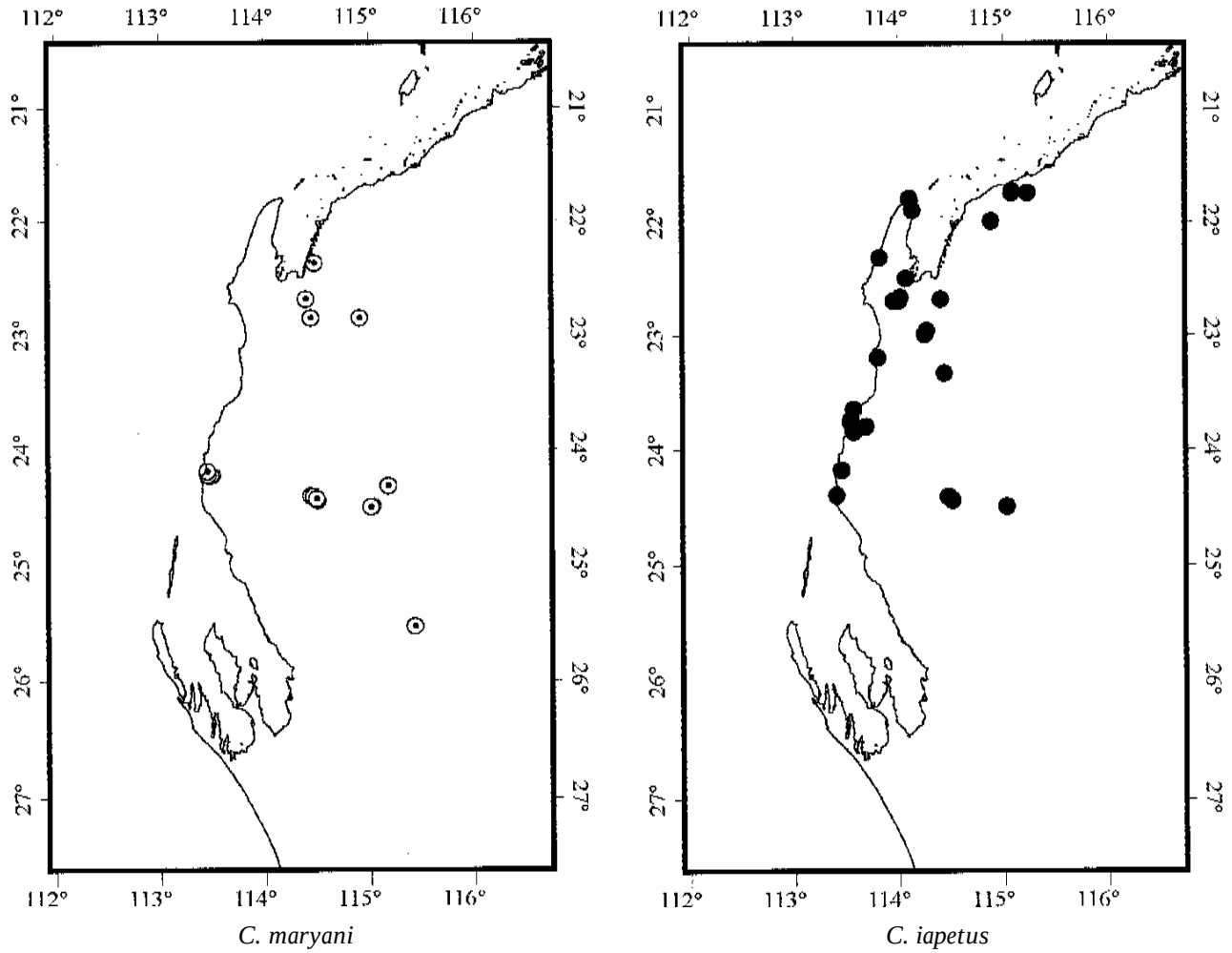


Figure 6. Distribution of *Ctenotus maryani* sp nov and *C. iapetus* in the Carnarvon Basin region of Western Australia. Both species are endemic to the region.

Table 3

Mensural and meristic data for *Ctenotus maryani* sp nov and *C. iapetus*. All values are mean ± standard deviation, followed by range and sample size. Sexual dimorphism was not present in any dimension so data are pooled for both sexes. *Ctenotus iapetus* evidently attains a larger overall size than *C. maryani* but sample means for SVL are not significantly different. *Ctenotus maryani* has a significantly higher mean number of paravertebral scales than does *C. iapetus*. The ratio data indicate that *Ctenotus maryani* has relatively shorter limbs than *C. iapetus*. Values are mean ± standard error with range and/or sample size (n), and with significance of interspecific difference by ANOVA with F-value and probability (P; NS indicates no significance).

	C. maryani	*C. iapetus*	ANOVA
SVL	47.56 ± 6.55 33-54 (n = 18)	49.20 ± 11.76 31-68 (n = 82)	$F_{1,99}$ = 0.326 (NS)
Tail	98.80 ± 19.98 64-119 (n = 10)	95.84 ± 24.61 60-149 (n = 44)	$F_{1,53}$ = 1.341 (NS)
ForelimbL	12.62 ± 1.77 8.1-14.9 (n = 18)	13.89 ± 2.59 8.9-18.1 (n = 81)	$F_{1,98}$ = 3.88 (NS)
HindlimbL	21.31 ± 2.43 14.8-23.9 (n = 18)	23.23 ± 4.47 15.5-31.0 (n = 77)	$F_{1,94}$ = 3.11 (NS)
Tail/SVL * 100	179-236 %	163-244 %	
ForelimbL/SVL*100	22.5-29.4 %	22.3-37.9 %	
HindlimbL/SVL*100	40.4-52.1 %	39.9-60.6 %	
PV	55.83 ± 3.31 51-62 (n = 18)	50.91 ± 2.90 44-61 (n = 70)	$F_{1,87}$ = 38.79(P < 0.001)
SDL-M3	16.0 ± 0.71 15-17 (n = 9)	15.66 ± 1.22 13-18 (n = 77)	$F_{1,85}$ = 0.668 (NS)
SDL-P4	25.22 ± 1.31 21-26 (n = 18)	26.17 ± 1.63 23-30 (n = 77)	$F_{1,94}$ = 5.288 (NS)

terminating in fine claw. Subdigital lamellae keeled and with small mucrons. SDL 14-17 on manal digit III, modal count 16 (56 % of sample); 24-26 on pedal digit IV, modal count 26 (61 % of sample).

Nasals and prefrontals both in broad medial contact. Loreals 2, anterior higher but less elongate than second (Fig 7). Supralabials 8-9, 5 or 6 of these making up discrete preorbital series. Postsupralabials [postlabials of Taylor (1935)] 2. Infralabials 8. Supraoculars 4, second wider than third, all but last in contact with frontal (Fig 8). Supraciliaries 7-8, either 1>2>3>>4-7 with anterior 3 in contact with first supraocular, or 1>2>>3-8 with anterior 4 in contact with first suprocular. Eyelid mobile, with three enlarged scales forming a divided window. Preoculars 2 [lower is anterior presubocular of Taylor (1935)]. Single presubocular, wedged between supralabials 5-6 or 6-7. Postsuboculars 3, abutting penultimate supralabial and primary temporal, in series with pretemporals. Single primary temporal, wedged between last two supralabials. Secondary temporals 2, upper much larger than lower. Frontoparietal larger than interparietal. Parietal eye clearly visible at rear of interparietal. Parietals in contact behind interparietal. Nuchals in 2-4 pairs, 83 % with 4 nuchals on at least one side.

Ear aperture moderately large. Usually with 2-3 large triangular lobules, bordered above and below by one or more smaller, rounded lobules (Fig 7).

Ground colour of body dark-brown on dorsum, paler reddish-brown on flanks. Dorsum with four continuous stripes (Fig 9); white paravertebral stripe (positioned centrally on SR-1), off-white dorsal stripe (centre SR-2), white dorsolateral (centre SR-3) and off-white upper lateral (lateral SR-4). Flank always with broad midlateral and lower lateral stripes; both are white, positioned on scale rows 6 + part 7 and 8 + part 9 respectively. Lower lateral stripe faintly delineated below by thin brown line (centre SR-9). Upper lateral zone variable: either solid brown, covering whole of SR-5 and intercalcating tips of rows 4 and 6 (*e.g.* R80299, R121555) or divided by off-white accessory upper lateral stripe (centre SR-5). Accessory stripe usually indistict, comprised of irregular

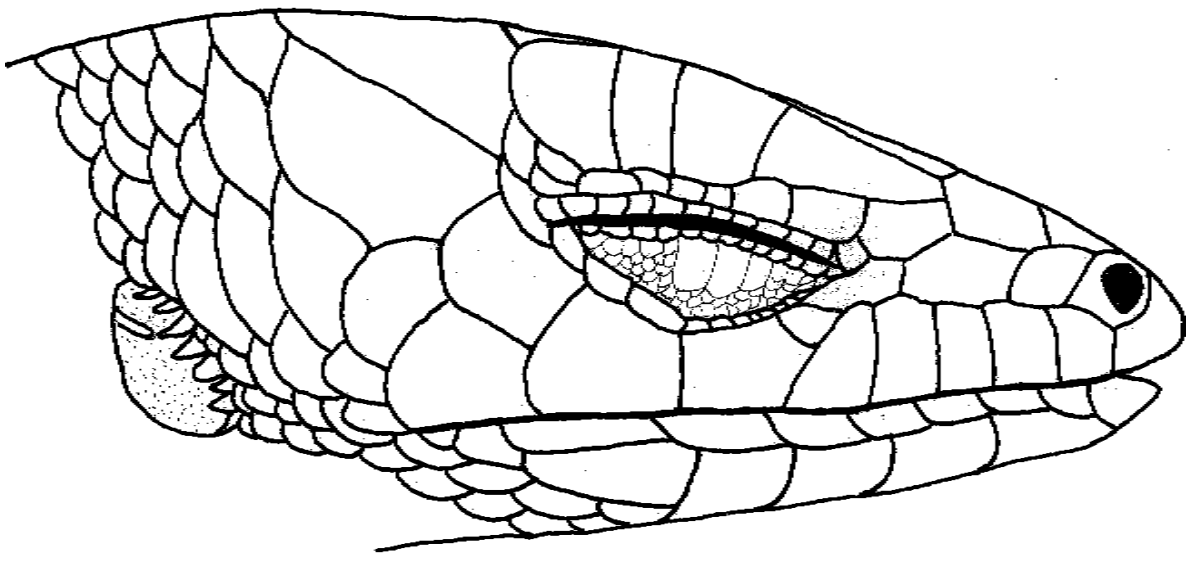


Figure 7. Scalation of the lateral surface of the head of *Ctenotus maryani* sp nov (WAM R126761).

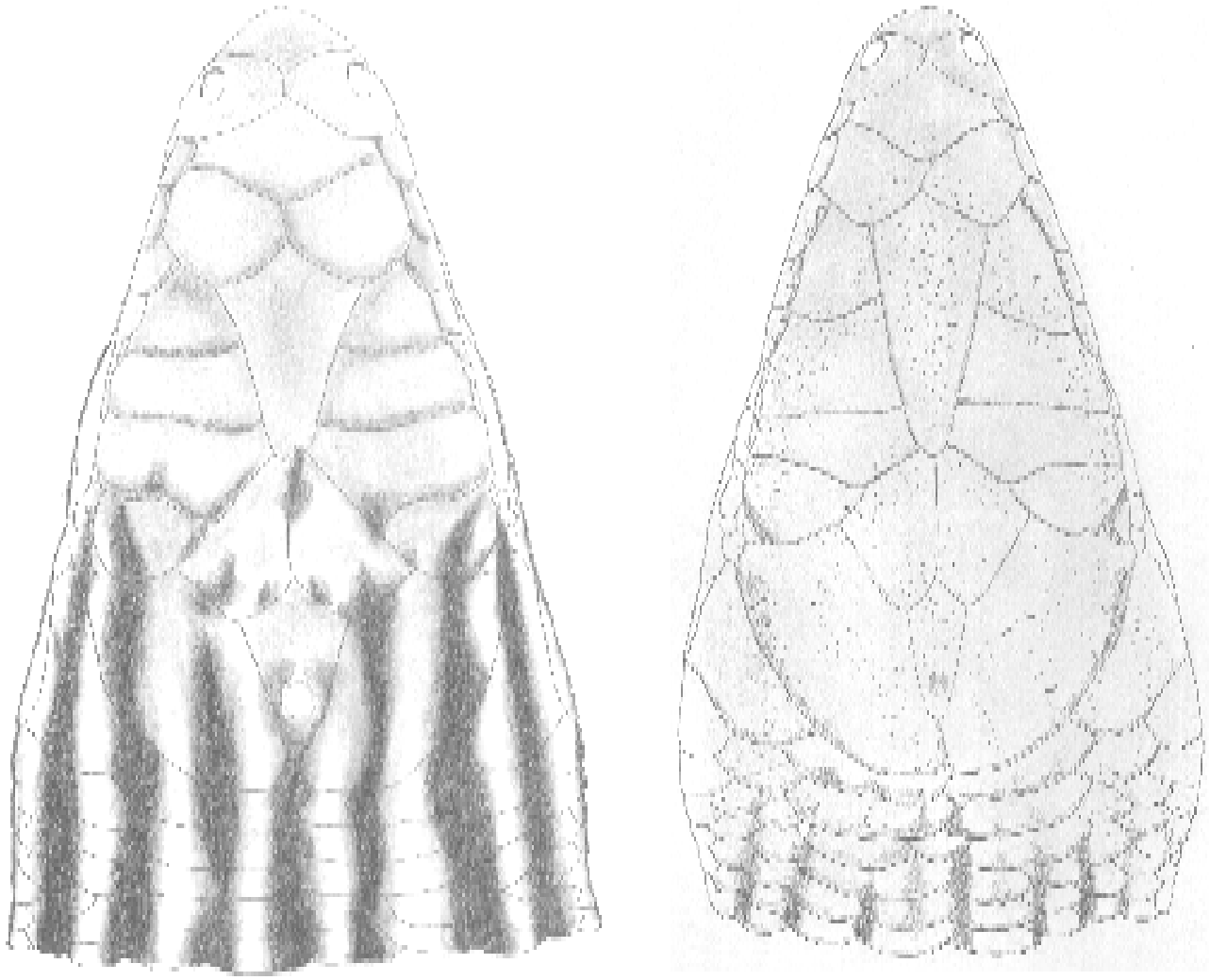


Figure 8. Scalation and patterning of the dorsal surface of the head and neck in *Ctenotus iapetus* (left; WAM R122921) and *C. maryani* sp nov (right; WAM R126761). Note the diagnostic discontinuation of the dorsal pattern at the level of the nuchal scales in *C. maryani*, compared with the continuation of dorsal patterning onto the parietal and frontoparietal scales in *C. iapetus*.

dashes (*e.g.* R114313, R126756, R126761), but occasionally continuous and well-defined (*e.g.* R120685).

Dorsal pattern terminates at level of nuchal scales (Fig 8). Lateral pattern extends forward of forelimb to terminate at level of ear aperture, ringed in white. Dorsum and sides of head pale brown, indistinctly marked as follows: lower temporal and postlabial scales with irregular white blotches; upper temporal scales and parietal scales with white flecking between eye and each of dorsal and dorsolateral stripes; subocular region with faint white streak; most scales and lower margin of orbital fossa with fine dark-brown emargination.

All pattern elements except dorsal stripe extend onto tail but with reduced intensity; tail paler than dorsum. Limbs with longitudinal dark-brown stripes, with occasional reticulation, extending onto digits. Venter immaculate throughout.

Details of Holotype

SVL 51 mm; Tail 118 mm; ForelimbL 15 mm; HindlimbL 24 mm; paravertebral scales 53; midbody scale rows 26; subdigital lamellae manus III 15; subdigital lamellae pes IV 25; supralabials 8; supraciliaries 8; upper ciliaries 10; ear lobules 4 on right, 3 on left; nuchals 3 pairs. Upper lateral zone with weakly defined accessory pale stripe. Testis regressed, efferent duct turgid.

Etymology

Named for Mr Brad Maryan, irrepressible enthusiast of the Australian herpetofauna, outspoken advocate of amateur reptile-keeping and a major contributor to the herpetological collections of the Western Australian Museum.

Distribution

Apparently restricted to the central and northern parts of the Carnarvon Basin, from the vicinity of Carey Downs HS, inland to the Kennedy Range and north to Giralia (Fig 6).

Genetic discrimination

Ctenotus maryani was compared genetically with *C.*

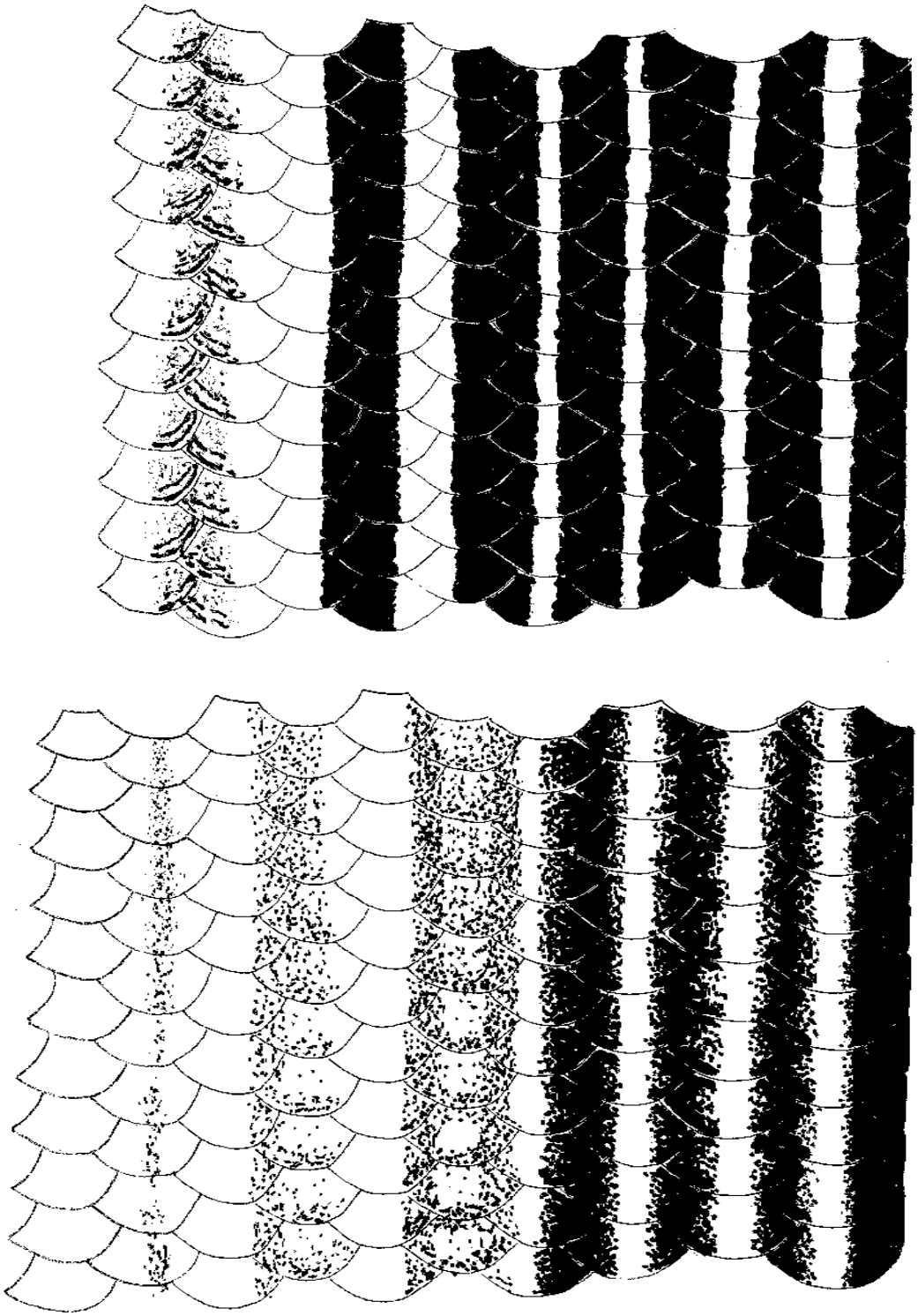


Figure 9. Semi-schematic diagram of the dorsal and lateral body pattern of *C. iapetus* (top; WAM R122911) and *Ctenotus maryani* sp nov (bottom; WAM R126761). The pattern is illustrated relative to the boundaries of longitudinal scale rows. The right hand margin corresponds with the dorsal midline.

iapetus Storr, the species with which it formerly was confused. *Ctenotus maryani* is morphologically quite distinct from all other species of the genus, hence broader genetic comparisons were not required to justify specific recognition.

A total of 10 individuals was screened at 46 presumptive loci. The sample comprised seven individuals of *C. iapetus* and three of *C. maryani*. The three individuals of *C. maryani* came from quadrats MR3 and MR4 on Mardathuna and quadrat KE1 on the slopes of the Kennedy Range. The seven individuals of *C. iapetus* included two from each of these sites and one

Table 4

Allozyme profiles of *Ctenotus iapetus* and *C. maryani* sp nov at 23 variable loci. Code for Carnarvon Basin survey sites: MR = Mardathuna Station, KE = Kennedy Range. A dash indicates that the genotype was not assignable at this locus due to poor sample activity.

Specimen Number	Site	*Acon1*	*Acon2*	*Adh1*	*Alb*	*Ca*	*Est2*	*Fdp*	*G6pd*	*Gapd*	*Got1*	*Hbdh*	*Idh1*	*Ldh*	*Me*	*PepA*	*PepB*	*PepD 1*	*PepD 2*	*6Pgd*	*Pgm*	*Pk2*	*Sod*	*Tpi*
C. iapetus																								
R123186	KE1	-	b	b	b	a	b	a	b	a	a	b	b	a	b	c	a	a	b	b	b	ab	a	b
R123187	KE1	a	b	b	b	a	b	a	b	a	ab	b	b	a	b	c	a	b	b	b	b	a	a	b
R122838	MR2	a	b	b	b	a	b	a	b	a	a	b	b	a	b	c	a	b	b	b	b	a	ab	b
R122725	MR3	ab	ab	b	b	a	b	a	b	a	a	b	b	a	b	c	a	b	b	b	b	a	a	b
R122728	MR3	a	b	b	b	a	b	a	b	a	a	b	b	a	b	c	a	ab	b	b	b	a	a	b
R120375	MR4	a	b	b	b	a	b	a	b	a	a	b	b	a	b	c	a	ab	b	b	b	a	a	b
R120698	MR4	a	b	b	b	ab	b	a	b	a	a	b	b	a	b	c	a	ab	b	b	b	a	a	b
C. maryani																								
R120530	KE1	a	ab	a	a	a	a	ab	a	b	a	a	a	b	a	b	b	b	a	a	b	ab	a	a
R122735	MR3	a	b	a	a	a	a	a	a	b	a	a	a	b	a	bc	b	b	a	a	ab	-	a	a
R120802	MR4	a	b	a	a	a	a	a	a	b	a	a	a	b	a	ab	b	b	a	a	b	a	a	a

from quadrat MR2 on Mardathuna. The sample is thus drawn from within an area of broad distributional overlap between the two taxa and includes material obtained in immediate sympatry.

Of the 46 loci examined, the following 23 were invariant; *Acp1, Acp2, Acyc, Adh2, Ak1, Dia, Enol, Est1, Fdp, Fum, Gda, Glo, Got2, Gpi, Gsr, Idh2, Mdh1, Mdh2, Mpi, Np, Pgam, Pgk* and *Srdh.* The allozyme profiles of all 10 individuals at the 23 variable loci are shown in Table 4.

The two taxa show fixed allelic differences at 13 loci; *Adh1, Alb, Est2, G6pd, Gapd, Hbdh, Idh1, Ldh1, Me2, PpB, PpD2, 6Pgd* and *Tpi*. This equates to a genetic distance of 28% FD or a Nei D of 0.328. The level of heterozygosity is very low in both species (H_o = 0.047 ± 0.021 for *C. maryani*; H_o = 0.028 ± 0.012 for *C. iapetus*) with the majority of loci having a single allele or one allele for each taxon. Accordingly, only one additional locus, *PepA*, displays a major difference in allele frequency between the two taxa. No obvious genetic differences exist between the two localities within either taxon.

The high level of genetic differentiation which exists between sympatric populations of *C. maryani* and *C. iapetus* amply confirms that that the two represent distinct biological species. Moreover, it gives cause for speculation that these species may not in fact represent true siblings, but might each be more closely related to some other taxon or cluster of taxa within the genus (see below).

Comparison with other species

Ctenotus maryani will be compared first with the sympatric *C. iapetus*, then with other small to medium-sized *Ctenotus* with 'simple' patterns and smooth to obtusely keeled subdigital lamellae (members of Storr *et al*.'s (1981) *Ctenotus atlas* group).

Ctenotus iapetus attains a larger size than *C. maryani* and has a heavier build and slightly longer-limbs (Table 3). It has a lower modal midbody scale count (26 *vs* 28 in *maryani*) and a significantly lower paravertebral scale count (Table 3). The digits of *C. iapetus* appear slightly longer and the subdigital lamellae have less prominent keels with smaller mucrons than those of *C. maryani*. *Ctenotus iapetus* typically has 2-3 pairs of nuchal scales (usually 4 pairs in *C. maryani*).

Although the body pattern is superficially similar in the two species, there are a number of significant differences (Fig 5A,B). In *C. iapetus* the longitudinal stripes are brilliant white and form a bold contrast with the uniform dark-brown to black ground colour; furthermore the dorsal and lateral stripes continue forward onto the dorsum and pretemporal regions of the head (the midlateral stripe passing below the eye to extend along the upper lip). In contrast, the pattern of *C. maryani* is more subdued, the variably white to off-white longitudinal stripes being less prominent against a dark-brown to reddish-brown ground colour, and the body pattern fading into an irregular mottling on the neck and head. The limbs in *C. iapetus* are also more boldly and regularly striped.

Ctenotus maryani and *C. iapetus* are both restricted to the Carnarvon Basin region, although the range of *C. iapetus* extends further north onto the Cape Range Peninsula and Onslow coastal plain (Fig 6).

Ctenotus quattuordecimlineatus (Sternfeld) of the central and northwestern Australian sand deserts is very similar to *C. iapetus* (see further comments below), hence it differs from *C. maryani* in essentially the same features which distinguish the latter species from *C. iapetus*. However, *C. quattuordecimlineatus* attains an even larger size (SVL to 70 mm), has a more sharply-defined reticulate (rather than lined) pattern on its limbs, and has a continuous, better-defined accessory upper lateral stripe (generally absent or weakly indicated in *C. maryani*). In some individuals of *C. quattuordecimlineatus*, a further incomplete stripe or row of dashes extends back from the axilla within the lower lateral zone, making a total of eight white stripes on each side compared with a maximum of seven in *C. maryani*.

Ctenotus ariadnae Storr of central Western Australia is readily distinguished from *C. maryani* by the strong black marbling of the frontoparietal and temporal regions. It also has a higher number of midbody scale rows (28-34) and longer digits with more finely keeled and mucronate subdigital lamellae. In adult *C. ariadnae*, the lateral pattern consists of numerous fine stripes anteriorly, breaking up into irregular spotting posteriorly. In juveniles, a more regular pattern of fine stripes is evident, with a continuous pale stripe running down the centre of each of SR-1 to SR-9.

Of the remaining members of Storr's *Ctenotus atlas* group, *C. atlas* Storr and *C. leae* (Boulenger) are similar to *C. maryani* in the absence of strong facial patterning, but each is readily distinguished on other criteria; *Ctenotus atlas* by its fewer pale stripes (maximum of 5 on each side) and higher number of midbody scales rows (28-34); and *C. leae* by its fewer pale stripes (3 on each side), generally fewer midbody scale rows (21-26), and larger presubocular and loreal scales (hence lower, more rectangular, anterior supralabials).

Ctenotus zastictus Storr, currently known only from an isolated patch of eucalpyt-*Triodia* habitat south of Shark Bay, is overall quite similar to *C. maryani* in limb and body proportions, head scalation and body pattern. It differs from *C. maryani* in having interrupted (*i.e.* dashed) rather than continuous dorsolateral and midlateral stripes, more regularly striped legs and a slightly lower midbody scale count (24-26). Storr (1984) noted the close resemblance between *C. zastictus* and *C. iapetus* (*sensu lato*) and referred both to his *C. atlas* species-group. His observations may have been due in part to confusion between *C. iapetus* and *C. maryani*.

Habitat and sympatry

In the Kennedy Range *C. maryani* was obtained from a red dune crest with a tall shrub layer of *Grevillea, Acacia* and *Banskia* over *Triodia.* On Mardathuna it occurs both on red dune and on red sand plain habitats, with *Acacia* woodland over *Plectrachne*. In the north (Giralia, Barradale & Merlinleigh) it appears to be associated specifically with interdune habitats with *Triodia.* On Carey Downs it was collected from *Triodia* beneath *Acacia* on 'fairly hard clay red soil' (notes accompanying specimen R114313). A specific association with hummock grasses may be reasonably inferred from its known distribution.

Ctenotus maryani is found in local sympatry in the Kennedy Range with *C. iapetus, C. pantherinus* and *C. rufescens.* On Mardathuna it is locally sympatric with these species and with *C. hanloni* and *C. piankai*.

Other remarks

Ehmann (1992: 202) figured an individual of *Ctenotus maryani* as *C. iapetus* but did not provide locality details. True *C. iapetus* has been illustrated by Storr *et al.* (1981; Plate 8.2) and by Wilson & Knowles (1988:362).

Removal of *C. maryani* from within *C. iapetus* makes it necessary to reconsider the relationship between the latter taxon and *C. quattuordecimlineatus*. Storr (1975) initially described *iapetus* as a subspecies of *C. quattuordecimlineatus* but later elevated the taxon to species level without comment (Storr & Hanlon, 1980). Interestingly, this action was taken following collection of the first specimens of *C. maryani* by Harold, Hanlon and others around Giralia and after examination of this new material in preparation for publication of "Lizards of Western Australia I. Skinks" (Storr *et al.* 1981; their account of *C. iapetus* is clearly based on a 'mixed' sample). Thus Storr's decision to dissociate *iapetus* from *quattuordecimlineatus* may have been influenced to some extent by characteristics of *C. maryani*. Interestingly enough, Cogger (1992; also Cogger *et al.* 1983) has continued to list *iapetus* as a subspecies of *quattuordecimlineatus*, which is mapped with a continuous distribution from Cape Range through to central Australia. Examination of WA Museum records indicates that the distribution is actually disjunct, with a gap of several hundreds of kilometers between the nearest specimens of *iapetus* and *quatturodecimlineatus*.

Preliminary morphological comparisons of *C. iapetus* (*sensu stricto*) with topotypic material of *C. quattuordecimlineatus* suggests that these taxa probably are closely related. Nevertheless, *iapetus* differs from *quattuordecimlineatus* in usually lacking any trace of an accessory dorsolateral stripe, and in having more boldly striped limbs and longer digits with higher subdigital lamellar counts. For the present, therefore, we prefer to maintain them as distinct species pending more detailed morphological and genetic studies of this group. Greer (1992) also favours recognition of two species.

***Menetia surda cresswelli* subsp nov**

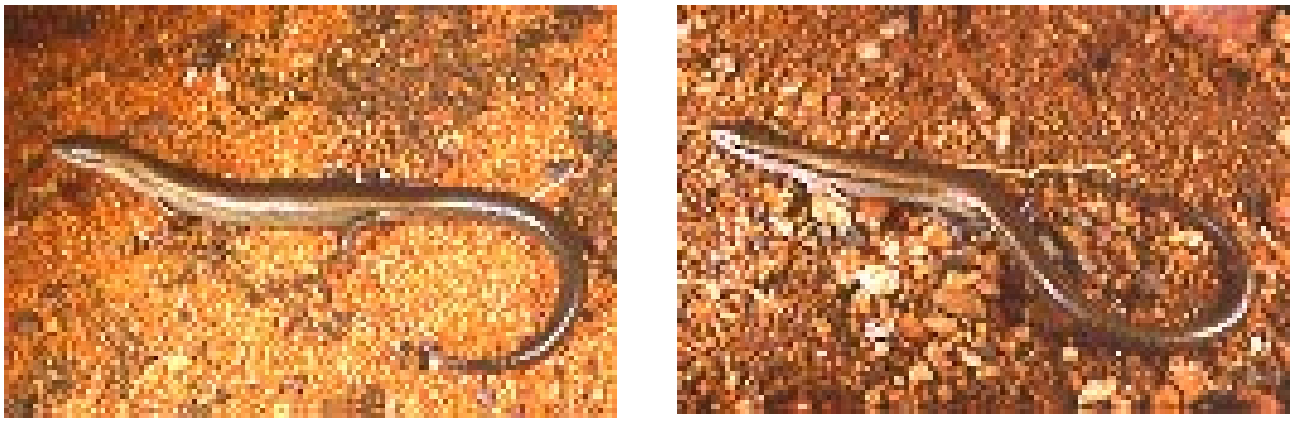
(Fig 10A)

Holotype

R101249 in the Western Australian Museum, an adult male collected by M Peterson on 25/5/1987 at 19 km N Yuna, WA, in 28° 10' S, 115° 03' E (Fig 11).

Paratypes

Bernier Island (24° 46' S, 113° 09' E): 20524-5; **PE2**, 3 km SSW Peron HS (25° 52' 31" S, 113° 33' 01" E): 121653; **PE5**, 13.5 km S Peron HS (25° 58' 33" S, 113° 34' 16" E): 121647-48, 123620, 123678-79; 25 km S Denham (26° 06' S, 113° 37' E): 54573-8, 54826; 8 km SE Nanga HS (26° 17' S, 113° 51' E): 54901-05; 12 km SW Hamelin HS (26° 29' S, 114° 05'40" E): 92465; **NA2**, 16 km SW Hamelin HS (26° 29' 23" S, 114° 03' 21" E): 120780; 48 km W Overlander Roadhouse (26° 30' S, 114° 02' E): 64358, 64367; 27 km E Tamala HS (26° 32' S, 113° 56' E): 18471; **NA4**, 27 km SW Hamelin HS



A. *Menetia surda cresswelli* B. *Menetia surda surda*

Figure 10. Individuals of *Menetia surda cresswelli* subsp nov and *Menetia surda surda* Storr, illustrating the differences in body patterning between these morphologically distinct but genetically closely related geographic isolates. Details of specimens as follows; *Menetia surda cresswelli* subsp nov, WAM R131779, an adult male from 12 km WNW Wandina Homestead, photographed by B Maryan; *M. surda surda*, WAMR132655, an adult male from Burrup Peninsula, photographed by B Maryan

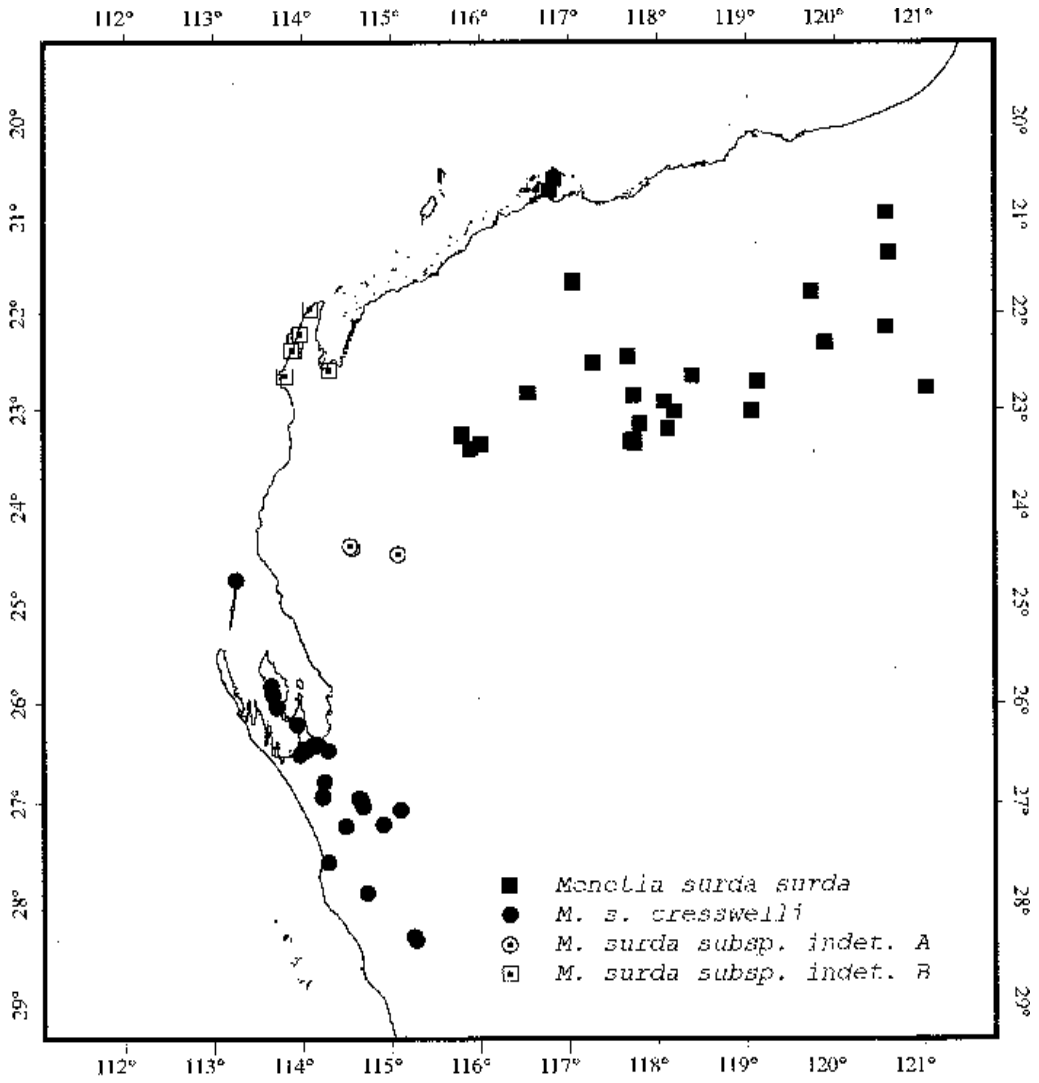


Figure 11. Distribution of the various, morphologically distinct populations of *Menetia surda* in Western Australia. Specimens from the Mardathunna/Kennedy Range area and from Cape Range Peninsula are regarded as *M. surda* subsp *incertae sedis* pending further field survey and analysis.

(26° 32' 47" S, 113° 57' 49" E): 121087, 121089, 122454; 18 km NW Coburn HS (26° 33' S, 114° 13' E): 96546; Nanga (26° 35' 32" S, 113° 53' 22" E): 127243; **NA5**, 35 km SW Hamelin HS (26° 35' 34" S, 113° 53' 23" E): 122474-76, 122508, 122523, 125506; 15 km WNW Cooloomia HS (26° 52' 30" S, 114° 09" E): 66340, 66351, 66373; 17 km SW Cooloomia HS (27° 01' 30" S, 114° 09' 00" E): 66377; 17.5 km SW Cooloomia HS (27° 02' S, 114° 09' E): 66353; **NE1**, 12 km NNW Nerren Nerren HS (27° 02' 50" S, 114° 34' 23" E): 120892; **NE2**, 9 km NNW Nerren Nerren HS (27° 03' 24" S, 114° 35' 21" E): 121315, 122981; **ZU1**, near Zuytdorp Cliffs (27° 15' 42" S, 114° 09' 11" E): 123545, 123598); 30 km SE Nerren Nerren HS (27° 19' S, 114° 51' E): 60638; 31 km SW Nerren Nerren HS (27° 20' S, 114° 25' E): 64327; 1 km SW Nerren Nerren HS (27° 20' S, 114° 37' E): 96551; Meanarra Hill, 7 km E Kalbarri (27° 42' S, 114° 13' E): 33536; 10 km NW Wandina HS (27° 56' S, 115° 30' E): 96678; 12 km WNW Wandina HS (27° 56' S 115° 32' E): 131779; 21 km S Galena (28° 01' S, 114° 40' E): 71048; East Yuna Nature Reserve, 30 km ESE Yuna (28° 28' S, 115° 13' E): 48109, 48112, 48124-25, 48225, 48235-37, 48253, 49927, 75558, 75561-62, 125956-961; Bindoo Hill Reserve, 30 km NNW Tenindewa (28° 30' S, 115° 14' E): 48194, 48203.

Diagnosis

A relatively plain *Menetia* with a subdued pattern of 8-10 longitudinal dark lines of subequal strength and spacing. Differs from nominate *M. surda* in having fewer scales along paravertebral series; paravertebral scale series wider than more lateral scales along entire length of body (posterior paravertebrals not widened in *surda*); claws on manus and pes shorter and recurved; lacking conspicuous laterodorsal stripe; and venter with faint longitudinal lines for posterior $^{1}/_{3}$ - $^{2}/_{3}$ of body length (immaculate in *surda*).

Description

A relatively plain *Menetia* with a subdued pattern of longitudinal dark lines. SVL to 30.3 mm; Tail to 52.6 mm; ForelimbL to 7.1 mm; HindlimbL to 10.7 mm. Other mensural and meristic data given in Table 5.

Paravertebral scales 50-60, mean = 55.6 ± 2.2 (sd); scales in 20-24 rows at midbody, modal count 22 (68 % of sample). Paravertebral scales remain wider than scales of more lateral rows along entire length of body.

Plantar surface of manus and pes with bluntly rounded scales. Digits slender, relatively elongate, all terminating in short, recurved claws. Subdigital lamellae with broad ventral calli. SDL 12-17 on manal digit III, modal count 15 (36 % of sample); 21-26 on pedal digit IV, modal count 24 (25 % of sample).

Preanal scales 4, lateral scales overlapping medial.

Nasals divided by posterodorsal cleft; widely separated medially. Prefrontals usually narrowly separated (40 % of sample) or in narrow medial contact (31 %); occasionally more widely separated (19 %) or in broad contact (10 %). Frontal small, shield-shaped, in point contact with frontoparietal. Loreals 2, subequal or anterior higher than posterior. Supralabials 6, 3 of these forming discrete preorbital series. First supralabial usually shorter than second or third. Posterior part of third supralabial wedged below anterior end of fourth. Postsupralabials 2. Infralabials 6. Supraoculars 3, first very large, in narrow contact with prefrontal, abutting supraciliaries 1-3. Second supraocular less than one half size of first, wider than third, abutting supraciliaries 3-4. Supraciliaries 4, first in broad contact with first supraocular; second largest, posterior end wedged between third supraciliary and enlarged ciliary; third more than twice size of fourth. One specimen (R123598) shows unilateral fusion of the first and second supracilairies. Eyelid forms fixed spectacle, entirely clear. Enlarged ciliary scale on posterodorsal margin of orbit, subequal to or slightly smaller than third supraciliary. Preoculars 2, upper scale very small, lower in series with single presubocular. Presubocular usually slightly smaller than lower preocular [both of these scales identified as presuboculars by Taylor (1935), Rankin (1979) and Storr *et al.* (1981)]. Single postsuboculars above fifth supralabial, in series with pretemporals. Upper pretemporal large, in series with supraoculars, narrowly separated from frontal. Primary temporals 2, lower larger than upper. Secondary temporals 2, upper much larger than lower. Frontoparietals fused into large shield. Interparietal distinct with centrally placed parietal eye. Parietals in contact behind interparietal. Nuchals usually in single pair, in lateral contact with upper secondary temporal.

Mental succeeded by large postmental and four pairs of chin-shields; first pair only in medial contact.

Ear aperture concealed by enlarged post-temporal scales [tympanum is not absent, as implied by Storr (1976)], at best a very faint groove to indicate position.

Ground colour of dorsum generally a drab brown, fading to pale grey on flanks; occasionally a darker brown (*e.g.* R123678-9) to almost black (R123545). Head concolorous with body. Dorsum and flanks with total of 8 distinct longitudinal black stripes on each side, running

Table 5

Mensural and meristic data for various subspecies and populations of ***Menetia surda*.** All values are mean ± standard deviation, followed by range and sample size. The two subspecifically unallocated populations are CRP - Cape Range Peninsula and MR/KE - Mardathunna / Kennedy Range. Values are mean ± standard error with range and sample size (n).

	M. surda surda	*M. s. cresswelli* subsp nov	*M. surda* subsp CRP	*M. surda* subsp MR/KE
SVL	26.94 ± 2.97 19.7-32.6 (n = 33)	26.00 ± 3.21 14.6-30.3 (n = 64)	25.14 ± 1.87 21.3-27.5 (n = 19)	31.87 ± 0.69 31.1-32.4 (n = 3)
ForelimbL	6.24 ± 0.66 4.5-7.4 (n = 33)	6.16 ± 0.63 4.4-7.1 (n = 64)	5.91 ± 0.40 5.1-6.6 (n = 21)	6.97 ± 0.38 6.7-7.4 (n = 3)
HindlimbL	8.91 ± 0.90 6.9 - 10.6 (n = 33)	9.19 ± 1.04 5.1-10.7 (n = 64)	8.55 ± 0.48 7.8-9.5 (n = 21)	10.23 ± 0.23 10.1-10.5 (n = 3)
PV	57.81 ± 1.97 50-60 (n = 31)	55.57 ± 2.19 50-60 (n = 61)	55.50 ± 2.70 51-60 (n = 20)	57.67 ± 2.08 56-60 (n = 3)
SDL-M3	14.63 ± 1.01 13-16 (n = 27)	15.14 ± 1.01 12-17 (n = 57)	15.63 ± 1.07 14-17 (n = 19)	14.67 ± 0.58 14-15 (n = 3)
SDL-P4	23.45 ± 1.46 21-26 (n = 31)	23.42 ± 1.69 20-26 (n = 59)	24.16 ± 1.30 21-26 (n = 19)	23.67 ± 2.08 22-26 (n = 3)

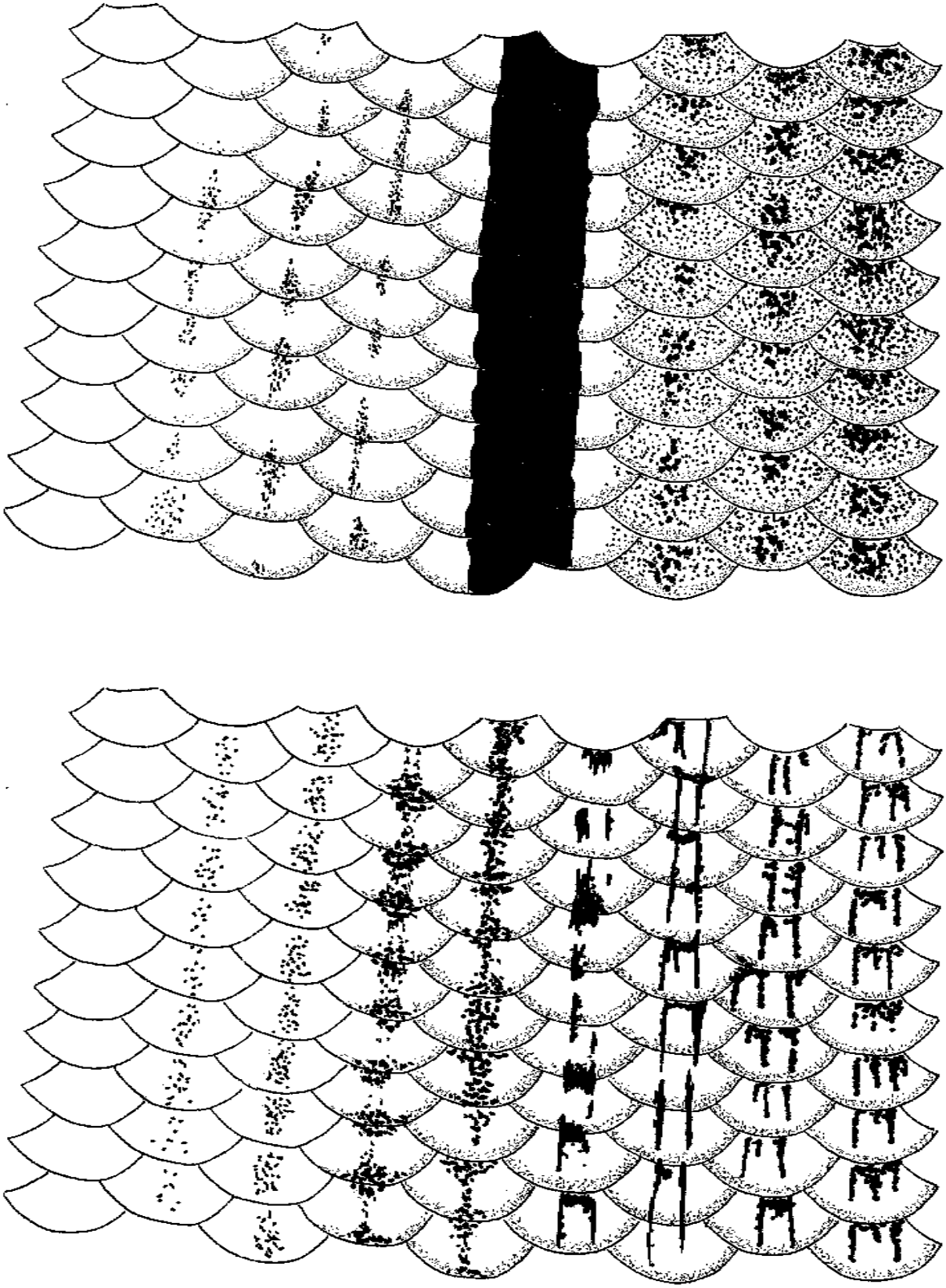


Figure 12. Semi-schematic diagram of the dorsal and lateral body pattern of *M. surda surda* (top; WAM R69777) and *M. s. cresswelli*. subsp nov (bottom; WAM R121089). The pattern is illustrated relative to the boundaries of longitudinal scale rows. The right hand margin corresponds with the dorsal midline.

Table 6

Allozyme profiles of *M. surda surda, M. surda cresswelli* subsp nov and two individuals of uncertain subspecific identity (MR) at 20 variable loci. Code for Carnarvon Basin survey sites: MR = Mardathuna , NA = Nanga, NE = Nerren Nerren, PE = Peron Peninsula. Other abbreviations for locality: RH = road-house; NR = Nature Reserve. A dash indicates that the genotype was not assignable at this locus due to poor activity. (The ' EBU-' prefix for Number refers to the accession number for the S.A. Museum's frozen tissue collection).

Specimen Number	Locality	*Acon2*	*Acyc*	*Adh*	*Ak*	*Dia*	*Est1*	*Est2*	*Fdp*	*G6pd*	*Gapd*	*Gda*	*Got1*	*Gpi*	*Me1*	*Me2*	*Mpi*	*PepB*	*6Pgd*	*Pgm1*	*Sordh*
M. s. surda																					
R120031	Hope Downs	a	b	a	b	ce	a	ab	ab	ac	-	b	a	b	b	b	ab	-	b	c	-
R119911	Mt Brockman	a	b	a	b	ac	ab	ab	a	ac	a	b	a	ab	b	b	a	ab	b	ac	c
EBU-S30	Millstream	ac	b	a	b	c	a	ac	ab	c	a	b	a	a	b	-	a	b	-	cd	bc
M. s. cresswelli																					
R122981	NE2	b	a	a	b	c	a	a	a	ab	a	b	a	a	b	b	a	bc	ab	cd	b
R121087	NA4	a	b	a	b	c	a	ab	a	a	a	ab	ab	a	b	b	a	ab	b	c	b
R122454	NA4	a	b	a	b	c	a	a	b	a	a	b	a	a	b	b	a	ab	b	c	b
R122523	NA5	ac	b	ab	b	c	a	a	b	a	a	b	a	a	ab	b	a	ab	b	c	b
R123678	PE5	ac	b	a	b	-	a	a	ab	a	a	b	a	a	b	b	a	ab	b	c	b
R36263	Billabong RH	a	b	a	b	cd	a	ab	b	a	ab	b	a	a	b	b	a	ab	b	c	b
R125956	East Yuna NR	a	b	b	b	c	a	b	ab	a	a	a	a	a	b	ab	a	b	bc	c	b
R125961	East Yuna NR	a	ab	a	ab	c	a	a	ab	a	a	ab	a	a	b	b	a	b	b	bc	b
M . s. subsp?																					
R120680	MR3	ac	b	a	b	c	a	a	ab	a	a	a	a	a	b	b	a	ab	b	c	b
R120724	MR4	a	b	a	b	bc	a	a	a	ab	a	a	a	a	b	b	a	a	b	c	ab

through centre of each of SR-1 to SR-8 (Fig 12). Stripes narrow but distinct against pale flanks, becoming wider but less distinct against darker dorsum. All stripes continue forward onto head and neck. Dorsolateral stripe positioned on SR-4; becoming noticably thicker and darker anterior of axilla, extending to posterior margin of eye and continued forward by thin subocular emargination. Distinct loreal stripe extends forward through nostril. Dorsum of head flecked with black. Upper lips barred, continued onto infralabials. Longitudinal lines present but not obvious on very dark individuals (*e.g.* R123545, R123598; both from Zuytdorp cliffs).

Undersurface of throat and anterior part of venter generally immaculate. Posterior $^{1}/_{2}$ to $^{2}/_{3}$ of venter with very faint longitudinal lines, continuing series of dorsum and flank. Tail with complete series of longitudinal lines. Two specimens from Zuytdorp Cliffs (as above) with venter diffusely pigmented to neck.

Limbs with longitudinal series of dark-brown spots, giving lined appearance. Upper surface of manus and pes spotted.

Details of Holotype

SVL 25.7 mm; Tail 43.5; ForelimbL 5.9 mm; HindlimbL 9.0 mm; paravertebral scales 54; midbody scale rows 22; subdigital lamellae manus III 15; subdigital lamellae pes IV 22; prefrontal scales narrowly separated; ear aperture entirely indistinct; nuchals 1 pair. Adult male with turgid testis and prominent efferent duct.

Etymology

Named for Mr Ian Creswell, formerly of the National Reserve Systems Cooperative Unit, Environment Australia, for his role in facilitating the Carnarvon-northern Irwin Biological Survey, and in particular for his support of systematic studies as a fundamental component of regional biological assessment.

Distribution and variation

The Shark Bay region of Western Australia including Peron Peninsula and Bernier Island, south to Bindoo Hill and East Yuna Nature Reserves, inland of Geraldton (Fig 11). With the exception of the Zuytdorp Cliffs specimens, all southern records are from inland localities although this may reflect access to the relevant sections of the coast. The nearest records of *M. surda surda* are from the Barlee Range.

The two specimens from Zuytdorp cliffs are unusually dark, both dorsally and ventrally. These specimens superficially resemble *M. amaura* Storr, an enigmatic taxon long known only from the holotype (Storr 1978), but more recently recognised from numerous coastal localities in the southern Carnarvon Basin (K Aplin, M Adams & M Cowan, unpublished observations). Interestingly enough, one of the Zuytdorp *cresswelli* specimens (R123598) also resembles the holotype of *M. amaura* in showing unilateral fusion of the first and second supraciliaries (this condition is bilateral in the holotype of *M. amaura*, but this appears to be an individual anomaly in a taxon which normally has a supraciliary arrangement like that of *M. greyii* Gray). In

all other respects the Zuytdorp specimens resemble *M. surda*, most notably in having distinct presubocular and lower preocular scales, an enlarged ciliary granule and distinct supraciliaries in contact with the frontal. Unfortunately, tissue samples are not available from either of the Zuytdorp specimens, hence the intriguing possibility that these specimens represent hybrids between *M. amaura* and *M. surda* could not be tested genetically.

Another distinctive population of *M. surda* is represented by three specimens obtained on Biological Survey quadrats on Mardathuna and in the Kennedy Range. With SVL of 31.1 - 32.4 mm, these specimens are larger than any *M. s. cresswelli*, and are larger than all but a few individuals of *M. s. surda*. The digits and claws are relatively long as in *M. s. surda*, but the dorsal pattern is more similar to that of *M. s. cresswelli*, consisting of indistinct black longitudinal lines on a dark brown ground colour. This population appears to be isolated from the main distribution of *M. s. cresswelli*, as no member of the group was obtained on any of the ten Biological Survey Quadrats on intervening Woodleigh and Meedo. The nearest records of typical *M. surda* are from the Barlee Range, approximately 200 km to the northeast of the Kennedy Range.

Genetic differentiation

Representative samples from various populations of *Menetia surda* were included in a broader investigation of genetic variation within *Menetia*. The results of this wider study will be presented elsewhere; for the present it need only be mentioned that the various populations of *M. surda* form a discrete clade which appears to be the sister taxon of an *M. greyii* 'complex', which itself consists of some three or four taxa including *M. amaura* and *M. maini* Storr. *Menetia alanae* Rankin and *M. concinna* Sadlier together form a third major clade.

Within *M. surda*, a total of 8 individuals of *cresswelli* from sites in the southern Carnarvon Basin were compared with three individuals of typical *surda* from the Pilbara and two specimens from Mardathuna. These animals were screened at 39 presumptive loci.

The allozyme profiles of all 13 individuals at the 20 loci found to be variable are shown in Table 6. The remaining 19 loci were invariant; *Acon1, Acp, Enol, Fum, Gdh, Glo, Got2, Gpd, Gpx, Idh1, Idh2, Lap, Ldh, Ndpk, Np, Pgam, Pgk, Pgm2* and *Tpi*.

Menetia s. surda and *M. s. cresswelli* show minimal genetic differentiation, with no fixed differences and a Nei D of 0.022. On Nei D, the Mardathuna population appears slightly closer genetically to *M. s. cresswelli* (Nei D = 0.018) than to *M. s. surda* (Nei D = 0.045). A few loci show differences in allele frequency (*e.g. G6pd, Gpi* and *Sordh* between *M. s. surda* and *M. s. cresswelli*; *Acon2, Acyc* and *Gda* between *M. s. cresswelli* and the Mardathuna population), but small sample sizes preclude any statistical analysis. It is possible that with screening of larger samples of these populations, some of these genetic markers may prove to be partly- or near-diagnostic (a common feature of many 'diagnostic' morphological characters). However, no amount of additional screening will change the general picture obtained in this study of low level genetic divergence among the various allopatric populations of *M. surda*. Elsewhere within *Menetia*, levels of genetic differentiation between sympatric species are somewhat higher, involving several fixed differences. However, there is also good evidence of active hybridization between some of the taxa (M Adams, M Hutchinson & K Aplin, unpublished observations).

The one genotyped specimen of *M. s. cresswelli* from Nerren Nerren is unusually divergent, with unique alleles at *Acon2, PepB, 6Pgd* and *Pgm1*. In contrast, the sample of two individuals from East Yuna Nature Reserve, even further to the south, is genetically consistent with the Nanga and Peron samples. The Nerren Nerren specimen is thus most likely individually anomalous.

Comparison with other taxa

Menetia surda cresswelli shares a number of unusual morphological features with nominate *M. surda* and it seems likely that these taxa are monophyletic to the exclusion of other species of *Menetia*. These include a large first supraciliary in contact with the first supraocular, an enlarged upper circumocular granule and a fully concealed ear aperture. Judging from the condition in other genera of skinks, the first of these characters is probably an ancestral state within *Menetia*, but the latter two are very likely derived conditions and the enlarged circumocular granule is uniquely derived within the genus. The results of the wider genetic data likewise support the monophyly of the populations here included within *M. surda*.

The type locality of *Menetia surda* is Budjan Creek, Corunna Downs, in the northeast Pilbara region; the nominate subspecies is here identified with certainty only from the wider Pilbara region (Fig 11 and Appendix 1 for list of material). The distinctive Mardathuna / Kennedy Range population of *M. surda* and another distinctive population from the Cape Range Peninsula are not clearly referrable to either the nominate subspecies or to *M. s. cresswelli* and are treated here as subspecies *incertae sedis*. Basic mensural and meristic data are contrasted in Table 5 for each population of *M. surda*.

Specimens of *M. s. surda* are similar to *M. s. cresswelli* in basic size and body proportions but differ in having a significantly higher mean number of paravertebral scales, narrower posterior paravertebral scales (*i.e.* not substantially broader than the second row scales) and longer, more projecting claws on the hands and feet. The prefrontal scales are in narrow medial contact in 48% of Pilbara region specimens, but have not been observed in broad contact (one specimen from Tom Price, R127711, has a separate, azygous scale). The body pattern of *M. s. surda* is distinctive, with a well-defined, continuous laterodorsal stripe which separates a plain or irregularly-dashed dorsum from the more boldly-patterned flank (Figs 10B, 12). Anterior to the forelimb, the laterodorsal stripe widens through amalgamation with the outer row of dorsal dashes which here forms a more-or-less continuous line. On the flank, the laterodorsal stripe is bordered below by white midlateral and dark-brown lower lateral zones (contrasting with five or six regularly-spaced stripes in *M. s. cresswelli*). The venter in *M. s. surda* is generally immaculate all the way to the cloaca

and the undersurface of the tail is usually lightly-dashed rather than strongly lined.

In some individuals of *M. s. surda* the laterodorsal line is solid and well-defined both anteriorly and posteriorly, extending onto the tail, but is divided into two, narrowly separated lines in the mid-body region (Fig 10B). This 'partially divided' laterodorsal line is observed on occasional specimens from throughout the Pilbara (*e.g.* R78569, Tom Price; R84276, R132655 Burrup Peninsula), but it appears to be especially prevalent in the northeast Pilbara ranges. The few available specimens from this area are also slightly larger on average and have somewhat lower paravertebral counts than specimens from elsewhere in the region.

The Cape Range Peninsula population of *M. surda* is similar to *M. s. cresswelli* in being relatively small with low paravertebral counts and relatively short claws. However, the body pattern is more consistent with that of *M. s. surda*, except that the the laterodorsal stripe is usually 'divided' in the midbody region and the ground colour is paler. The posterior paravertebral scales are unwidened (*i.e. surda*-like) in most individuals, but are broader than the second row scales (*i.e. cresswelli*-like) in some individuals (*e.g.* R61070, R95719). The Cape Range population has an unusually high incidence of moderate to broad contact between the prefrontal scales (38%), accentuating the trend for medial contact observed in *M. s. cresswelli*. In some respects, this distinctive population thus combines features of each of *M. s. surda* and *M. s. cresswelli* and is not readily grouped with either one or the other.

As noted above, the Mardathuna/Kennedy Range population of *M. surda* also shares features with both *surda* and *cresswelli*, although on balance it appears closer to the latter. The prefrontal scales are narrowly separated in two of the specimens but meet in point contact in the third.

Habitat and sympatry

Menetia s. cresswelli was obtained from eight of the Biological Survey quadrats and is otherwise broadly distributed in the southern part of the Carnarvon Basin and south to the Geraldton sandplain. On Nanga it was collected from eucalypt and *Acacia* shrublands over spinifex (*Plectrachne drummondii*) and from eucalypt/bowgada scrub. On Nerren Nerren it was obtained from sandplain quadrats with eucalypts, banksias and *Allocasuarina* over *Plectrachne* or low shrubland, but not from sites with a heavier, sandy-loam substrate. On Peron Peninsula, it was once again present in sandplain habitats with *Acacia* over *Plectrachne*. Somewhat anomalously at Zuytdorp, *M. s. cresswelli* was obtained from a near-coastal limestone slope supporting a low heath, but was absent from quadrats further away from the coast (note that these specimens are also morphologically distinctive).

Earlier capture records indicate that *M. s. cresswelli* has most commonly been obtained by burning 'spinifex'. However, it has also been collected from within and below litter beds over sand in various shrubland communities. Storr & Hanlon (1980:370) summarised the habitat of *M. s. cresswelli* in the Zuytdorp hinterland as follows: "Mainly in soft spinifex (*Plectrachne*) and leaf litter on yellow, brown and red sandplains". Pilbara and Cape Range specimens of *M. s. surda* are also generally noted as coming from spinifex tussocks; however in these areas, the substrate is typically hard stony ground or heavy soils.

Menetia s. cresswelli shows broad distributional overlap with various representatives of the *M. greyii* 'complex'. During the Biological Survey it was obtained in sympatry with members of this group on two of the Nanga quadrats (NA2, NA4) and on both Nerren Nerren quadrats (NE1, NE2). On Peron Peninsula (PE2) and at Zuytdorp (ZU1) it was found in sympatry with *M. amaura*. The genetic data provide no indication of hybridization between *M. s. cresswelli* and any member of the *M. greyii* complex (M Adams, M Hutchinson & K Aplin, unpublished observations), but certain morphological features noted above for Zuytdorp specimens hint at possible interspecific interaction (with *M. amaura*?) in this area.

Other remarks

Storr (1976:198) commented on variation in prefrontal scale contact in *M. surda*; "almost as often contiguous as separated" in the north *vs* "always separated" in the south; and he also noted the distinctively 'striate' pattern of southern individuals. However, Storr's 'northern' sample probably included specimens of both *M. s. surda* and *M. s. cresswelli* (*e.g.* Bernier Island) as well as material from the Cape Range Peninsula. His 'southern' sample consisted of specimens here distinguished as *M. s. cresswelli*. As indicated above, the frequency of medial contact between the prefrontals is slightly lower in *cresswelli* than in nominate *surda*; however, in both populations the frequency of medial contact is greater than 40 % with broad contact present in 10 % of individuals of *M. s. cresswelli*.

Storr *et al.* (1981:165) illustrated the geographic range of *M. surda* as most likely continuous from the Pilbara region south to Geraldton. The more extensive collecting undertaken through the region since that time indicates that the geographic distribution of *M. surda* is actually quite disjunct, consisting of separate northern and southern ranges along with several probable isolates on the Cape Range Peninsula and in the central Carnarvon Basin (Mardathuna/Kennedy Range). Each of these regional populations of *M. surda* is morphologically distinctive, with significant differences in overall size, meristic features and body pattern. These differences might conceivably relate to ecological differences associated with the contrasting substrate and vegetation of these environmentally diverse regions.

Menetia surda surda is widely distributed within the Pilbara region but appears to be nowhere especially common. Although the combined Pilbara sample is still not large, there is some indication of intra-regional variation in size, body pattern and meristics, with specimens from the northeast Pilbara appearing particularly distinctive. In contrast, *M. s. cresswelli* appears to be locally abundant in the southern sandplain habitats and shows very little morphological variation across a large geographic area, except possibly in the peripheral Zuytdorp area. As indicated earlier, the Cape Range Peninsula population appears to combines features of each of typical *surda* and *cresswelli*.

The allozyme data demonstrate that the various populations of *M. surda* are genetically very close. This most likely points to a very recent origin of the various isolated populations, either by range fragmentation (vicariance) or by dispersal with rapid local adaptation and morphological differentiation. However, other, more complex scenarios might also warrant consideration, such as the possibility that morphological differentiation within *M. surda* was present prior to the fragmentation of the species range, perhaps in the form of a north-south cline along the coastal hinterland. The morphological intermediacy of the Cape Range population of *M. surda* could be viewed as consistent with this latter scenario, yet caution is urged by the fact that clines are not readily distinguished from zones of secondary contact on the basis of either morphological or allozyme characters (Endler 1977). This and other questions regarding the evolution of *M. surda* must await analysis of more sensitive nuclear and mitochondrial markers.

In our view, the combined morphological and genetic evidence is best expressed taxonomically through recognition of the Shark Bay population as a distinct subspecies within *M. surda*. This makes it clear that *cresswelli* belongs with *M. surda*, yet gives expression to the significant morphological differences between them. Admittedly, by the same argument, each of the Mardathuna/Kennedy Range and Cape Range populations might also warrant subspecific recognition. However, the former population is too poorly represented for statistical analysis of morphology, and the latter might yet prove to be connected via intermediate populations with the main Pilbara populations. Until the distributions and affinities of each of these outlying populations are more firmly established, we suggest that they be listed formally as *Menetia surda* subsp *incertae sedis*.

Discussion

Many of the recent advances in Australian vertebrate systematics have come through the combined application of morphological and genetic methods of investigation. Morphological studies alone can be effective at identifying patterns of variation, but it is often difficult to decide exactly where boundaries should be drawn between species and/or subspecies. Genetic studies, on the other hand, may give a clear indication of interrupted gene flow and a lack of interbreeding in the case of sympatric comparisons, but they are usually carried out on relatively small numbers of individuals derived from large geographic areas. Moreover, genetic studies alone will rarely lead to taxonomic conclusions owing to the lack of genetic data for type specimens or even topotypic specimens.

Each of the new taxa described in this paper was detected initially through careful and systematic study of museum voucher specimens. However, in each case, allozyme electrophoresis played a critical role in the taxonomic process. For each of *Ctenotus maryani* and *Diplodactylus klugei*, the genetic data were essential in the confirmation of specific status. Both taxa are morphologically cryptic and both had been collected on prior occasions but overlooked by highly experienced field collectors and taxonomists. Indeed, were it not for the confirmation provided by the genetic data, the variation observed in sympatry might easily have been dismissed as polymorphism and individual variation.

In the case of *Menetia surda cresswelli*, the senior authors' initial judgement was that the southern populations were very likely specifically distinct from *surda* on account of the extent of morphological divergence within what is generally regarded as a morphologically conservative genus. The genetic data indicated that specific distinction is probably not warranted; subspecific distinction was chosen as an appropriate level of taxonomic discrimination for *cresswelli*.

The common lack of congruence between morphological and genetic levels of divergence has been noted for various groups of vertebrates (Baverstock & Adams 1984; Ohta 1992; Sheldon & Bledscoe 1993; see Omland 1997 for a contrary view). Among the present series of taxa, the two skinks illustrate this very clearly. In morphological terms, *Ctenotus maryani* and *Menetia surda cresswelli* differ from *C. iapetus* and *M. s. surda* in very similar ways, namely slight changes in meristic values and body proportions (limb lengths, claw size) and subtle but noticeable differences in body patterning. Yet the level of genetic differentiation between the related taxa differs by an order of magnitude, *i.e.* Nei D = 0.022-0.045 between *Menetia s. cresswelli* and *M. s. surda*; and Nei D = 0.328 between *Ctenotus maryani* and *C. iapetus*. The level of genetic differentiation between the newly recognised *Diplodactylus klugei* and *D. pulcher* lies between these values at Nei D = 0.258; yet morphologically, the two species are perhaps as close, if not closer, than any other currently recognised sibling pair within the genus *Diplodactlyus*.

Ctenotus maryani and *Diplodactylus klugei* both qualify as 'cryptic' species in the sense that they exhibit only very subtle morphological differences from, and have been previously 'buried' within, other species, namely *C. iapetus* and *D. pulcher*. However, each of these species pairs suggests a quite different evolutionary scenario. The two *Diplodactylus* species are moderately well-differentiated genetically and have broadly overlapping geographic ranges. They may well be true sibling species which have diverged very little from a common ancestral morphology. In contrast, the two *Ctenotus* species are more distant genetically and may not be true siblings (*C. iapetus* is probably more closely related to *C. quattuordecimlineatus*; and *C. maryani* may be closest to *C. zasticus*); yet *C. maryani* and *C. iapetus* are remarkably similar in morphology. In this case, the morphological similarity could either be due to conservatism (*i.e.* both species retaining an ancestral morphology) or to parallelism (*i.e.* both species having independantly evolved the same form), or perhaps to some combination of the two (*e.g.* conservatism of body proportions, parallel evolution of dorsal and flank pattern). *Ctenotus maryani* is undeniably 'cryptic', yet its crypticity is unusual in that it may well owe as much to morphological parallelism as it does to morphological conservatism.

Elsewhere we have individually argued that the recognition of 'cryptic' species should be a high research priority for Australian herpetology (Aplin & How 1993; Donnellan *et al.* 1993). Here we would like to turn that

plea around to deliver a cautionary message for conservation biology.

The steady and ongoing recognition of new species of reptiles, mammals and frogs in Australia makes it abundantly clear that we are still a long way short of a full inventory of species-level diversity in these groups. Keogh & Smith (1996:687) recently expressed the view that "Australia is still a virtual frontier of taxonomic research". This statement was made in the context of a traditional morphometric study of a genus of snakes, but is perhaps even more appropriate in the context of genetic assessment of species-level diversity. The number of genera which have been subjected to anything like a comprehensive genetic assessment is extremely low for all major groups. More commonly, genetic data are available for only one part of a complex genus or as pilot data across a selection of the total available species, and for many other genera of vertebrates (birds included here) there is quite simply no information (published or otherwise) on levels of genetic variation, even between currently recognised species.

Given the current spate of regional assessments being conducted in advance of land acquisition and rehabilitation and for general resource management, we believe that it is essential that we objectively re-examine species-level diversity within the Australian vertebrate fauna. As exemplified by the ongoing studies of the Carnarvon Basin herpetofauna, allozyme electrophoresis can provide the necessary objectivity, but it is most effectively applied to the testing of specific hypotheses generated by prior morphological assessment. To implement such an approach for wider-scale regional biodiversity assessment requires an open-minded approach to ecological theory and zoogeography, a willingness to collect the necessary tissue samples for genetic analysis and a carefully structured protocol for the efficient application of both morphological and genetic techniques. Knowledge only rarely ever comes so cheaply.

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Appendix 1

Other material examined

Ctenotus iapetus Storr 1975

18 KM SE Onslow (21°45'S, 115°14'E): 80314; Vlaming Head (21°48'S, 114°06'E): 61422, 61440; 13 KM S North West Cape (21°54'S, 114°08'E): 27887; 26 KM S Urala (22°00'S, 114°53'E): 30324; 2.5 KM N Yardie Creek (22°19'S, 113°49'E): 611363; 21.5 KM N Bullara HS (22°30'S, 114°04'E): 11691; KM NW Bullara HS (22°40'S, 114°01'E): 50290, 51018; 3 KM E Giralia HS (22°41'S, 114°24'E): 60992-3, 60999, 61148; 30 KM E Ningaloo (22°42'S, 113°57'E): 16883; 30 KM E Ningaloo (22°42'S, 114°00'E): 61310; 16 KM W Marrilla HS (22°58'S, 114°16'E): 63692; 1 KM N Minga Bore (23°00'S, 114°15'E): 116920; 32 KM N Warroora (23°12'S, 113°48'E): 21776; 6 KM N Mia Mia HS (23°20'S, 114°26'E): 71353-4; 10 KM SE Gnaraloo (23°39'S, 113°34'E): 81714-15; 3KM SE Gnaraloo (23°45'S, 113°32'E): 76725-76726; 5 KM SE Gnaraloo (23°46'S, 113°32'E): 71745; 17 KM ENE Gnaraloo (23°48'S, 113°41'E): 81693; 5 KM SE Gnaraloo (23°51'S, 113°34'E): 71594; 9 KM NE Cape Cuvier (24°11'S, 113°27'E): 117225; **CU5**, 8 KM NE Cape Cuvier (24°11'35"S, 113°27'19"E): 119867, 121465, 121473, 126850, 126879, 126906; **CU2**,11 KM E Cape Cuvier (24°13'22"S, 113°30'12"E): 119861, 122909; **CU3**, 8 KM E Cape Cuvier (24°13'23"S, 113°29'29"E): 120405,122911; **CU4**, 6 KM E Cape Cuvier (24°13'26"S, 113°27'41"E): 119877, 119879-80, 119883, 119886, 120406, 125279-80, 126877-78, 126880; Quobba (24°24'S, 113°24'E): 60524; **MR5**, 14.7 KM W Mardathuna Homestead (24°24'21"S, 114°26'40"E): 122892; **MR4**, 11.8 KM W Mardathuna Homestead (24°24'26"S, 114°28'24"E): 120375, 120698, 121547, 122748, 122776, 122778, 126756; **MR3**, 7.7 KM W Mardathuna HS (24°25'44"S, 114°29'60"E): 120407, 120716, 120718, 122725-26, 122728, 122734, 122736, 122858-59, 126196, 126801; **MR2**, 5.6 KM W Mardathuna HS (24°26'36"S, 114°30'43"E): 122838-39; **KE1**, 41 KM from Binthalya Homestead (24°29'36"S, 115°01'51"E): 120524, 121334, 12386-87, 123194, 123219, 123280, 123291, 124169, 125168; **KE2**, 38.9 KM from Binthalya Homestead (24°30'04"S, 115°01'03"E): 120515, 123376-78, 126209.

Menetia surda surda Storr 1976

Dolphin Island, Dampier Archipelago (20° 29' S, 116° 51' E): 14329-30; Burrup Peninsula (20° 36' S, 116° 48' E): 84274-78, 132655; Warrawagine (20° 51' S, 120° 42' E): 13248; Ripon Hills (21° 17' S, 120° 44' E): 13247; Millstream HS (21° 35' S, 117° 04' E): 94620; 1 km SE Millstream HQ (21° 36' S, 117° 04' E): 99808; 3 km S Millstream HS (21° 37' S, 117° 04' E): 81395; Budjan Creek, Corunna Downs (21° 42' S, 119° 50' E): 13249; 5 km ENE Kurrana Well (22° 02' E, 120° 29' E): 73950; 2 km W Rove Hills Mine (22° 05' S, 120° 42' E): 74086; Between Nullagin and Roy Hill (22° 15' S, 120° 00' E): 68365; 17 km S Riotinto Gorge (22° 21' S 117° 53' E): 114446; 24 km NNW Tom Price (22° 24' S, 117° 42' E): 76569; 3.5 km NE Mt Brockman (22° 28' S, 117° 18' E): 119911,119917; Curran Curran Rockhole (22° 32' S, 121° 56' E): 42209; 10 km NW Windell (22° 36' 00" S, 118° 27' 35" E): 102122, 102146; 21 km WSW Marillana HS (22° 40' S, 119° 13' E): 71653; Junction Well. Upper Oakover River (22° 44' S, 121° 10' E): 42228-29, 42239-40; 25 km ESE Kooline HS (22° 47' 28" S, 116° 32' 46" E): 116888; 5 km S Mt Tom Price Mine (22° 48' 40" S, 117° 46' 03" E): 127711; Coppin Pool Turee Creek (22° 53' S, 118° 08' E): 69717, 69755, 69810; Hope Downs (22° 58' 00" S, 119° 08' 20' E): 120031; 1 km N Mt Trevarton (22° 59' S, 118° 15' E): 69710; 21 km NE Paraburdoo (23° 07' S, 117° 51' E): 83725, 83728-29; O'Brien Creek Tributary of Turee Creek (23° 10' S, 118° 10' E): 69810; 9.4 km N Joy Helen Mine (23° 13' 00" S, 115° 46' 30" E): 102021; 5.4 km N Joy Helen Mine (23° 14' 15" S, 115° 46' 30" E): 102014; 0.5 km N Joy Helen Mine (23° 14' 40" S, 115° 46' 30" E): 102007-008; 6 km S Paraburdoo (23° 16' S, 117° 40' E): 83723; 14 km SE Paraburdoo (23° 17' S, 117° 46' E): 83779; 4 km N Mount Maguire (23° 18' S, 117° 44' E): 94859; 4 km ENE Mt Maguire (23° 19' 30" S, 117° 47' 00" E): 94874; 21 km NW Ullawarra (23° 20' S, 116° 00' E): 25263-64; Barlee Range Nature Reserve (23° 22' 45" S, 115° 52' 50" E): 102369, 102260.

Menetia surda subsp *incertae sedis*

Mardathuna/Kennedy Range population: **MR4**, 11.8 km W Mardathuna HS (24° 24' 26" S, 114° 28' 24" E): 120724; **MR3**, 7.7 km W Mardathuna HS (24° 25' 44" S, 114° 29' 60" E): 120680; **KE1**, 41 km from Binthalya HS (24° 29' 36" S, 115° 01' 51" E): 125895.

Cape Range population: Yardie Creek HS (21° 53' S, 114° 01' E): 13192, 27980; 65 km NNE Ningaloo HS (22° 08' 52" S, 113° 53' 36" E): 95719; 14 km N Yardie Creek HS (22° 13' S, 113° 51' E): 61260; 9 km N Yardie Creek HS (22° 15' S, 113° 50' E): 61244; Yardie Creek Mouth (22° 20' S, 113° 48' E): 61455-61462, 61491; Yardie Creek (22° 20' S, 113° 49' E): 27981-83, 61069-71, 61119, 121405; 20 km NW Giralia HS (22° 33' S, 114° 14' E): 61233; 3 km E Norwegian Bay, Ningaloo (22° 36' S, 113° 43' E): 32030; 50 km S Yardie Creek HS (21° 53' S, 114° 01' E).