Systematics of *Diplodactylus* (Squamata: Diplodactylidae) from the south-western Australian biodiversity hotspot: redefinition of *D. polyophthalmus* and the description of two new species

Paul Doughty[1] and Paul M. Oliver[2]

[1] Department of Terrestrial Zoology, Western Australian Museum, 49 Kew St, Welshpool, Western Australia 6106, Australia. Email: Paul.Doughty@museum.wa.gov.au

[2] University of Melbourne, Melbourne, Victoria 3000, and Museum Victoria, Melbourne, Victoria 3001, Australia. Email: Paul.Oliver@unimelb.edu.au

ABSTRACT – The Australian gecko genus *Diplodactylus* is characterised by morphologically similar but genetically divergent lineages and taxa. Recent molecular analysis indicated the presence of an undescribed *Diplodactylus* from the Geraldton Sandplain on the western coast of Australia, and a relatively deep divergence between populations of *D. polyophthalmus* on the Swan Coastal Plain (around Perth) and the Darling Range (inland and south of Perth). Here we present a more detailed investigation of genetic and morphological variation among these forms. The two genetically divergent populations of *D. polyophthalmus* do not differ appreciably in morphology but differ in dorsal colouration and ecology. Since the lectotype of *D. polyophthalmus* was collected from 'Champion Bay' (near Geraldton) and is in agreement with specimens collected from there, we redescribe this species and restrict its range to the coastal sandplain from Perth to Eneabba. The Darling Range population, regarded as typical *D. polyophthalmus* since Storr's 1979 ressurrection, differs in that it is consistently darker with a rusty-brown colouration and occurs on hard surfaces such as laterite. As the lectotype of *D. polyophthalmus* refers to the coastal sandplain form, we describe the Darling Range form as a new species, *D. lateroides* sp. nov. Genetic and morphological evidence also confirmed the existance of a highly divergent lineage that forms a polytomy with *D. capensis* and *D. granariensis*. This lineage, here described as *Diplodactylus nebulosus* sp. nov., has a restricted range, occurring from near Geraldton in the north to Mt Lesueur ~200 km to the south. Like its close genetic relatives, the new species has enlarged labial and supranasal scales, making it relatively easy to distinguish from the regionally sympatric *D. ornatus* and *D. polyophthalmus*. The conservation status of some species of *Diplodactylus* in south-western Australia need to be carefully considered, especially southern populations of the redefined *D. polyophthalmus*.

KEYWORDS: Darling Range, *Diplodactylus lateroides* sp. nov., *Diplodactylus nebulosus* sp. nov., Geraldton Sandplain, Swan Coastal Plain, taxonomy, Western Australia

INTRODUCTION

Diplodactylus Gray, 1832 is a genus of small and relatively generalised terrestrial Australian geckos, which currently includes 18 recognized species. Recent genetic work has revealed that species diversity within *Diplodactylus* had been significantly underestimated (Oliver et al. 2007a, 2009). Although five species of *Diplodactylus* have been described or resurrected from synonomy in as many years (Doughty et al. 2008, 2010; Hutchinson et al. 2009), our studies have identified a number of additional divergent genetic lineages, the taxonomic status of which requires further investigation.

Two of the lineages requiring taxonomic attention identified by Oliver et al. (2009) are from the southern coastal sandplains of Western Australia, between the greater Perth region in the south and Shark Bay in the north. One of these, *Diplodactylus* 'Yetna' is a divergent and apparently isolated lineage that was recognised as a 'candidate species', but which at the time was known only from Yetna, near Geraldton (approximately 400 km north of Perth). In this same paper, samples assigned to the south-western endemic species *D. polyophthalmus* Günther, 1867 included two divergent sister lineages. Oliver et al. (2009) did not recognise either of these lineages as candidate species, but noted

urn:lsid:zoobank.org:pub:9E8A1F4F-104F-4056-AC9B-6F18BF0264B8

that the genetic divergences between them were deep and required further investigation. One of these lineages was represented by a single individual from remnant *Banksia* woodland on the Swan Coastal Plain near Perth, whereas the other lineage was represented by a number of samples from the lateritic, stony environments on the Darling Range inland and south of Perth (Storr et al. 1990; Bush et al. 2007, 2010).

Here we assess the taxonomic status of these divergent lineages of *Diplodactylus* from south-western Australia. We have expanded sampling for the mitochondrial *ND2* gene to include all avaliable localties from the region of interest and carried out a detailed morphological investigation of these populations, including examination of the lectotype of *D. polyophthalmus* housed at the Natural History Museum, London (BMNH). Based on the results of this work we present a revised taxonomy, including a redescription and redefinition of *D. polyophthalmus* and the description of two new *Diplodactylus* species.

MATERIALS AND METHODS

MOLECULAR GENETICS

Genetic analyses included mitochondrial data from 55 *Diplodactylus* including exemplars from all populations from mid coastal Western Australia for which tissues samples were available, and additional Western Australian species which are known to be closely related, such as *D. mitchelli* and *D. granariensis* (Appendix 1). *Diplodactylus calcicolus*, *D. ornatus* and *D. klugei* were also included as more distant outgroups. New sequences generated in this study were aligned with data presented in Doughty et al. (2008) and Oliver et al. (2009) and available on GenBank. Previously unsampled tissues were extracted using a high throughput QIAxtractor robot (QIAGEN™) at Museum Victoria and the standard manufactorer protocol for tissue extractions. A 900–1200 bp region of the *ND2* gene and surrounding tRNAs was amplified using one of the following two combinations of primers: 1) AAG CTT TCG GGG CCC ATA CC (L4437; Macey et al. 1997) and CTA AAA TRT TRC GGG ATC GAG GCC (Asn-tRNA; Read et al. 2001); or 2) GCC CAT ACC CCG AAA ATS TTG and TTA GGGTRG TTA TTT GHG AYA TKC G (Oliver et al. 2007). PCR products were amplified for 40 cycles at an annealing temperature of 55ºC. Unpurified products were sent to a genetic services company (Macrogen, Korea) and sequenced in both directions using tradional Sanger Sequencing approachs.

Our final alignment included 816 bp of data and was aligned using the MUSCLE algorithm (Edgar 2004) implemented in Geneious version 6.0.5 (Biomatters 2012), and subsequently checked by eye. Our final alignment included a single three base pair deletion towards the 5’ end of the *ND2* gene in *D. mitchelli*. Phylogenetic trees were computed using standard maximum Likelihood (RAxML v7.2.8; Stamakakis 2006) analyses implemented on the CIPRES web portal version 3.1 for online phylogenetic analysis (www.phylo.org/portal2). Data were not partitioned by codon (e.g. first, second and third base positions) and analyses were run using the default settings for RAxML on the CIPRES portal; namely the GTRGAMMA model of sequence evolution and ceasing bootstrapping when MRE-bootstrapping criteria had been reached.

MORPHOLOGICAL ASSESSMENT

We examined all specimens of *Diplodactylus* from south-western Australia held in the Western Australian Museum, Perth (WAM). A subset of these were chosen to be measured based on quality, whether a tissue sample had been sequenced and geographic coverage (Appendix 2 and type lists in Systematics section). Table 1 presents the characters measured and their abbreviations. We measured 15 *D. ornatus*, 13 *D. polyophthalmus*, 19 *D. lateroides* sp. nov. and 21 *D. nebulosus* sp. nov. We compared these data to those of other *Diplodactylus* taxa reported in Doughty et al. (2008) and Hutchinson et al. (2009). We provide means, *S.D.* and ranges, and discuss qualitative differences among taxa in the Results and Systematics sections.

RESULTS

MOLECULAR GENETICS

Genetic analyses identified three highly divergent lineages of *Diplodactylus* in the coastal area between Perth and Shark Bay. A summary of phylogenetic relationships is shown in Figure 1 and a summary of genetic distances data is given in Table 2. Of the three lineages identified in the region, one is clearly referable to *D. ornatus*, a well characterised species that has been the focus of recent phylogeographic study with a range that extends from Jurien Bay in the south to the North West Cape (Storr et al. 1990; Edwards et al. 2012).

The second lineage from the region of interest included the single sample of *Diplodactylus* ‘Yetna’ sampled by Oliver et al. (2009), plus additional specimens from the Moresby Range just to the north, and a more distant population from the Mt Lesueur area to the south. The mean uncorrected mitochondrial sequence divergence between these two areas was 3.8%. This lineage lies within a well supported group in which *D. mitchelli* is the sister to an unresolved trichotomy that includes *Diplodactylus* ‘Yetna’, *D. capensis* and *D. granariensis*. The mean genetic distances between *Diplodactylus* ‘Yetna’ and these two recognised taxa were 8.4% and 8.5%, respectively.

The third lineage from the region included two specimens referred to *D. polyophthalmus* from a single locality on the Swan Coastal Plain in the northern suburbs of Perth. This lineage is sister to samples from throughout the Darling Range and associated areas of the south-west that are also currently referred to *D. polyophthalmus*. The relative genetic uniformity of the better-sampled and widespread Darling Range *‘polyophthalmus’* clade (mean uncorrected difference of 1.5% over a range of >200 km) differs markedly

TABLE 1 Morphological characters measured in this study.

Character	Description
SVL	Snout-vent length
TrunkL	Trunk length: from axilla to groin
TailL	Tail length: from cloaca to tip (unbroken tails only)
TailW	Tail width: at widest point (unbroken tails only)
HeadL	Head length: measured obliquely from tip of snout to angle of lower jaw (retroarticular process)
HeadW	Head width: measured at the widest point
HeadD	Head depth: measured behind eyes on top of head
RadL	Radius length: from elbow to base of hand
TibL	Tibia length: from knee to base of foot
IO	Inter-orbital distance: measured at anterior of eye socket
NarEye	Nare-eye distance: from posterior edge of nare to anterior corner of eye socket
IntNar	Internarial distance: from inner edges of nostrils
RosCre	Proportion of crease relative to height of rostral scale
No. PN	Number of postnasal scales
MentL	Mental length: measured obliquely from mouth to posterior edge of scale
MentW	Mental width: measured at anterior edge along mouth
SNas	Proportion of supranasals in contact (0 – not in contact; 1 – full contact)
SupLab	Number of supralabial scales
InfLab	Number of infralabial scales
4FLam	Number of enlarged rows of subdigial lamellae under fourth finger
4TLam	Number of enlarged rows of subdigial lamellae under fourth toe
No. SC	Number of supracaudal scales, from first scale of tail (defined by transition from rounded dorsal scale to rectangular scale at fracture plane) to tail tip (unbroken tails only)

TABLE 2 Uncorrected *ND2* sequence divergences between seven species of *Diplodactylus* known from south-western Australia. Mean intraspecific divergence values for each species are shown in bold.

	1	2	3	4	5	6	7
1 *D. calcicolus*	**0.063**						
2 *D. capensis*	0.154	**0.001**					
3 *D. granariensis*	0.135	0.083	**0.023**				
4 *D. ornatus*	0.146	0.156	0.142	**0.053**			
5 *D. polyophthalmus*	0.154	0.173	0.163	0.153	**0.015**		
6 *D. lateroides* sp. nov.	0.152	0.181	0.166	0.16	0.085	**0.003**	
7 *D. nebulosus* sp. nov.	0.144	0.084	0.085	0.145	0.165	0.173	**0.021**

from the deep genetic split between this population and samples from localities on the Swan Coastal Plain (mean genetic divergence 8.5%, despite occuring within 20 km of each other in the Perth region).

MORPHOLOGICAL ASSESSMENT

Table 3 presents the morphological comparisons among taxa measured here. There were few morphological differences among the genetically distinctive lineages, however, various combinations of labial scalation and colouration were diagnostic. Along the coastal plain, the 'Yetna' lineages are diagnosable by the possession of tall labial scales (scales roughly as tall as wide), a character shared by the related but geographically distant *D. capensis*, *D. granariensis* and *D. mitchelli*. Other characters that differed between the 'Yetna' lineage and the other three taxa measured were greater contact of the supranasals (SNas) and fewer clocal spurs in males. Populations of *D. polyophthalmus* from the Swan Coastal plain and Darling Range showed no conspicuous differences in body size and shape, or scalation on the head or digits (characters typically useful for distinguishing gecko species) other than slightly more numerous postnasals (Table 3).

Dorsal colouration and pattern differed consistently among all major lineages (Figures 2, 4). The 'Yetna'

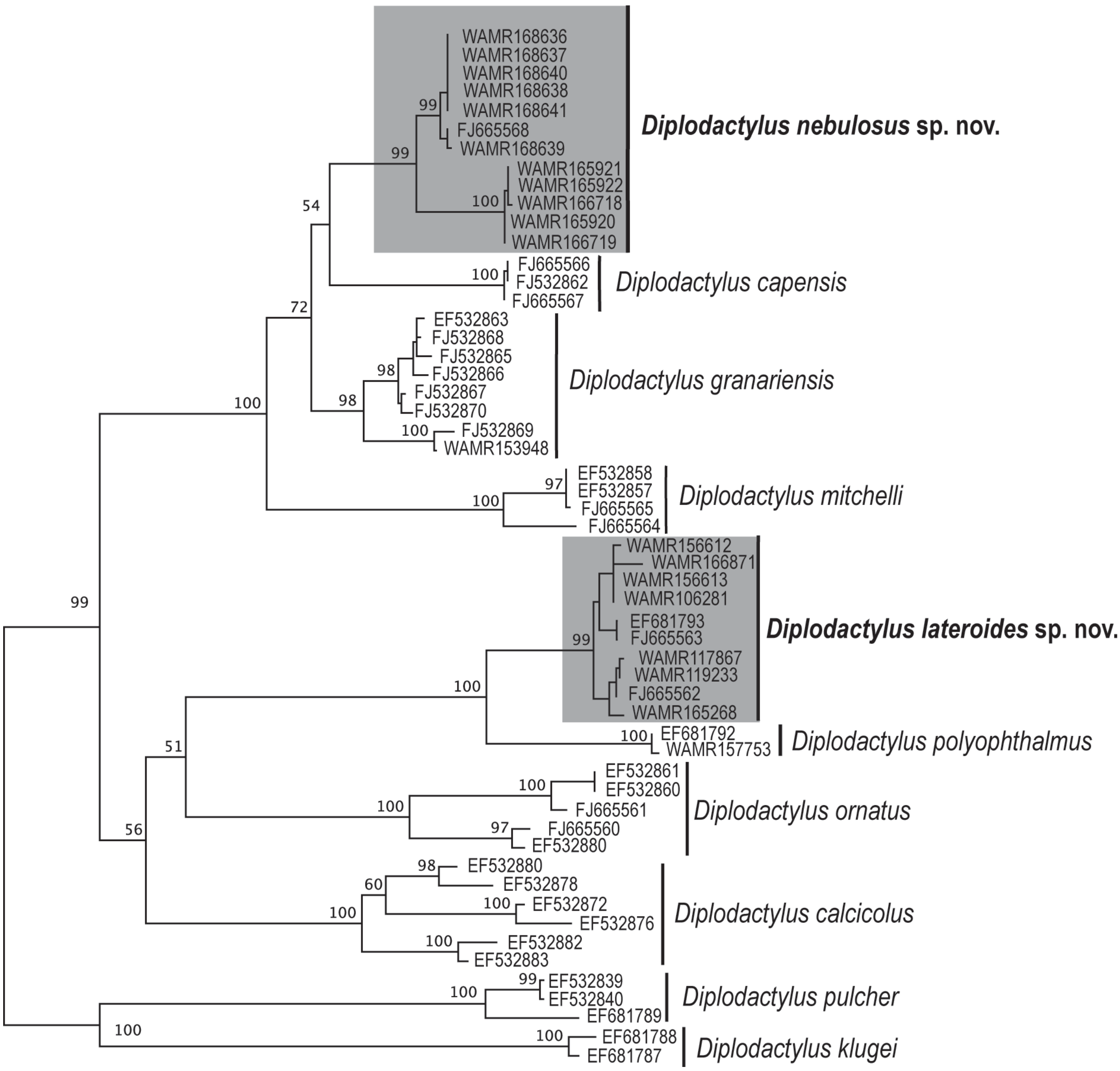

FIGURE 1 Maximum likelihood phylogeny for *Diplodactylus* species found in south-west and coastal Western Australia estimated using 816 base pairs of the mitochondrial *ND2* gene.

TABLE 3 Summaries of characters measured for *Diplodactylus* species. All measurements in mm. Mean±*S.D.* (range). See Table 1 for abbreviations. Sample sizes are listed in column headings, unless noted for individual characters below.

Character	*D. polyophthalmus* N: 10♀, 3♂	*D. lateroides* sp. nov. N: 7♀, 12♂	*D. nebulosus* sp. nov. N: 9♀, 12♂	D. ornatus N: 5♀, 10♂
SVL	♀♀: 49.9±3.7 (44.0–54.0) ♂♂: 45.7±3.2 (42.0–48.0)	♀♀: 46.8±1.5 (45.0–49.0) ♂♂: 45.1±3.1 (40.5–51.0)	♀♀: 51.5±4.0 (43.5–56.0) ♂♂: 47.9±4.9 (37.0–52.0)	♀♀: 53.4±1.6 (51.0–54.0) ♂♂: 45.8±4.7 (42.5–54.0)
TrunkL	22.2±2.0 (20.0–25.6) N=12	19.6±1.5 (17.2–22.9)	21.3±1.5 (15.6–25.4)	21.2±3.5 (16.1–28.2) N=14
TailL	30.4±1.1 (29–31) N=5	26.3±2.0 (24–30) N=6	30.1±3.2 (22–36) N=15	34.3±4.6 (28–41) N=4
TailW	5.6±1.0 (4.4–7.0) N=5	5.3±0.7 (4.4–6.4) N=6	4.9±0.8 (3.9–6.5) N=15	6.0±1.0 (4.6–7.5) N=4
HeadL	12.8±1.0 (11.1–14.0)	12.5±0.7 (5.8–9.5)	13.6±1.2 (8.1–10.9)	13.1±1.1 (7.5–10.1)
HeadW	8.9±0.7 (8.3–10.7)	8.6±0.8 (5.8–9.5)	9.4±0.8 (8.1–10.9)	8.9±0.9 (7.5–10.1)
HeadD	5.9±0.6 (4.7–7.3)	5.5±0.4 (4.7–6.2)	6.3±0.7 (4.9–7.2)	5.7±0.7 (4.3–6.8)
RadL	7.2±0.5 (6.3–8.0) N=11	6.9±0.3 (6.6–7.4) N=14	7.9±0.8 (5.6–9.1)	7.2±0.7 (5.6–8.2) N=14
TibL	8.5±0.9 (7.6–10.8)	8.3±0.5 (7.2–9.5) N=18	9.3±0.9 (7.3–10.3) N=19	8.5±0.8 (7.1–9.6)
IO	4.6±0.3 (4.1–5.1)	4.6±0.3 (4.3–5.1)	4.8±0.4 (4.0–5.3)	4.9±0.4 (4.2–5.4)
NarEye	3.4±0.4 (2.9–4.2)	3.5±0.2 (3.2–3.9)	3.9±0.3 (3.1–4.2)	3.6±0.3 (3.0–4.1)

Character	*D. polyophthalmus* N: 10♀, 3♂	*D. lateroides* sp. nov. N: 7♀, 12♂	*D. nebulosus* sp. nov. N: 9♀, 12♂	D. ornatus N: 5♀, 10♂
IntNar	1.7±0.1 (1.5–1.9)	1.8±0.1 (1.7–2.1)	1.7±0.2 (1.4–2.1)	1.8±0.1 (1.7–2.0)
RosCre	0.5±0.1 (0.2–0.65) N=11	0.4±0.2 (0.25–0.75) N=18	0.4±0.1 (0.25–0.67) N=20	0.5±0.1 (0.2–0.67)
No. PN	5.9±0.6 (5–7) N=12	4.7±0.7 (3–6)	3.6±0.6 (3–5)	4.0±0.7 (3–5)
MentL	1.2±0.1 (0.8–1.4) N=12	1.4±0.1 (1.2–1.6)	1.5±0.1 (1.2–1.7)	1.1±0.1 (0.9–1.3)
MentW	1.4±0.2 (1.1–1.9) N=12	1.5±0.2 (1.2–1.9)	1.5±0.2 (1.2–1.8)	1.4±0.2 (1.2–1.7)
SNas	0.19±0.25 (0–0.60)	0.34±0.27 (0–0.67)	0.78±0.16 (0.25–1)	0.08±0.20 (0–0.5)
SupLab	11.3±0.8 (10–13)	11.0±0.9 (9–12)	11.3±0.8 (10–13)	11.3±0.8 (10–12)
InfLab	10.5±0.7 (9–11)	10.4±0.7 (9–11)	11.1±0.9 (9–11)	11.5±0.9 (10–13)
CSpurs	8.3±3.1 (5–11) N=3	7.8±2.1 (7–11.5) N=12	5.1±0.5 (4.5–6) N=12	6.2±1.9 (4.5–10) N=10
4FLam	7.0±0.7 (6–8)	6.8±0.8 (5–8)	6.7±0.9 (5–8)	5.9±0.9 (7–9)
4TLam	8.5±0.9 (7–10)	8.7±0.7 (8–10)	8.8±0.7 (8–10)	7.9±0.8 (7–9)
NoSC	89.4±12.5 (78–102) N=5	81.3±6.8 (69–88) N=6	78.4±4.8 (73–88) N=15	81.4±6.9 (73–91) N=11

FIGURE 2 Photographs in life of *Diplodactylus* from Western Australia treated here. Top row – *Diplodactylus polyophthalmus* (left: Cataby – S. Cherriman; right: Dianella – B. Maryan); middle row – *D. lateroides* sp. nov. (left: Mt Dale – B. Maryan; right: Harvey – P. Doughty); bottom row – *D. nebulosus* sp. nov. (Morseby Range – B. Maryan).

taxon differed from all geographically proximate congeners (*D. ornatus*, *D. polyophthalmus* and *D. pulcher* further inland) in possessing an irregular cloud-like series of pale blotches that covered nearly the entire dorsum. This taxon is also unique within *Diplodactylus* by usually having a short transverse row of fine white spots within the blotches.

Differences in dorsal colouration and pattern between the two '*D. polyophthalmus*' populations were also apparent: individuals from the coastal plain were a pale brownish-grey, whereas individuals from the Darling Range possessed a rusty-brown hue over the body (Figure 2). This difference was less apparent in preserved specimens owing to the leaching of colours in ethanol. A subtle difference in the pattern was also discernible, with coastal sandplain populations possessing more contrasting spots on the dorsum and lateral surfaces, in contrast to the Darling Range population where the spots are not as clear, especially on the sides (Figures 2, 4–6).

TAXONOMIC CONCLUSIONS

Based on the consistent morphological, colour and pattern differences and the genetic data presented here, we conclude the 'Yetna' taxon is taxonomically distinct from *D. capensis* and *D. granariensis* and describe it as a new species. In Storr's (1979) revision of the *D. vittatus* species-group, he designated 11 specimens of this new taxon as paratypes of *D. granariensis* (Appendix 3). He commented that 'the vertebral stripe is deeply sinuous or broken into blotches' (p. 400), but that these specimens otherwise agreed with northern *D. granariensis*. Storr (1979) made significant progress in his revision by splitting off three species from *D. vittatus*, but lacked sufficient material to fully resolve the species-group at the time.

The two populations of *D. polyophthalmus* are similar in overall size, appearance and scalation (Table 3). They differ, however, in several aspects. As noted above there are consistent differences in colouration and to a lesser extent pattern (Figure 2). The two populations also occur in largely different habitats. The north coast individuals have been collected from sandy substrates such as in *Banksia* woodlands and sandplains. In contrast, the Darling Range populations occur on stony soils, usually laterite. In addition to these differences in appearance

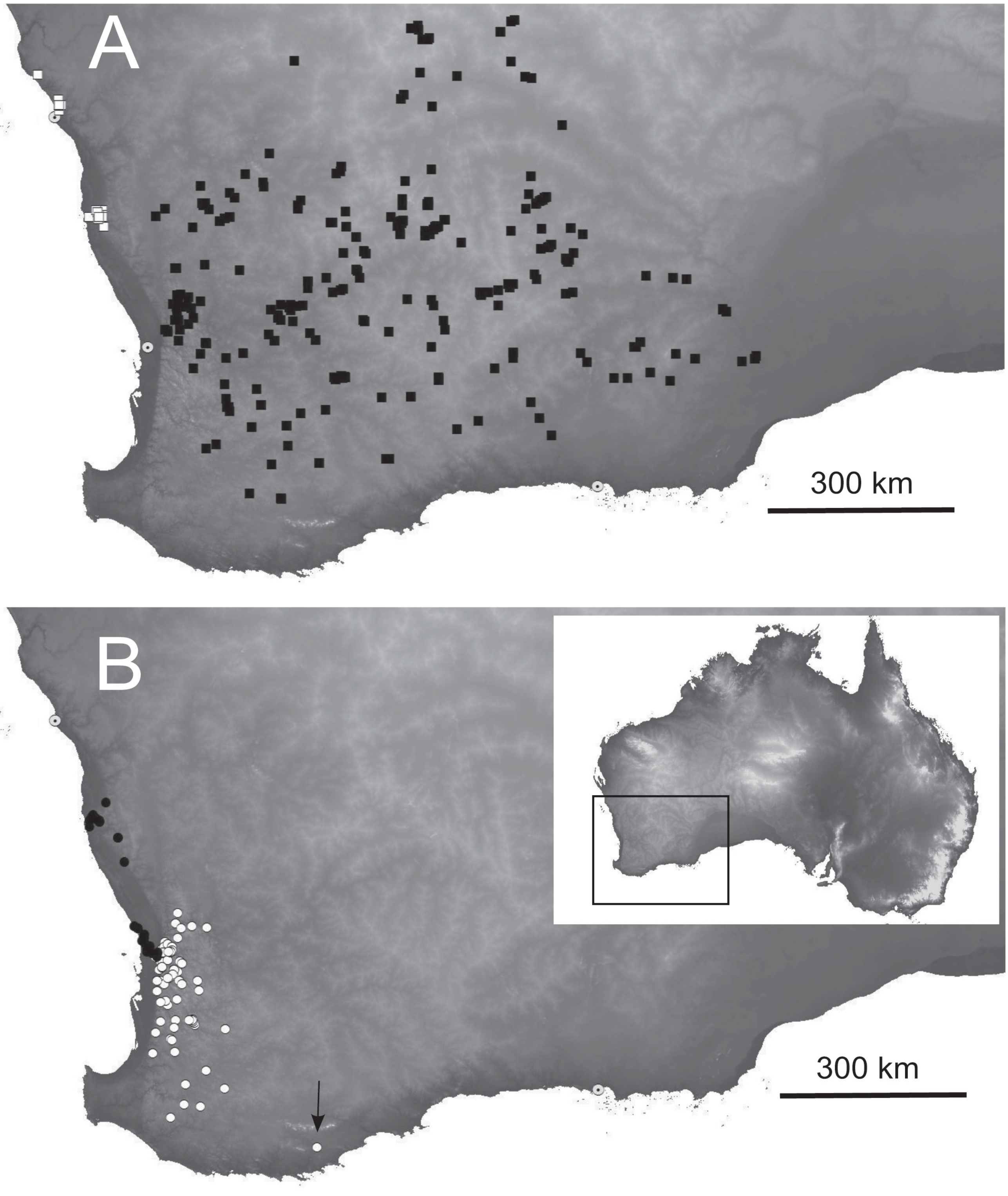

FIGURE 3 Distribution maps of *Diplodactylus* occuring in far south-western Australia. A) *D. nebulosus* sp. nov. – white squares, *D. granariensis* – black squares. B) *D. polyophthalmus* – black circles, *D. lateroides* sp. nov. – white circles. White circles with a black dot represent Geraldton (upper left), Perth (lower left) and Esperance (lower right).

and habitat preference, the genetic data indicates that populations from these two areas have a long history of isolation. Although we only had tissue samples of the coastal lineage from Perth, they differed by an average mitochondrial sequence divergence of 8.5% from all material collected from the Darling Range (Table 2).

The lectotype of *D. polyophthalmus* and its collection data were examined to resolve the application of the name to the correct population of *Diplodactylus* from the western coastal plain. Kluge (1967) examined the two syntypes from the original description and chose as lectotype BMNH 67.2.19.16 collected from 'Champion Bay' (near Geraldton) by F.H. DuBoulay. Kluge designated as paralectotype BMNH 67.2.19.51, collected from 'Nickol Bay' (= Karratha in the Pilbara region); this specimen corresponds to *Lucasium stenodactylum* Boulenger (= *L. woodwardi* Fry, currently in synonomy of *L. stenodactylum*; Pepper et al. 2006, unpublished data). The lectotype of *D. polyophthalmus* (Figure 5) is distinguished from the other lineages of *Diplodactylus* which occur in the Geraldton area. The low labial and supranasal scales of this specimen distinguish it from the 'Yetna' lineage which has tall labial and supranasal scales, and the scattered spots on the body distinguish it from *D. ornatus* which has a clearly-defined vertebral stripe.

Given the lack of morphological differentiation between the two genetic sister lineages of *D. 'polyophthalmus'* populations and the loss of colour in ethanol (the main distinguishing morphological feature), we consider here the collection location of the lectotype of *D. polyophthalmus* in assigning it to either of the sister lineages formerly under this species (based on correspondance with G.M. Shea, Univeristy of Sydney). Francis H. DeBoulay was an avid amateur entomologist based at Minnannooka (or Minnenooka) Station from around 1857 until 1872, when he left permanently for Victoria to pursue a career in the concertina. The station was approximately 30 km west-south-west of Geraldton, where 'Champion Bay' is located. Examination of the list of DeBoulay's collections (>80 specimens) donated to the BMNH indicates many reptile and frog species typical of the Western Australian mid-west, with the odd specimen from the Pilbara and Kimberley regions (likely donated to him by other early explorers). Although some of these species' ranges also extend to south-western Australia (i.e. south of Perth), none are true south-western endemics. The sandplain population of *D. polyophthalmus* occurs as close as 120 km south of Minnannooka Station, close enough to be within the broad environs that DeBoulay would have explored while collecting invertebrates and the occasional vertebrate. We therefore conclude that the lectotype specimen was most likely collected from the coastal sandplain population, and apply the name *D. polyophthalmus* to this lineage. This action results in the Darling Range population lacking an available name, despite this form being considered to be typical *D. polyophthalmus* in the previous work of Kluge (1967), King (1977) and Storr (1979) and illustrated in most field guides (e.g. Storr 1990; Cogger 2000; Wilson & Swan 2011; but see Bush et al. 2007, 2010 for photographs of both forms). Therefore, we describe this taxon as a new species, *D. lateroides* sp. nov.

SYSTEMATICS

Genus *Diplodactylus* Gray, 1832

TYPE SPECIES

Diplodactylus vittatus Gray, 1832, by monotypy.

DIAGNOSIS

A genus of Diplodactylidae (sensu Han et al. 2004) characterized by robust habitus, wide scansors, short (<80% SVL) stout tails, absence of precloacal pores, numerous (typically >5) clocal spurs, two pairs of cloacal bones and anteriorly enlarged jugal bone entering floor of lacrimal foramen (Oliver et al. 2007a).

Diplodactylus polyophthalmus Günther, 1867

Spotted Sandplain Gecko

Figures 2, 4, 5

Lectotype

Australia: ***Western Australia*:** BMNH 67.2.19.16 from Champion Bay; designation by Kluge (1967).

DIAGNOSIS

A relatively small *Diplodactylus* characterised by flat, triangular head with low labial scales, first supralabial taller than second, rostral in contact with nostril, supranasals wider than tall and separated by an internasal in point or narrow contact, ≥5 postnasals, mental and infralabials similar in length, dorsal scales small and similar in size to ventrals, and short and cylindrical tail. Dorsum ground colouration brownish-grey with weakly-defined pale light brown spots often connecting to form irregular larger blotches and occasionally a weakly-defined vertebral stripe.

MEASUREMENTS OF LECTOTYPE

All measurements in mm. SVL – 46.5; TrunkL – 21.5; TailL – 27.5; TailW – 6.8; ArmL – 6.5; LegL – 8.2; HeadL – 12.2; HeadW – 9.8; HeadD – 6.2; IO – 4.8; NarEye – 3.5; Internar – 1.7; RosCre – 0.39; PostNas – 8; MentalL – 1.2; MentalW – 1.5; SupNas – 0 (= not in contact); SupLab – 12; InfLab – 11; CSpurs – 5; 4FLam – 8; FTLam – 8; No. SC – 81.

DESCRIPTION

A small (to SVL 54 mm) *Diplodactylus* with a slight build and small flattened head; arms and legs slender and of moderate length; head moderately wide (HeadW/HeadL – mean = 0.70 and deep (HeadD/HeadL – 0.46); snout triangular when viewed dorsally but rounded in profile at tip; adductor muscles of jaw moderate; eyes moderately large, usually not protruding above top of

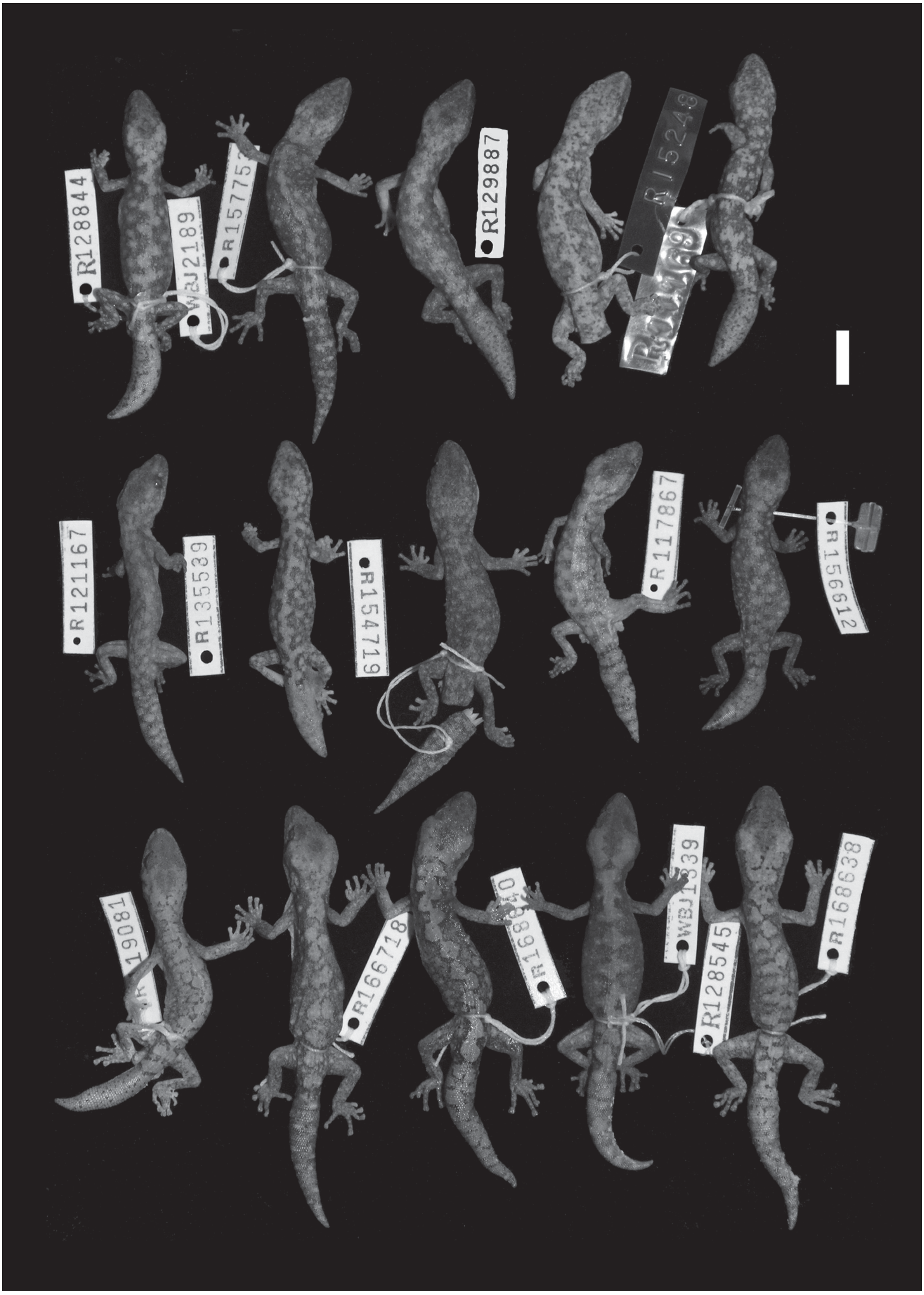

FIGURE 4 Preserved specimens showing variation in dorsal patterning. Top row – *Diplodactylus polyophthalmus*; middle row – *D. lateroides* sp. nov.; bottom row – *D. nebulosus* sp. nov. Scale bar = 1 cm.

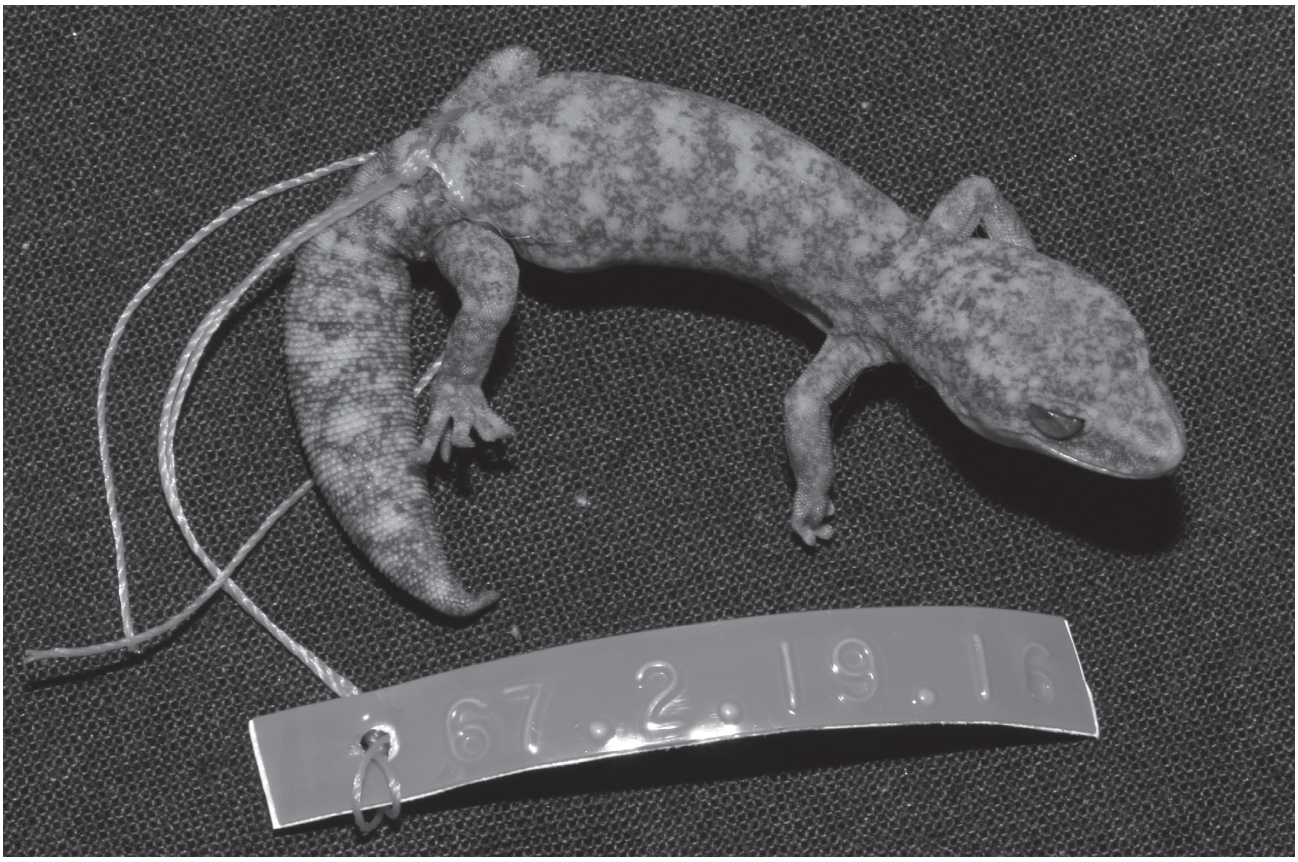

FIGURE 5 Lectotype of *Diplodactylus polyophthalmus* Günther (BMNH 67.2.19.16).

head; 2–5 spinose scales towards the posterior edge of eyelid margin.

Usually 11 (range: 9–13) upper and lower labial scales; nostril in contact with rostral, 2 supranasals, 5–8 postnasals and first labial; first labial taller than second, sloping posteriorly; rostral crease extending from one-fifth to two-thirds down from top of scale; nostrils separated by 2 lower supranasals that are wider than tall (supranasals usually separated by 1 or 2 internasals or in point or narrow contact) and 7–10 smaller, upper supranasals; mental scale triangular with straight sides and with pointed or blunt posterior edge, slightly wider than long; gular scale rows adjacent to infralabials slightly enlarged (in comparison to other gulars) and reducing to fine scales in central gular region.

Scales on dorsum and venter small and similar in size, dorsal scales conical with rounded apex directed posteriorly, ventral scales flattened; crown of head, gular region and limbs with small granular scales; proximal subdigital lamellae usually circular and paired (occasionally single and transversely oblong); distal lamellae singular and circular or occasionally transversely oblong; 6–8 rows of subdigital lamellae on fourth finger and 7–10 on fourth toe; paired moderately enlarged terminal pads on either side of claw; plantar surface of manus and pes covered in protruding rounded scales.

Mature males with 5–11 sharp cloacal spurs with acute tips, females with enlarged rounded scales instead of cloacal spurs. Tail short (TailL%SVL – 66.3), ranging from thin to moderately thick, covered by rectangular rows of scales much larger than those on dorsum.

Colouration

In life, ground pattern of dorsal surfaces to latero-ventral edge light brownish-grey, heavily stippled with darker flecks; poorly defined (lacking dark border) pale off-white irregular blotches on dorsum, usually forming a weak vertebral stripe or chain of blotches; smaller light blotches in upper lateral zone to either side of vertebral stripe or chain; on flanks, pale white small blotches or spots; on head, vertebral stripe bifurcating and extending to eyes to form weakly-defined fork, bordered below by a diffuse dark temporal stripe posterior to eye; anterior to eye a dark loreal stripe; top of snout darkly pigmented, bordered below by pale canthal stripe; labial scales pale white with moderately dense small dark spots; upper surface of limbs same ground colour of dorsum and with small off-white spots as for flanks; venter and ventral surfaces of limbs and tail pale creamy white; original tails with an irregular pale off-white medial stripe or chain of blotches as for dorsum; regenerated tails with light grey background colour and scattered dark flecks. In preservative, ground colour darker brown with fine stippling lost.

HABITAT AND REPRODUCTION

All specimens for which there is location or collection data indicate this species prefers sandy substrates, especially *Banksia* and *Eucalypt* woodlands, but woodlands also including Jarrah, Marri and Tuart trees as well (B. Maryan, W.B. Jennings, pers. comm.). A female collected in October (WAM R15244) had two enlarged follicles (7.6 x 4.9 mm, 7.0 x 5.2 mm).

ETYMOLOGY

The specific name *polyophthalmus* means 'many eyes' in Latin, in reference to the spots on the dorsum that resemble eyes.

DISTRIBUTION

Diplodactylus polyophthalmus is restricted to the coastal and adjacent inland colluvial sandplains (associated with sandstone and laterite) north of the Swan River, with collection records from two widely-separated areas (Figure 3). Records from the Perth region include Thornlie in the Canning River catchment area, King's Park, East Victoria Park and Dianella just north of the Swan River, and extending through to Duncraig, Wanneroo, Woodvale and Yanchep National Park. The second cluster of loaclities begins near Cataby, 100 km north of Yanchep, and there are more recent specimens that have been collected from Lesueur and Badgingarra National Parks, with the most northern record from Eneabba (WAM R78106), 230 km north of Perth. All known records are from the Swan Coastal Plain and the adjacent inland quartz sandplains derived from sandstone and laterite, with records inland as far as 30 km (Cataby, Eneabba) and 40 km (Badgingarra). Most of the northern population specimens are from the inland sandplain, but with a record near Padbury Station 6 km from the coast. It is not known whether the disjunct distribution of the two populations represents a true absence of the species, lack of survey effort or recent extirpation of populations owing to land clearing. Further survey work is required in intervening regions.

COMPARISONS WITH OTHER SPECIES

Diplodactylus polyophthalmus can be differentiatied from all other *Diplodactylus* as follows; from *D. conspicillatus*, *D. galaxias, D. kenneallyi, D. klugei, D. pulcher* and *D. savagei* in having nostrils in contact with rostral scale (v. widely excluded), large labial scales (v. labials similar in size to adjacent scales or only slightly enlarged) and mental not longer than infralabials; from *D. mitchelli* in having dorsals approximately the same size as ventrals (v. dorsal much larger than ventrals), smaller adult body size (mean SVL: 49 v. 65 mm) and different appearance (*D. mitchelli* has a wide, dorsoventrally compressed head and long limbs); from *D. calcicolus*, *D. capensis*, *D. furcosus*, *D. granariensis*, *D. vittatus* and *D. wiru* by labial scales much wider than high (v. width and height similar); from *D. fulleri* and *D. tessellatus* by possessing a vertebral zone of blotches (v. at most diffuse streaks and scattered markings on dorsum); from *D. furcosus* and *D. galeatus* by lacking dark borders around blotches; from the sympatric *D. ornatus* by scattered spots on dorsum (v. clearly-demarcated vertebral stripe); and from the similar, closely-related *D. lateroides* sp. nov. by possessing brownish-grey pigmentation (v. rusty-brown colouration) and more conspicuous spots on dorsum and flanks.

CONSERVATION

Diplodactylus polyophthalmus as it is redefined is restricted to the coastal sandplain in two widely-separated areas. The southern population is only know from from scattered locations north of the Swan River within the city of Perth (population 1.8 million). Populations in Perth are largely extirpated by urban development owing to clearing of habitat for housing and industry. How and Dell (2000) found that although *D. polyophthalmus* was once widespread on the Swan Coastal Plain, by the mid-1990s they only occurred on 5 of nearly 40 bushland remants they examined. Survey work in the last five years has failed to detect any further specimens from these remnants (R. How, pers. comm.). We consider the Perth population to be threatened and at risk of being extirpated in the near future. The large parks and reserves within the Perth footprint are important refugia for many species, yet they are isolated and can be subject to frequent bushfires. The conservation outlook in the northern area is more optimistic, as some of the distribution is included in reserves and national parks that may be less subject to frequent fires.

Diplodactylus lateroides **sp. nov.**

Speckled Stone Gecko

Figures 2, 4, 6

urn:lsid:zoobank.org:act:026E9484-19E2-4F5D-9AFC-CBDA8DA5FA55

Holotype

Australia: ***Western Australia*:** *WAM R156613, an adult male collected from Mount Dale (32.13°S; 116.30°E) on 4 June 2005 by B. Maryan and P. Orange.

Paratypes

Australia: ***Western Australia*:** *WAM R117867 (male), Byford (32.217°S; 116.000°E); WAM R121167 (male), Cooliabberra Spring (32.18°S; 116.03°E); WAM R135539 (female), Kingston State Forest (34.0742°S; 116.3286°E); WAM R154719 (male), Dwellingup area (32.7041°S; 116.1103°E); *WAM R156612 (female), as for holotype.

DIAGNOSIS

A relatively small *Diplodactylus* characterised by flat, triangular head with low labial scales, first supralabial taller than second, rostral in contact with nostril, supranasals usually slightly wider than tall and seperated by internasals or in short contact, 3–6 postnasals, mental similar in length to infralabials, small and similarly sized dorsal and ventral scales and short cylindrical tail. Dorsum with dark-brownish black ground colouration with scattered irregularly shaped and sized lighter blotches, interior of blotches with rusty-brown colouration with paler centres; dorsal blotches usually connecting to form a weakly-defined irregular vertebral stripe or broken series along midline.

MEASUREMENTS OF HOLOTYPE

All measurements in mm. SVL – 47.0; TrunkL – 19.8; ArmL – 6.7; LegL – 7.8; HeadL – 12.0; HeadW – 9.0; HeadD – 5.1; IO – 4.6; NarEye – 3.4; Internar – 1.8; Rost 0.33; PostNas – 3; MentalL – 1.4; MentalW – 1.4; SupNas – 0 (= not in contact); SupLab – 12; InfLab – 11; CSpurs – 11.5; 4FLam – 6; FTLam – 10.

DESCRIPTION

A small (to 51 mm SVL) *Diplodactylus* with a slight build and small flattened head; arms and legs slender and of moderate length; head moderately wide (HeadW/HeadL – mean=0.70) and deep (HeadD/HeadL – 0.44); snout in dorsal view triangular when viewed dorsally, rounded at tip; adductor muscles of jaw moderate; eyes moderately large, usually not protruding above top of head; 2–5 spinose scales towards the posterior fold of the eyelid margin.

Supralabials usually 11 or 12 (range: 9–12); infralabials 10 or 11 (9–11); nostril surrounded by rostral, 2 supranasals, 3–6 postnasals and first supralabial; first supralabial slightly taller or equal in height to second; rostral crease extending from one-fifth to three-quarters down from top of scale; nostrils separated by 2 lower supranasals that are not taller than wide (supranasals usually in point contact or separated by internasals) and 5–9 smaller, upper supranasals; mental scale triangular with blunt or flat posterior edge (usually straight-sided), slightly wider than long; gular scale rows adjacent to infralabials only slightly enlarged and reducing to fine scales in central gular region.

Scales on dorsum similar in size to those on venter, but more rounded (v. flattened); crown of head, gular region and limbs with small granular scales; proximal subdigital lamellae usually circular and paired; distal lamellae circular to transversely oblong; from 5–8 rows of subdigital lamellae on fourth finger and 8–10 under fourth toe; two moderately enlarged apical pads to either side of claw; protruding rounded scales cover plantar surface of manus and pes.

Males with 7–11.5 cloacal spurs with acute tips, females with enlarged rounded scales; tail short (Tail%SVL – 57.5), cylindrical with a slight constriction near the base, ranging from thin to moderately thick, covered by rows of rectangular scales much larger than those on dorsum.

FIGURE 6 Holotype of *Diplodactylus lateroides* sp. nov. (WAM R156613). Scale bar = 1 cm.

Colouration

In life, ground pattern of dorsal surfaces to latero-ventral edge dark brownish-grey heavily stippled with black flecks, extending to latero-ventral edge; lighter, poorly defined (lacking dark border) irregular blotches extend along dorsum, usually connecting to form vertebral stripe or chain of blotches; blotches consist of a rusty-brown band of colouration enclosing a pale off-white central region; smaller blotches in upper lateral zone to either side of vertebral stripe also with rusty-brown interior layer; flanks with small pale white blotches or spots with less conspicuous rusty-brown internal toning; crown of head rusty-brown with dark markings, a poorly-defined dark temporal stripe extends anteriorly past eye as dark loreal stripe, slightly paler stripes above along canthal ridge; labial scales pale but moderately darkly pigmented; ground colour of upper surface of limbs same as dorsum with small paler spots as for flanks; ventral surfaces a pale creamy white; original tails with an irregular median pale stripe or chain of blotches as for dorsum; regenerated tails are light grey with scattered dark brownish-black markings. In preservative, ground colour dark brown and the fine stippling is lost.

HABITAT AND REPRODUCTION

Specimens for which habitat, vegetation or substrate details are noted indicate an association with Jarrah, Marri or Wandoo open *Eucalyptus* woodlands on hard stony surfaces, usually lateritic ridges or granite outcrops in the Darling Range. Individuals have been collected while sheltering under exfoliated granite or laterite rocks and under fallen timber, or from pit-traps in gullies.

Bush et al. (2010) report females (as *D. polyophthalmus*) laying two eggs measuring 15 x 7 mm.

ETYMOLOGY

The specific name *laterioides* means 'resembles laterite' in Latin, in reference to the similarity of the colour pattern of many individuals of this species to the lateritic surfaces on which they occur (Figure 2).

DISTRIBUTION

Diplodactylus lateroides sp. nov. occurs on the Darling Range inland and largely south of Perth (Figure 4). There are two old records from the Stirling Range: WAM R1995 collected around 1927, and a karyotyped individual mentioned in King (1977) (whereabouts unknown). However, a recent search for this species in the Stirlings resulted in the collection of several more specimens.

COMPARISONS WITH OTHER SPECIES

Diplodactylus lateroides sp. nov. can be differentiatied from all other *Diplodactylus* as follows; from *D. conspicillatus*, *D. galaxias, D. kenneallyi, D. klugei, D. pulcher* and *D. savagei* in having nostrils in contact with rostral scale (v. widely excluded), large labial scales (v. labials similar to adjacent scales) and mental not longer than adjacent infralabials; from *D. mitchelli* in having dorsals approximately the same size as ventrals (v. dorsal much larger than ventrals), smaller adult body size (mean SVL: 46 v. 65 mm), different shape (*D. mitchelli* has a wide, dorsoventrally compressed head and long limbs); from *D. calcicolus*, *D. capensis*, *D. furcosus*, *D. granariensis*, *D. vittatus* and *D. wiru* by labial scales wider than tall (v. approximately square); from *D. fulleri* and *D. tessellatus* by possessing a vertebral zone of blotches (v. at most diffuse streaks and scattered markings on dorsum); from *D. furcosus* and *D. galeatus* by lacking dark brown borders around dorsal and lateral blotches; from the sympatric *D. ornatus* by scattered spots on dorsum (v. clearly-demarcated vertebral stripe); and from the similar, closely-related *D. polyophthalmus* by possessing dark rusty-brown (v. pale brownish-grey) colouration with less contrasting spots on the dorsum and flanks.

CONSERVATION

Diplodactylus lateroides sp. nov. is broadly distributed in the Darling Range, a series of low rugged ranges that occur near Perth and extend south and inland in south-western Australia (Figure 3). The Stirling Range is a likely outlying population, but further survey effort is required to confirm its occurrence there and assess any populational variation. We believe this species is more secure than *D. polyophthalmus* owing to relatively less land-clearing on the poor agricultural land and rugged terrain where it occurs, and the presence of many national parks within its range.

***Diplodactylus nebulosus* sp. nov.**

Cloudy Stone Gecko

Figures 2, 4, 7

urn:lsid:zoobank.org:act:D1097213-D1DC-433C-A3B5-E31CAD78A405

Holotype

Australia: ***Western Australia***: *WAM R168639, an adult male collected from Moresby Range (28.6275°S; 114.6703°E) on 16 June 2009 by B. Maryan and D. Algaba.

Paratypes

Australia: ***Western Australia***: WAM R61318 (male), 20 km east of Green Head (30.066°S; 115.167°E); WAM R100225 (male), ~7 km north-east of Mt Lesueur (30.13°S; 115.25°E); *WAM R119081 (male), Yetna (28.62°S; 114.7°E); WAM R128545 (male) and WAM R128551 (female), Lesueur National Park (30.0938°S; 115.1789°E); *WAM R166718 (female), Mt Lesueur (30.1619°S; 115.1992°E); *WAM R168638 (female), as for holotype; *WAM R168640 (female), Moresby Range (28.6194°S; 114.6700°E); *WAM R168641 (male), Moresby Range (28.6163°S; 114.6619°E).

DIAGNOSIS

A medium-sized *Diplodactylus* characterised by stout head with tall labial scales (as tall as wide), ≤5

FIGURE 7 Holotype of *Diplodactylus nebulosus* sp. nov. (WAM R168639). Scale bar = 1 cm.

postnasals, mental similar size to adjacent infralabials, first supralabial equal or slightly taller than second, rostral in contact with nostril, dorsal scales only slightly larger than ventral scales, and tail long, cylindrical and tapering to a fine point. Dorsal ground colour light to dark brown with a series of large irregular pale blotches along midline, blotches usually containing a short transverse row of fine pale spots.

MEASUREMENTS OF HOLOTYPE

All measurements in mm. SVL – 45.5; TrunkL – 17.8; TailL – 36.0; TailW – 6.5; ArmL – 8.0; LegL – 10.3; HeadL – 13.6; HeadW – 9.5; HeadD – 7.0; IO – 5.1; NarEye – 3.9; Internar – 1.6; Rost – 0.25; PostNas – 3; MentalL – 1.5; MentalW – 1.2; SupNas – 1 (= full contact); SupLab – 11; InfLab – 9; CSpurs – 5; 4FLam – 7; FTLam – 9; No. SC – 77.

DESCRIPTION

A medium-sized (to 56 mm SVL) *Diplodactylus* with a moderate build and medium-large head; arms and legs slender and of moderate length; head moderately wide (HeadW/HeadL – mean = 0.69) and deep (HeadD/HeadL – 0.46); snout triangular when viewed dorsally, rounded in profile at tip; adductor muscles of jaw prominent; eyes moderately large and slightly protruding above top of head; ~5 spinose scales towards the posterior fold of the eyelid margin.

Usually 11 or 12 (range: 9–13) upper and lower labial scales; nostril surrounded by rostral, 2 supranasals, 2–5 postnasals and first supralabial; first supralabial slightly taller or equal in height to second; rostral crease extending from one-quarter to two-thirds down from top of scale; nostrils separated by 2 lower supranasals in broad contact and 4–6 smaller, upper supranasals; mental scale sharply triangular or lanceolate, approximately as long as wide; gular scale rows adjacent to infralabials slightly enlarged, reducing to fine scales in central gular region.

Scales on dorsum slightly larger than on venter; ventral and chin scales flatter than scales on head, dorsum and tail which are more rounded; head scales smaller and more rounded than dorsal scales; limbs with small granular scales; subdigital lamellae circular or rarely tranversely oblong, flanked by slightly smaller, rounded scales to either side usually 6–7 (range: 5–8) unbroken subdigital lamellae on fourth finger and 8–9 (8–10) under fourth toe; two enlarged apical pads to either side of claw; protruding rounded scales cover plantar surface of manus and pes.

Males have 5–6 spinose scales (cloacal spurs) arranged in 1–2 rows; females have rounded scales where the male spurs occur; tail moderately thick and long (TailL%SVL – 65.9); cylindrical with a slight constriction near the base, covered by regular rows of rectangular scales much larger than those on dorsum.

Colouration

In life, ground colouration on upper surfaces, sides and limbs heavily stippled dark brownish-grey; the vertebral zone has a series of large pale blotches that either join to form a continuous stripe with a wavy highly irregular border, or form a series of isolated blotches; inside each dorsal blotch there tends to be a transverse row of fine white spots; the vertebral stripe or blotches continue anteriorly to the nape and form a pale cap or two broad pale streaks to the eyes; below this and above the pale upper labials a dark temporal streak extends through the ventral portion of eye, continuing anterior to eye as a dark loreal stripe; on flanks a row of irregular pale spots blotches separated from vertebral blotches, occasionally containing fine white spots; limbs same ground colour as dorsum with smaller white spots or blotches; ventral surface and the lower flanks creamy white; original tails with dorsal vertebral blotches extending length of tail; regenerated tails grey with dark stippling and lacking the patterns and blotches of original tails. In preservative, the original pattern is largely retained, but overall hue is a dark brown and the transverse row of fine white spots is often not apparent.

HABITAT AND REPRODUCTION

Most collection data indicate a preference for *Eucalypt* and Wandoo woodlands on harder surfaces, such as rocky ridges, sandstone outcrops and lateritic breakaways. Some have also been observed on softer substrates such as sandplains and clay soils (B. Jennings, pers. comm.). Many individuals were collected under rocks or fallen timber during the day (A. Desmond, B. Jennings, B. Maryan, pers. comm.). Examining records from the survey of Cockleshell Gully (Dell and Chapman 1977) indicated that *D. nebulosus* sp. nov. specimens were collected to the east of Mt Peron, whereas both *D. ornatus* and *D. polyophthalmus* were found on softer substrates, including the Spearwood Dunes towards the coast.

No females examined were gravid, but reproduction should be similar to other *Diplodactylus*.

ETYMOLOGY

nebulosus is derived from the Latin *nebula*, meaning ‘cloud’, owing to the large irregular blotches on the dorsum that resemble billowing clouds. Used as a noun in apposition.

DISTRIBUTION

Diplodactylus nebulosus sp. nov. is restricted to the southern portion of the western coast of Australia. It occurs on harder substrates inland of the coastal sandplain. There are two main areas of distribution, with a large intervening area of approximately 160 km where no individuals have been collected (Figure 3). The southern collection area includes Lesueur National Park (Burbidge et al. 1990), and records 20–30 km inland of Jurien and Green Head. The northern collection area is near Geraldton and includes Yetna, Moresby Range and Howatharra Nature Reserve, with the northernmost records from near the mouth of the Lower Hutt River. The linear distance between the southern and northernmost records is about 240 km. The moderate genetic divergence between these two collecting areas (~3.8%) suggests these populations have a history of isolation and that the observed disjunction may represent a true absence.

COMPARISONS WITH OTHER SPECIES

Diplodactylus nebulosus sp. nov. differs from *D. conspicillatus*, *D. galaxias, D. kenneallyi, D. klugei, D. pulcher* and *D. savagei* by nostrils in contact with rostral scale, enlarged labial scales, longer tail, and mental not longer than infralabials; from *D. mitchelli* by dorsals approximately the same size as ventrals, smaller adult body size, stouter head and shorter limbs; from *D. lateroides* sp. nov., *D. ornatus*, *D. polyophthalmus* by possessing relatively tall labials (as tall as wide). *Diplodactylus nebulusus* sp. nov. differs from the remaining *Diplodactylus* largely in aspects of dorsal pattern and colouration. It differs from *D. granariensis*, *D. ornatus*, *D. vittatus*, *D. wiru* and some *D. calcicolus* by having an irregular vertebral zone comprised of blotches (the other taxa have straight or scalloped edges to the vertebral stripe). It differs from *D. furcosus*, *D. galeatus* and some *D. calcicolus* by usually having a tranverse row of fine white spots within the blotches (unique in *Diplodactylus*). It differs from *D. fulleri* and *D. tessellatus* by possessing a vertebral zone of blotches (v. at most diffuse streaks and scattered markings on dorsum). It differs from *D. capensis* and *D. mitchelli* by lacking rich reddish colouration with pale transverse bars extending from vertebral stripe.

CONSERVATION

The populations of *D. nebulosus* in Lesueur and Badgingarra National Parks would seem to be secure given the protection afforded to these areas, bearing in mind that such places are also subject to modified burning regimes and feral animals (Burbidge et al. 1990). The species appears to be abundant and widespread in both parks, and distributed over a variety of habitats (B. Jennings, pers. comm.). The populations near Geraldton are generally not in national parks or reserves, and the area is being subject to increased industrial and housing developments. One significant reserve is the proposed Moresby Range Conservation Park where specimens have been collected. The species’ preference for hard surfaces is different from the sandy surfaces preferentially cleared by industrial and housing developments in Western Australia.

DISCUSSION

BIOGEOGRAPHY OF SOUTH-WESTERN AUSTRALIA

The South-west Australian Floristic Region (south-west hotspot) is a relatively wet continental refuge covering approximately 300,000 km^2, bordered on two sides by ocean, and by arid lands to the north, north-east, and east (Hopper and Gioia 2004). This region is recognised globally as a 'biodiversity hotspot', and a centre of diversity and endemism for many plant and (to a lesser extent) animal groups (Myers et al. 2000; Hopper and Gioia 2004). Why the south-west is so biodiverse is a major recurring question in Australian biogeography (Hopper and Gioia 2004; Melville et al. 2008; Hopper 2009; Edwards et al. 2012).

Diplodactylus is the most diverse gecko genus in the south-west. The region is also a centre of diversity for the genus (7 out of a probable Australian total of ~30 species [Oliver et al. 2009]). This includes the three regionally endemic species treated here (*D. lateroides*, *D. nebulosus* and *D. polyophthalmus*) and four more wide-ranging species (*D. calcicolus*, *D. granariensis*, *D. ornatus* and *D. pulcher*). The distribution of many of these taxa overlap, and in at least one region in the south-west (around Mt Lesueur) three species are regionally sympatric (*D. nebulosus*, *D. ornatus* and *D. polyophthalmus*; Figure 3; W.B. Jennings, pers. comm.). Below we examine how the distribution of *Diplodactylus* species in the south-west compares to broad phytogeographic patterns reported by Hopper and Gioia (2004).

Hopper and Gioia (2004) suggested that there has been a history of repeated faunal interchange between the south-west and surrounding biomes. Our data supports this concept: many *Diplodactylus* lineages in the south-west are clearly related to arid zone lineages. Many *Diplodactylus* species that occur in the south-west hotspot (4 of 7) occur outside this region, consistent with another hypothesis that the overlap of arid, semi-arid and temperate niches contributes to overall biodiversity indices (Hopper and Gioia 2004). More broadly, an emerging pattern is that the entire lizard fauna of the south-west includes few highly divergent relictual taxa; for instance only two recognised genera are endemic or near endemic (*Hesperoedura* and *Pletholax*) and show evidence of moderately long term persistence (since the around late Miocene) in complete isolation from any living relatives (Jennings et al. 2003; Oliver et al. 2012).

Hopper and Gioia (2004) noted that flora of the south-west region was most diverse and endemic in the Transitional Rainfall Province (300–800 mm rainfall per year). Inter- and intraspecific lineage divergence within south-western *Diplodactylus* is also concentrated within this zone (the split of *D. lateroides* and *D. polyophthalmus*, and lineages within *D. nebulosus* and *D. ornatus*), supporting the idea that this area has been the most important zone of *in situ* diversification in the south-west. A final pattern apparent in the distribution of *Diplodactylus* and other lizards is that genetic turnover and levels of endemism are much higher along the western coastal region than the southern coastal region (Melville et al. 2008). If additional short range endemic *Diplodactylus* from the Carnarvon Basin (*D. klugei*) and North West Cape (*D. capensis*) are also considered, the number of endemics along the west coast is even more marked (Aplin and Adams 1998; Doughty et al. 2008).

The mechanisms that have shaped the biodiversity of the south-west are probably many and synergistic (Hopper 2009). Edwards et al. (2012) presented a detailed analysis of patterns of genetic divergence among west coast reptiles, and suggested that they were broadly (and often idiosyncratically) shaped by the interplay of historical environmental change and ecological specialisation, especially substrate preference. *Diplodactylus* species in the south-west are often associated with different substrates and where multiple taxa occur in close regional proximity they usually utilise different substrates (e.g. at Lesueur National Park – *D. ornatus* and *D. polyophthalmus* on sandy substrates and *D. nebulosus* on harder surfaces; W.B. Jennings, pers. comm.). The distribution of the only two sister species of *Diplodactylus* endemic to the south-west (*D. lateroides* and *D. polyophthalmus*) also meets at an ancient and sharp geological border where the Darling Range meets the Swan Coastal Plain. The correlation between divergent lineages and different substrates supports the hypothesis that habitat variation has played an important role in the diversification and persistence of multiple lineages of *Diplodactylus* in the south-west.

SPECIES DIVERSITY AND CONSERVATION IN THE SOUTH-WEST HOTSPOT

Resolution of taxonomic boundaries among the species treated here has required targeted surveys of key areas to obtain new material, an assessment of genetic diversity and re-examination of older voucher specimens. In the absence of this background data, specimens of *D. nebulosus* and *D. polyophthalmus* from the coastal sandplain of south-western Australia were often incorrectly assigned to *D. granariensis* or *D. ornatus*. Indeed, several *D. nebulosus* specimens are paratypes of *D. granariensis* (Appendix 3). Recent revisions of *Diplodactylus* (Doughty et al. 2008, 2010; Hutchinson et al. 2009) also relied heavily on genotyped specimens assigned to divergent lineages to facilitate the search for diagnostic morphological characters. While the taxonomy of *Diplodactylus* remains incomplete (Oliver et al. 2009), each iteration of revisionary work has improved our understanding of the nature of variation within and between taxa. In other regions of Australia where there is similar evidence of unresolved taxonomic complexity, targeted surveys to fill collecting gaps are necessary as current sampling (especially tissues for genetic analyses) is probably inadequate to properly understand patterns of variation.

Many new taxa of *Diplodactylus* remain to be described from elsewhere in Australia (Oliver et al. 2009). It seems unlikely, however, that completely unknown and distinctive populations of *Diplodactylus* remain undiscovered in the south-west. Nevertheless, there are additional populations within established taxa that are of note and may in some cases require further taxonomic study. The two isolated populations of *D. nebulosus* on the Geraldton Sandplain show a level of genetic divergence indicative of a significant history of isolation and probably warrant recognition as Evolutionary Significant Units (Moritz 1994). *Diplodactylus polyophthalmus* also includes two apparently isolated populations. Further fieldwork is required to determine the extent of the disjunction between these populations, and genetic analyses are required to determine their history of divergence. The status of an apparently disjunct population of *D. lateroides* from the Stirling Range also requires assessment. Finally, there is evidence of significant morphological and genetic differentiation between *Diplodactylus g. granariensis* from the Darling Ranges and those from plains further to the east that requires investigation (Doughty et al. 2008; Hutchinson et al. 2009).

The Swan Coastal Plain has a distinctive geology and highly diverse and endemic biota, but is also the location of Western Australia's rapidly expanding state capital of Perth (1.8 million people) and thus one of the most heavily modified regions of Western Australia (How and Dell 2000). Likewise, much of the Geraldton Sandplain has been cleared for agriculture and large areas of remaining habitat are significantly degraded (e.g. Desmond and Chant 2001). Our genetic studies have highlighted the presence of two endemic species of *Diplodactylus* in these coastal sandplains which require further study to adequately assess their conservation status. While both occur in protected areas and may not be immediately threatened, a large percentage (if not a majority) of their habitat has been cleared, and they have most certainly undergone concomitant population declines since European settlement.

As noted above, the southern population of the redefined *D. polyophthalmus* is of particular concern. There have been few recent records of this species from Perth, and all have been from small patches of habitat that may not be viable in the long term. Expanding urban sprawl in this region also continues to threaten other areas of potentially suitable habitat. The southern population of *D. polyophthalmus* is certainly under threat, and there is a pressing need to develop a better understanding of its distribution, habitat requirements, and evolutionary divergence from probable conspecific populations further to the north.

More broadly, this paper adds two vertebrates to the large number of taxa endemic to the heavily disturbed coastal sandplain bioregions of the south-west. Four other endemic species have been described in relatively recent times (*Cyclodomorphus branchialis* and *C. celatus* Shea and Miller, 1995; *Arenophryne xiphorhyncha* Doughty and Edwards, 2008; *Ctenotus ora* Kay and Keogh, 2012). Two of these taxa are also considered to be of conservation concern. Ongoing work suggests the presence of additional unrecognised endemic reptile taxa in this region (PD, pers. obs.; B. Maryan, pers. comm.). These previously undocumented endemic vertebrate taxa demonstrate that there remains much to learn about the diverse but highly disturbed coastal sandplains of south-west Western Australia.

ACKNOWLEDGEMENTS

We thank A. Desmond, B. Maryan, B. Bush, W.B. Jennings, R. Browne-Cooper, P. Orange and W.H. Butler for collecting the key specimens that were necessary for this study, and for sharing observations on habitat and ecology on the taxa treated here. We thank K. Smith for generating sequence data, Z. Squires, R. Laver and J. Sumner for additional help with molecular labwork. For examination of specimens we thank D. Bray of Museum Victoria, C. McCarthy and P. Campbell of the Natural History Museum, London and Glenn Shea for measurements of the lectotype of *D. polyophthalmus*. We thank B. Maryan and S. Cherriman for use of photographs of live animals, L. Kealley for help with photography of preserved specimens and G. Shea for sharing his voluminous knowledge of early collections of Australian reptiles with us which greatly contributed to establishing the collecting location of *D. polyophthalmus*. This work was supported by a McKenzie Postodoctoral Fellowship from Melbourne University (Oliver), a grant from the Australian Biological Resources Survey to P. Oliver, P. Doughty, M. Adams and M.S.Y Lee and a Churchill Fellowship (Doughty). For helpful comments on drafts of the manuscript we thank R. How, W.B. Jennings and B. Maryan.

REFERENCES

Aplin, K.P. and Adams, M. (1998). Morphological and genetic discrimination of new species and subspecies of gekkonid and scincid lizards (Squamata: Lacertilia) from the Carnarvon Basin of Western Australia. *Journal of the Royal Society of Western Australia* **81**: 201–223

Biomatters. (2012). Geneious version R6. Available from http://www.geneious.com.

Burbidge, A.A., Hopper, S.D. and van Leeuwen, S. (1990). A report to the Environmental Protection Authority from the Department of Conservation and Land Management. CALM: Perth.

Bush, B., Maryan, B., Browne-Cooper, R. and Robinson, D. (2007). *Reptiles and frogs in the bush: Southwestern Australia*. University of Western Australia Press: Crawley, Australia.

Bush, B., Maryan, B., Browne-Cooper, R. and Robinson, D. (2010). *Field guide to reptiles and frogs of the Perth region.* Western Australian Museum Press: Perth.

Cogger, H.G. (2000). *Reptiles and amphibians of Australia.* Reed: Sydney.

Dell, J. and Chapman, A. (1977). Reptiles and frogs of Cockleshell Gully Reserve. In: *A vertebrate survey of Cockleshell Gully Reserve, Western Australia*. *Records of the Western Australian Museum*, Supplement **4**: 75–85.

Desmond, A. and Chant, A. (2001). Geraldton Sandplain 3 (GS3 – Lesueur Sandplain subregion) (pp. 293–313). *In:* May, J.E. and Mckenzie, N.L. (eds). *A biodiversity audit of Western Australia's biogeographical subregions in 2002.* Department of Conservation and Land Management: Perth.

Doughty, P. and Edwards, D. (2008). A new species of sandhill frog (Myobatrachidae: *Arenophryne*) from the western coast of Australia. *Records of the Western Australian Museum* **24**: 121–131.

Doughty, P., Oliver, P. and Adams, M. (2008). Systematics of stone geckos in the genus *Diplodactylus* (Reptilia: Diplodactylidae) from northwestern Australia, with a description of a new species from the Northwest Cape, Western Australia. *Records of the Western Australian Museum* **24**: 247–265.

Doughty, P., Pepper, M. and Keogh, J.S. (2010). Morphological and molecular assessment of the *Diplodactylus savagei* species complex in the Pilbara region, Western Australia, with a description of a new species. *Zootaxa* **2393**: 33–45.

Edgar, R.C. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**: 1792–1797.

Edwards, D.L, Keogh, J.S. and Knowles, L.L. (2012). Effects of vicariant barriers, habitat stability, population isolation and environmental features on species divergence in the south-western Australian coastal reptile community. *Molecular Ecology* **21**: 3809–3822.

Günther, A. (1867). Additions to the knowledge of Australian reptiles and fishes. *Annals and Magazine of Natural History* (3), **20**: 45–68.

Han, D., Zhou, K. and Bauer, A.M. (2004). Phylogenetic relationships among gekkotan lizards inferred from *C-mos* nuclear DNA sequences and a new classification of the Gekkota. *Biological Journal of the Linnaean Society* **83**: 353–368.

Hopper, S.D. (1979) Biogeographical aspects of speciation in the southwest Australian flora. *Annual Review of Ecology and Systematics* **10**: 399–422.

Hopper, S.D. (2009). OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically-buffered, infertile landscapes. *Plant and Soil* **322**: 49–86.

Hopper, S.D. and Gioia, P. (2004). The Southwest Australian Floristic Region: evolution and conservation of a global hotspot of biodiversity. *Annual Review of Ecology, Evolution and Systematics* **35**: 623–650.

How, R. and Dell, J. (2000). Ground vertebrate fauna of Perth's vegetation remanants: impact of 170 years of urbanization. Pacific *Conservation Biology* **6**: 198–217.

Hutchinson, M.N., Doughty, P. and Oliver, P.M. (2009). Taxonomic revision of the stone geckos (Squamata: Diplodactylidae: *Diplodactylus*) of southern Australia. *Zootaxa* **2167**: 25–46.

Jennings, B., Pianka, E.R. and Donnellan, S.C. (2003). Systematics of the lizard family Pygopodidae with implications for the diversification of Australian temperate biotas. *Systematic Biology*, 52: 757–780.

Kay, G.M. and Keogh, J.S. (2012). Molecular phylogeny and morphological revision of the *Ctenotus labillardieri* (Reptilia: Squamata: Scincidae) species group and a new species of immediate conservation concern in the southwestern Australian biodiversity hotspot. *Zootaxa* **3390**:1–8.

King, M. (1977). Chromosomal and morphometric variation in the gecko *Diplodactylus vittatus* (Gray). *Australian Journal of Zoology* **25**: 42–57.

Kluge, A.G. (1967). Systematics, phylogeny and zoogeography of the lizard genus *Diplodactylus* Gray (Gekkonidae). *Australian Journal of Zoology* **15**: 1007–1108.

Macey, J.R., Larson, A., Ananjeva, N.B., Fang, Z. and Papenfuss, T.J. (1997). Two novel gene orders and the role of light strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution* **14**: 91–104.

Melville , J., Shoo, L.P. and Doughty, P. (2008). Phylogenetic relationships of the heath dragons (*Rankinia adelaidensis* and *R. parviceps*) from the southwestern Australian biodiversity hotspot. *Australian Journal of Zoology* **56**:159–171.

Moritz, C. (1994). Definning 'Evolutionarily Significant Units' for conservation. *Trends in Ecology and Evolution* **9**: 373–375.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403:** 853–858.

Oliver, P.M., Hutchinson, M.N. and Cooper, S.J.B. (2007a). Phylogenetic relationships in the lizard genus *Diplodactylus* Gray and resurrection of *Lucasium* Wermuth (Gekkota, Diplodactylidae). *Australian Journal of Zoology* **55**: 197–210.

Oliver, P., Hugall, A., Adams, M., Cooper, S.J.B. and Hutchinson, M. (2007b). Genetic elucidation of ancient and cryptic diversity in a group of Australian geckos: the *Diplodactylus vittatus* complex. *Molecular Phylogenetics and Evolution* **44**: 77–88.

Oliver, P.M., Adams, M., Lee, M.S.Y., Hutchinson, M.N. and Doughty, P. (2009). Cryptic diversity in vertebrates: molecular data double estimates of species diversity in a radiation of Australian lizards (*Diplodactylus*, Gekkota). *Proceedings of the Royal Society B* **276**: 2001–2007.

Oliver, P.M., Bauer, A.M., Greenbaum, E., Jackman, T. and Hobbie, T. (2012). Molecular phylogenetic evidence for the paraphyly of the arboreal Australian gecko genus *Oedura* Gray 1842 (Gekkota: Diplodactylidae): yet another plesiomorphic grade? *Molecular Phylogenetics and Evolution* **63**: 255–264.

Pepper, M., Doughty, P. and Keogh, J.S. (2006) Molecular systematics and phylogeography of the Australian *Diplodactylus stenodactylus* (Gekkota: Reptilia) species-group based on mitochondrial and nuclear genes reveals an ancient split between Pilbara and non-Pilbara *D. stenodactylus*. *Molecular Phylogenetics and Evolution* **41**: 539–555.

Read, K., J.S. Keogh, I.A.W. Scott, J.D. Roberts and P. Doughty. (2001). Molecular phylogeny of the Australian frog genera *Crinia* and *Geocrinia* and allied taxa (Anura:Myobatrachidae). *Molecular Phylogenetics and Evolution* **21**: 294–308.

Shea, G.M. and Miller B. (1995). A taxonomic revision of the *Cyclodomorphus branchialis* species group (Squamata: Scincidae). *Records of the Australian Museu*Stamatakis, A. (2006). RaxML–VI–HPC: Maximum Likelihood–based Phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.

Storr, G.M. (1979). The *Diplodactylus vittatus* complex (Lacertilia, Gekkonidae) in Western Australia. *Records of the Western Australian Museum* **7**: 391–402.

Storr, G.M., Smith, L.A. and Johnstone, R.E. (1990). *Lizards of Western Australia III: geckos and pygopods.* Western Australian Museum Press: Perth.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. and Kumar, S. (2011). MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* **28**: 2731–2739.

MANUSCRIPT RECEIVED 5 APRIL 2013; ACCEPTED 12 JULY 2013.

APPENDIX 1 Specimens details for samples included in genetic analyses.

Species	Registration #	Locality	State	Latitude	Longitude	GenBank
D. calcicolus	WAM R91756	15 km SSE Haig	WA	-31.1402	126.1450	EF532880
D. calcicolus	SAMA R22923	Coomalbidgup, Lort River	WA	-33.63	121.30	EF532883
D. calcicolus	SAMA R36643	Venus Bay	SA	-33.23	134.67	EF532876
D. calcicolus	SAMA R39473	3 km NW of Harriot Hill	SA	-35.20	139.05	EF532872
D. calcicolus	SAMA R44119	St Peter Island	SA	-32.25	133.62	EF532878
D. calcicolus	WAM R140941	27.5 km SSE Peak Eleanora	WA	-33.1666	121.2667	EF532882
D. capensis	WAM R132465	Cape Range National Park	WA	-22.0500	114.0169	EF532862
D. capensis	WAM R132467	Cape Range National Park	WA	-22.0500	114.0169	FJ665566
D. capensis	WAM R132468	Cape Range National Park	WA	-22.0500	114.0169	FJ665567
D. granariensis	WAM R112102	86 km N Meekatharra	WA	-25.9347	118.8433	EF532865
D. granariensis	WAM R112103	86 km N Meekatharra	WA	-25.9347	118.8433	EF532863
D. granariensis	WAM R113191	35 km S Kumarina	WA	-24.9166	119.3667	EF532866
D. granariensis	WAM R140415	3 km S Vivien Mine	WA	-28.0166	120.7167	EF532868
D. granariensis	WAM R144551	Mount Jackson	WA	-30.2497	119.2386	EF532870
D. granariensis	WAM R153946	Bindoon Military Training Area	WA	-31.2380	116.2503	EF532869
D. klugei	WAM R120715	10 km ESE Mardathuna Homestead	WA	-24.5113	114.6367	EF681788
D. klugei	WAM R120870	Woodleigh Station	WA	-26.1955	114.4231	EF681787
D. lateroides sp. nov.	WAM R106281	Mount Cooke	WA	-32.4166	116.3000	KF197024
D. lateroides sp. nov.	WAM R117867	Byford, Perth	WA	-32.2166	116.0000	KF197025
D. lateroides sp. nov.	WAM R119233	Bungendore, Perth	WA	-32.1911	116.0356	KF197026
D. lateroides sp. nov.	WAM R121167	Cooliabberra Spring, Bungendore, Perth	WA	-32.1833	116.0333	FJ665563
D. lateroides sp. nov.	WAM R135539	Kingston State Forest	WA	-34.0752	116.3286	FJ665563
D. lateroides sp. nov.	WAM R144178	4 km S Collie	WA	-33.3533	116.2064	EF681793
D. lateroides sp. nov.	WAM R156612	Mount Dale	WA	-32.1333	116.3000	KF197027
D. lateroides sp. nov.	WAM R156613	Mount Dale	WA	-32.1333	116.3000	KF197028
D. lateroides sp. nov.	WAM R165286	Harvey Reserve	WA	-33.0833	115.9500	KF197030

Species	Registration #	Locality	State	Latitude	Longitude	GenBank
D. lateroides sp. nov.	WAM R166871	Red Hill	WA	-31.8341	116.0783	KF197031
D. mitchelli	SAMA R60439	Roy Hill area	WA	-22.75	119.92	FJ665564
D. mitchelli	WAM R113642	37 km NNE Auski Roadhouse	WA	-22.05	118.82	FJ665565
D. mitchelli	WAM R146632	198 km S Port Hedland	WA	-22.1022	118.9900	EF532857
D. mitchelli	WAM R152704	Chichester Range	WA	-22.0900	118.9919	EF532858
D. nebulosus sp. nov.	WAM R119081	Yetna	WA	-28.6166	114.7000	FJ665568
D. nebulosus sp. nov.	WAM R165920	Mount Lesueur	WA	-30.1627	115.1992	KF197032
D. nebulosus sp. nov.	WAM R165921	Mount Lesueur	WA	-30.1627	115.1992	KF197033
D. nebulosus sp. nov.	WAM R165922	Lesueur National Park	WA	-30.1433	115.1817	KF197034
D. nebulosus sp. nov.	WAM R166718	Mount Lesueur	WA	-30.1619	115.1992	KF197035
D. nebulosus sp. nov.	WAM R166719	Mount Lesueur	WA	-30.1619	115.1992	KF197036
D. nebulosus sp. nov.	WAM R168636	Moresby Range	WA	-28.6275	114.6703	KF197037
D. nebulosus sp. nov.	WAM R168637	Moresby Range	WA	-28.6275	114.6703	KF197038
D. nebulosus sp. nov.	WAM R168638	Moresby Range	WA	-28.6275	114.6703	KF197039
D. nebulosus sp. nov.	WAM R168639	Moresby Range	WA	-28.6275	114.6703	KF197040
D. nebulosus sp. nov.	WAM R168640	Moresby Range	WA	-28.6194	114.6700	KF197041
D. nebulosus sp. nov.	WAM R168641	Moresby Range	WA	-28.6163	114.6619	KF197042
D. ornatus	WAM R100000	False Entrance Well	WA	-26.3333	113.2833	EF532861
D. ornatus	WAM R120060	3 km E Greenough River Mouth	WA	-28.8500	114.6833	EF532859
D. ornatus	WAM R135081	18 km WSW Marchagee	WA	-30.1166	115.9000	FJ665560
D. ornatus	WAM R141587	Gnaraloo Homestead	WA	-23.8211	113.5258	FJ665561
D. ornatus	WAM R99299	False Entrance Well, Shark Bay	WA	-26.3333	113.2833	EF532860
D. polyophthalmus	WAM R129887	Dianella, Perth	WA	-31.9000	115.8669	EF681792
D. polyophthalmus	WAM R157753	Dianella, Perth	WA	-31.8900	115.8764	KF197029
D. pulcher	SAMA R26383	Near Cook	SA	-29.92	130.03	EF532839
D. pulcher	SAMA R32183	47 km N Muckera Roadhouse	SA	-29.58	130.13	EF532840
D. pulcher	WAM R120668	8 km NW Mardathuna Homestead	WA	-24.4289	114.5000	EF681789

APPENDIX 2 Additional material examined. All specimens are from the WAM (prefixes excluded) and from Western Australia. Specimens that were genotyped are indicated by an asterisk.

'*D. polyophthalmus*

R388 (female), R11169 (female), R15244 (female), R15248 (female), R26856 (female), R29194 (female), R49049 (female), R59389 (male), R62172 (female), R128844–5 (males), R129887 (female), *R157753 (female).

D. lateroides sp. nov.

R70694 (male), R70695 (female), R71695 (male), R71720 (male), R71721 (male), R76575 (male), R96850 (female), R103709 (female), R119233 (male), R143367 (male), R156610 (male), R156611 (female), *R166871 (female).

D. nebulosus sp. nov.

R61319 (female), R61371 (female), R128544 (male), R128548 (male), R128550 (female), R128554 (male), R164371 (male), *R165922 (female), *R166719 (female), *R168636 (male), *R168637 (male), *R168641 (male).

D. ornatus

R71105 (male), R71584 (male), R97295 (female), R100000 (female), R116928 (male), R128556 (male), R128559 (female), R128561 (female), R141587 (male), R156907 (female), R164162 (male), R164208 (male), R164209 (male), R165823 (male), R166801 (male).

APPENDIX 3 Paratypes of *Diplodactylus g. granariensis* Storr, 1979 that are now *D. nebulosus* sp. nov. All specimens are from the WAM (prefixes excluded) and from Western Australia.

R22277, R25286, R25287, R27397, R27398, R27399, R49002, R49003, R49015, R49021, R49022, R49023, R49100.