

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

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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 resurrection, 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 existence 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 synonymy 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

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 available localities 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 QIAextractor robot (QIAGEN™) at Museum Victoria and the standard manufacturer 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 55°C. Unpurified products were sent to a genetic services company (Macrogen, Korea) and sequenced in both directions using traditional Sanger Sequencing approaches.

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; Stamatakis 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 subdigital lamellae under fourth finger |
| 4TLam | Number of enlarged rows of subdigital 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 <i>D. calcicolus</i> | 0.063 | | | | | | |
| 2 <i>D. capensis</i> | 0.154 | 0.001 | | | | | |
| 3 <i>D. granariensis</i> | 0.135 | 0.083 | 0.023 | | | | |
| 4 <i>D. ornatus</i> | 0.146 | 0.156 | 0.142 | 0.053 | | | |
| 5 <i>D. polyophthalmus</i> | 0.154 | 0.173 | 0.163 | 0.153 | 0.015 | | |
| 6 <i>D. lateroides</i> sp. nov. | 0.152 | 0.181 | 0.166 | 0.16 | 0.085 | 0.003 | |
| 7 <i>D. nebulosus</i> 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 occurring 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 cloacal 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’

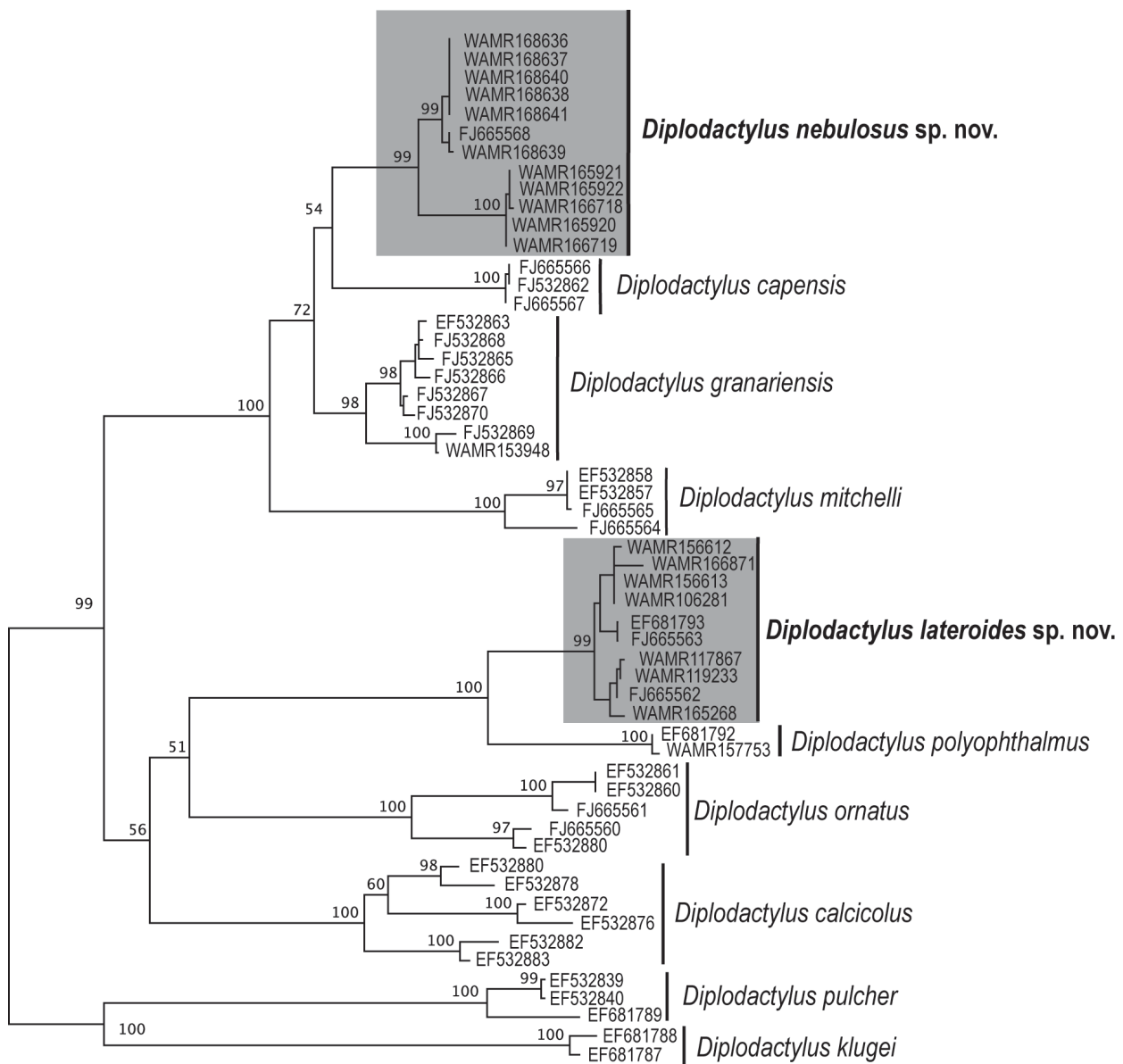


FIGURE 1 Maximum likelihood phylogeny for *Diplodactylus* species found in south-west and coastal Western Australia estimated using 816 base pairs of the mitochondrial *ND2* gene.

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

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

| Character | <i>D. polyopthalmus</i> N: 10♀, 3♂ | <i>D. lateroides</i> sp. nov. N: 7♀, 12♂ | <i>D. nebulosus</i> sp. nov. N: 9♀, 12♂ | <i>D. ornatus</i> 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

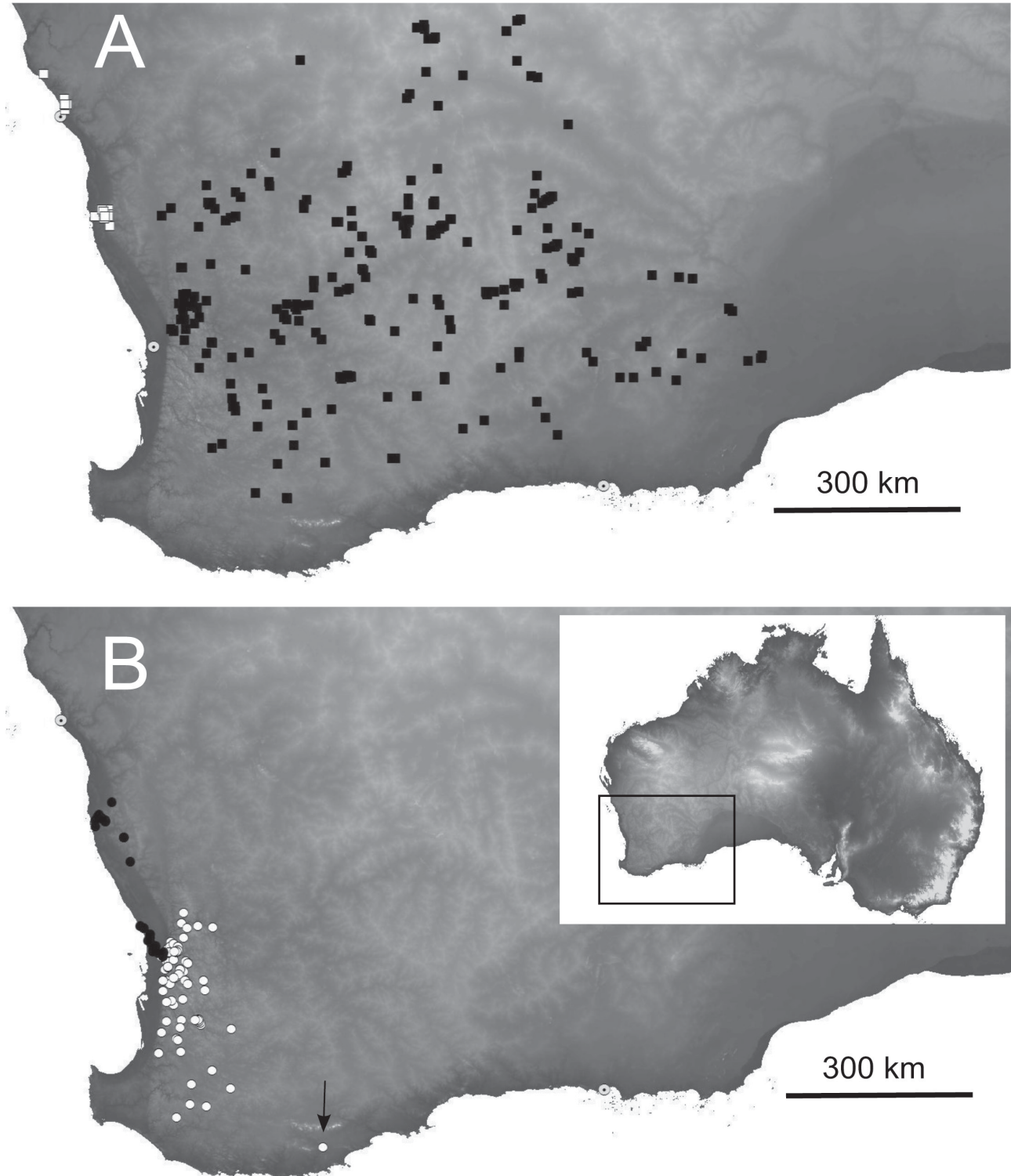


FIGURE 3 Distribution maps of *Diplodactylus* occurring in far south-western Australia. A) *D. nebulosus* sp. nov. – white squares, *D. granariensis* – black squares. B) *D. polyophthalmus* – black circles, *D. lateroides* sp. nov. – white circles. White circles with a black dot represent Geraldton (upper 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 synonymy 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 preloacal pores, numerous (typically >5) cloacal 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

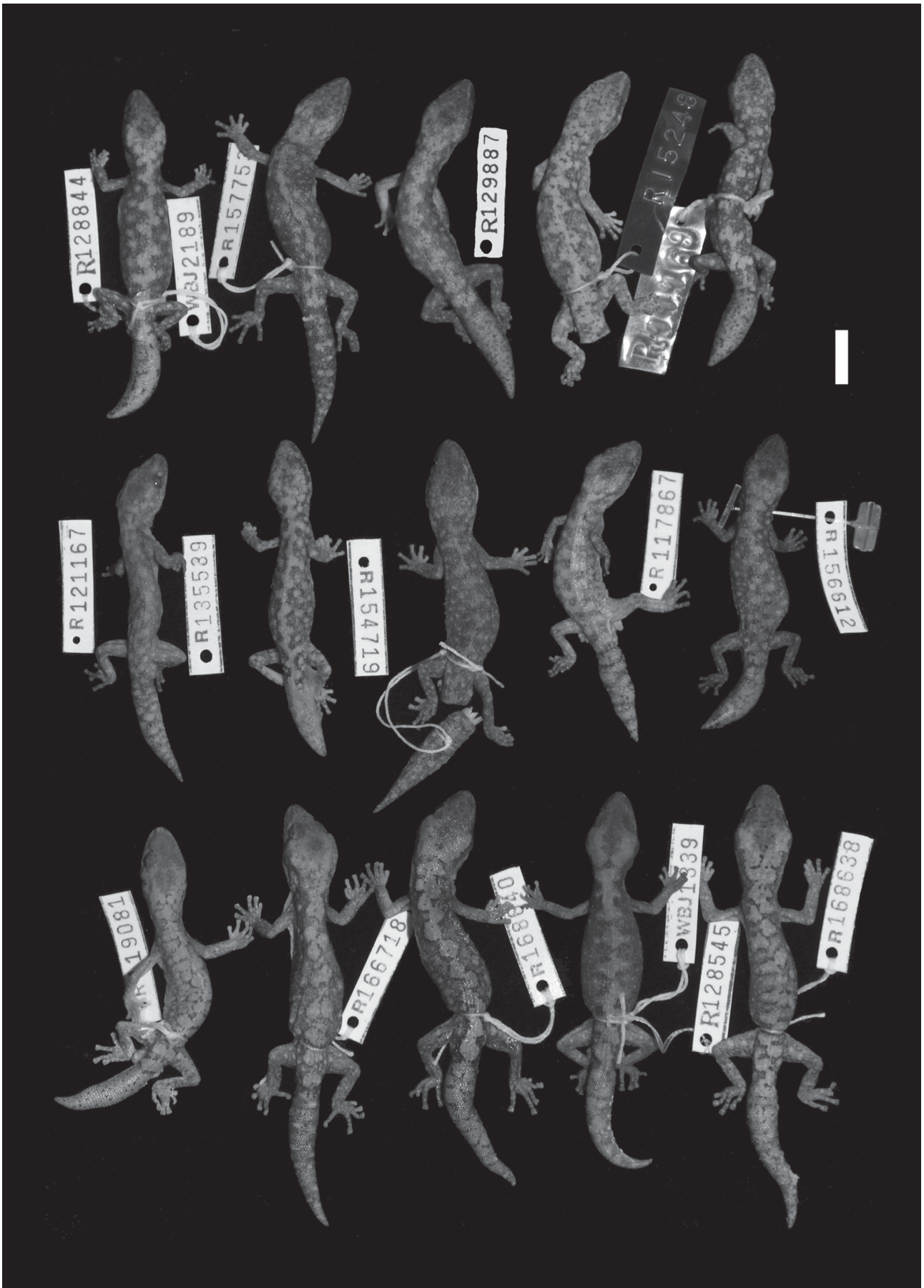


FIGURE 4 Preserved specimens showing variation in dorsal patterning. Top row – *Diplodactylus polyophthalmus*; middle row – *D. lateroides* sp. nov.; bottom row – *D. nebulosus* sp. nov. Scale bar = 1 cm.



FIGURE 5 Lectotype of *Diplodactylus polyophthalmus* Günther (BMNH 672.19.16).

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 ($\text{TailL}\% \text{SVL} = 66.3$), 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 localities 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 differentiated 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 known 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 remnants 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), Coolibberra 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 separated 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 laterioides 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 laterioides sp. nov. can be differentiated 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 laterioides 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 transversely 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 nebulosus* 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 transverse 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 km², 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 phylogeographic 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. kluzei*) 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.

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APPENDIX 1 Specimens details for samples included in genetic analyses.

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

| Species | Registration # | Locality | State | Latitude | Longitude | GenBank |
|-------------------------------|----------------|--------------------------------|-------|----------|-----------|----------|
| <i>D. lateroides</i> sp. nov. | WAM R 166871 | Red Hill | WA | -31.8341 | 116.0783 | KF197031 |
| <i>D. mitchelli</i> | SAMA R60439 | Roy Hill area | WA | -22.75 | 119.92 | FJ665564 |
| <i>D. mitchelli</i> | WAM R 113642 | 37 km NNE Auski Roadhouse | WA | -22.05 | 118.82 | FJ665565 |
| <i>D. mitchelli</i> | WAM R 146632 | 198 km S Port Hedland | WA | -22.1022 | 118.9900 | EF532857 |
| <i>D. mitchelli</i> | WAM R 152704 | Chichester Range | WA | -22.0900 | 118.9919 | EF532858 |
| <i>D. nebulosus</i> sp. nov. | WAM R 119081 | Yetna | WA | -28.6166 | 114.7000 | FJ665568 |
| <i>D. nebulosus</i> sp. nov. | WAM R 165920 | Mount Lesueur | WA | -30.1627 | 115.1992 | KF197032 |
| <i>D. nebulosus</i> sp. nov. | WAM R 165921 | Mount Lesueur | WA | -30.1627 | 115.1992 | KF197033 |
| <i>D. nebulosus</i> sp. nov. | WAM R 165922 | Lesueur National Park | WA | -30.1433 | 115.1817 | KF197034 |
| <i>D. nebulosus</i> sp. nov. | WAM R 166718 | Mount Lesueur | WA | -30.1619 | 115.1992 | KF197035 |
| <i>D. nebulosus</i> sp. nov. | WAM R 166719 | Mount Lesueur | WA | -30.1619 | 115.1992 | KF197036 |
| <i>D. nebulosus</i> sp. nov. | WAM R 168636 | Moresby Range | WA | -28.6275 | 114.6703 | KF197037 |
| <i>D. nebulosus</i> sp. nov. | WAM R 168637 | Moresby Range | WA | -28.6275 | 114.6703 | KF197038 |
| <i>D. nebulosus</i> sp. nov. | WAM R 168638 | Moresby Range | WA | -28.6275 | 114.6703 | KF197039 |
| <i>D. nebulosus</i> sp. nov. | WAM R 168639 | Moresby Range | WA | -28.6275 | 114.6703 | KF197040 |
| <i>D. nebulosus</i> sp. nov. | WAM R 168640 | Moresby Range | WA | -28.6194 | 114.6700 | KF197041 |
| <i>D. nebulosus</i> sp. nov. | WAM R 168641 | Moresby Range | WA | -28.6163 | 114.6619 | KF197042 |
| <i>D. ornatus</i> | WAM R 100000 | False Entrance Well | WA | -26.3333 | 113.2833 | EF532861 |
| <i>D. ornatus</i> | WAM R 120060 | 3 km E Greenough River Mouth | WA | -28.8500 | 114.6833 | EF532859 |
| <i>D. ornatus</i> | WAM R 135081 | 18 km WSW Marchagee | WA | -30.1166 | 115.9000 | FJ665560 |
| <i>D. ornatus</i> | WAM R 141587 | Gnaraloo Homestead | WA | -23.8211 | 113.5258 | FJ665561 |
| <i>D. ornatus</i> | WAM R 99299 | False Entrance Well, Shark Bay | WA | -26.3333 | 113.2833 | EF532860 |
| <i>D. polyphthalmus</i> | WAM R 129887 | Dianella, Perth | WA | -31.9000 | 115.8669 | EF681792 |
| <i>D. polyphthalmus</i> | WAM R 157753 | Dianella, Perth | WA | -31.8900 | 115.8764 | KF197029 |
| <i>D. pulcher</i> | SAMA R26383 | Near Cook | SA | -29.92 | 130.03 | EF532839 |
| <i>D. pulcher</i> | SAMA R32183 | 47 km N Muckera Roadhouse | SA | -29.58 | 130.13 | EF532840 |
| <i>D. pulcher</i> | WAM R 120668 | 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.