

## 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

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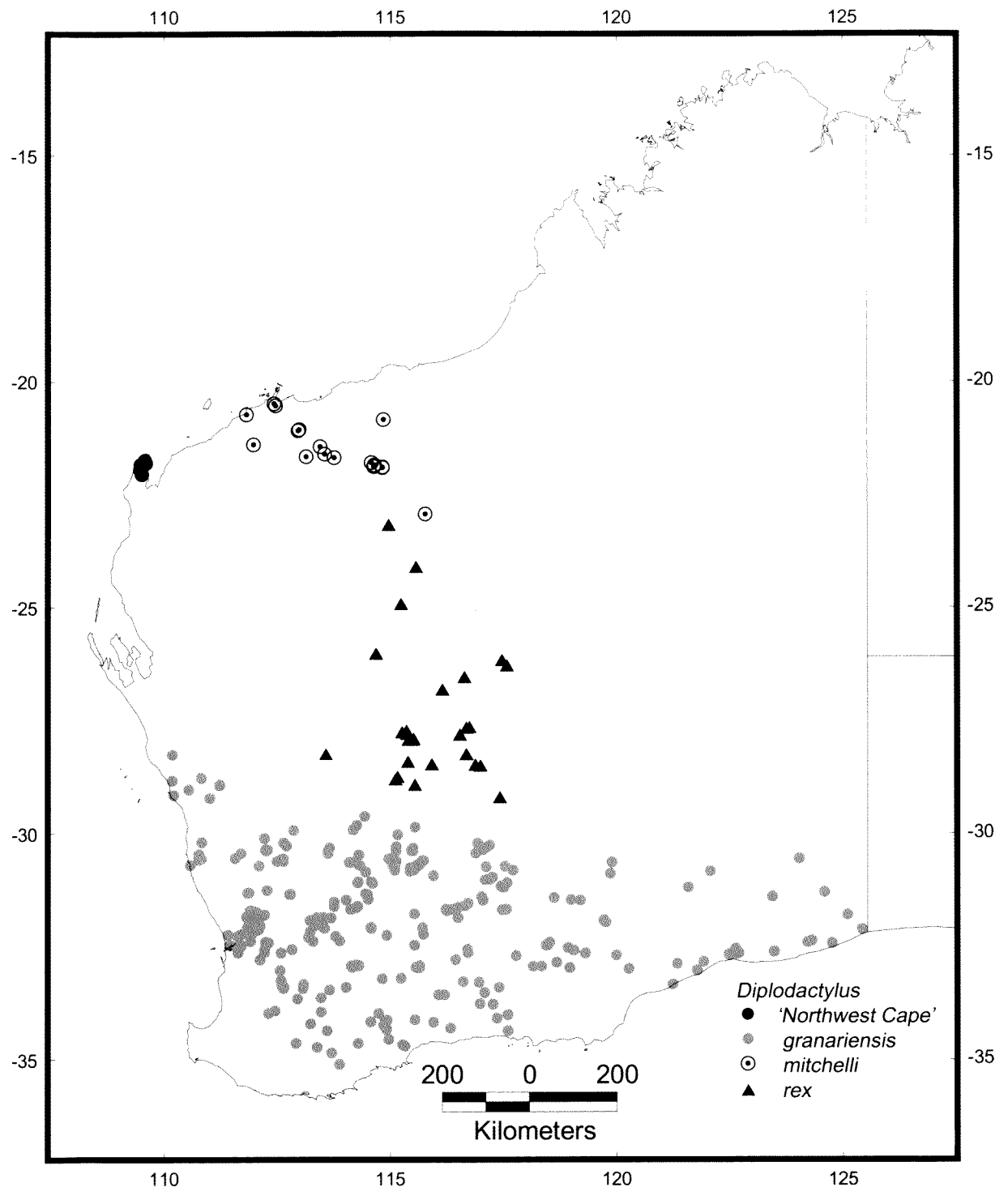
**Abstract** – Stone geckos (*Diplodactylus* spp.) are a small group of moderately robust geckos that occur on hard soils in southern and arid regions of Australia. We present a morphological and molecular assessment of the systematics of *D. g. granariensis*, *D. g. rex* and *D. mitchelli*, including an isolated population of *D. 'mitchelli'* from the Northwest Cape. Genetic data from allozyme analysis and 757bp of the mitochondrial *ND2* gene provided evidence for very recent divergence between the subspecies of *D. granariensis*, despite the morphological distinctiveness of *D. g. rex* from other stone geckos owing to large size, massive head, different pattern and scalation. In contrast, morphological and molecular data indicated that the isolated population of *D. 'mitchelli'* from the Northwest Cape was distinct at the species level and also more closely allied to *D. granariensis*. The new species differs from *D. mitchelli* in having smaller dorsal scales, fewer vertebrae and cloacal spurs, from *D. g. granariensis* in larger size, shorter tail and unincreased rostral scale, from *D. g. rex* by smaller body and head size and from both subspecies by fewer undivided subdigital lamellae, reddish colouration and distinctive dorsal stripe with transverse bands. The Northwest Cape has several other endemic species of reptiles indicating that this region is biogeographically significant and hence of special conservation value.

**Keywords:** Australia, *Diplodactylus mitchelli*, *Diplodactylus g. granariensis*, *D. g. rex*, Pilbara, wheatbelt

### INTRODUCTION

The Australian continent has a diverse gecko fauna stemming from both ancient Gondwanan lineages (Carphodactylidae, Diplodactylidae and Pygopodidae) and more recent arrivals (Gekkonidae) (Han *et al.* 2004). Until recently the most speciose genus of Australian geckos was *Diplodactylus*. The only comprehensive taxonomic treatment of this group was by Kluge (1967), with significant taxonomic changes occurring since then. The arboreal spiny-tailed species were transferred to the genus *Strophurus* (Russell and Rosenberg 1984; Melville *et al.* 2004) and recently Oliver *et al.* (2007a) resurrected the genus *Lucasium* for the clade of more gracile, narrow-toed, long-tailed and highly terrestrial species based on molecular and morphological analyses. The genus *Diplodactylus* is now restricted to a group of species with a distinctive larger jugal, generally shorter tails and larger terminal scancers.

Within the redefined *Diplodactylus* there are thirteen recognized species (Cogger 2000; Wilson and Swan 2003; Bush *et al.* 2007). Recent genetic studies using mtDNA, however, have uncovered considerable evidence for high levels of unrecognized cryptic diversity (Oliver *et al.* 2007a,b). Stone geckos of the genus *Diplodactylus* refer to a moderately robust terrestrial lineage of geckos with primarily a southern distribution. Currently recognized members in Western Australia include *D. g. granariensis*, *D. g. rex*, *D. mitchelli*, *D. ornatus* and *D. polyophthalmus*. Here we focus on the systematics of Western Australian stone geckos from northwestern and central Western Australia. These are *D. mitchelli* (Kluge 1963) from the Pilbara and presumably an isolated population from the Northwest Cape, *D. g. granariensis* (Storr 1979) from the wheatbelt and *D. g. rex* (Storr 1988) which occurs between the previous two taxa (Figure 1). *Diplodactylus*



**Figure 1** Distribution of *Diplodactylus mitchelli*, *D. g. granariensis*, *D. g. rex* and the isolated population of *D. 'mitchelli'* in Western Australia.

*mitchelli* is the most morphologically divergent of these taxa and can be readily diagnosed by its large size, long limbs, vertebral stripe with transverse bars on reddish background colour and enlarged dorsal scales (Storr *et al.* 1990; Cogger 2000). *Diplodactylus granariensis* from southwestern Australia was separated from the widespread *D. vittatus* by Storr (1979). *Diplodactylus g. rex* was described by Storr (1988) and diagnosed on the

basis of its substantially larger size, uncreased rostral and distinctive pattern. At the time of its description, *D. g. rex* was believed to be allopatric from the nominate species. However, further collecting has shown the two taxa to be contiguous with morphology not always showing a clear demarcation between subspecies.

The isolated *Diplodactylus* population from the Northwest Cape was assigned to *D. mitchelli* by

Kluge (1963, 1967), who noted that it differed in possessing smaller dorsal scales and restricted dorsal pattern. The genetic study of Oliver *et al.* (2007a) found that this population was not aligned to *D. mitchelli*, but instead was more closely related to *D. granariensis*. Limited sampling also indicated that there was little genetic support for the recognition of *D. g. rex* as distinct from *D. g. granariensis*. Here we use evidence from two different molecular techniques (mtDNA and allozymes) and morphology to elucidate the relationships and taxonomic status of the currently recognized taxa of northwestern stone geckos, with emphasis on the Northwest Cape population of *D. mitchelli*.

## METHODS

### Materials

Genetic studies were performed using frozen tissue samples in the collection of the Western Australian Museum (WAM) and the South Australian Museum (SAMA). Multiple samples from all key populations were included in order to assess intraspecific geographic variation. Morphological examination was performed using formalin-fixed ethanol-preserved specimens in the WAM collection (Appendix 1).

### Allozyme analyses

Analyses were undertaken on raw allozyme data generated previously for *D. granariensis*, *D. 'NW Cape'*, *D. mitchelli*, and *D. ornatus* (Oliver *et al.* 2007b). All procedures relating to the use of stepwise Principle Co-ordinates Analysis (PCoA) and the estimation of genetic distances follow those detailed therein. Genetic distance matrices for both percent fixed differences (%FD) and Nei's Distance (Nei D) were used to explore the phenetic and phylo-genetic affinities among taxa, the former via UPGMA dendrograms and the latter via NJ networks. Horner and Adams (2007) provide details of how dendrograms and trees were constructed. The level of statistical support for nodes was assessed by non-parametric bootstrapping for 1,000 pseudo-replicates using BASIC computer programs written by M. Adams.

### Mitochondrial DNA

Mitochondrial DNA data were obtained from a subset of the animals used in the allozyme analyses. This sampling included all allozyme localities for nominal *D. mitchelli* and most localities for *D. granariensis*. These data were used to provide an independent assessment of genetic divergence and evolutionary relationships. The final mitochondrial dataset was comprised of 11 nominal *D. granariensis*, 4 *D. mitchelli* and 3 specimens of the

Northwest Cape population. Two specimens of three different species were included as outgroups based on the analyses of Oliver *et al.* (2007b): *D. ornatus*, *D. pulcher* and an undescribed *Diplodactylus* from the southern coast of Australia. The majority of sequences included in this study have already been published in Oliver *et al.* (2007b).

DNA extraction and amplification protocols for the *ND2* gene follow those outlined in Oliver *et al.* (2007a,b). An approximately 900-bp segment of coding region was amplified using the following primers; light strand 5'-GCC CAT ACC CCG AAA ATS TTG-3' (modified from Jennings *et al.* 2003) and heavy 5'-TTA GGG TRG TTA TTT GHG AYA TKC G-3' (Oliver *et al.* 2007b). This fragment of the *ND2* gene has been successfully used to examine intrageneric relationships in many diplodactyline gecko groups (Jennings *et al.* 2003; Melville *et al.* 2004; Pepper *et al.* 2006; Bauer *et al.* 2006; Oliver *et al.* 2007a,b). PCR products were amplified using Hotmaster Taq (Eppendorf) using the following conditions: denaturing 94°C, annealing 55°C and for extension 72°C for 34 amplification cycles. Newly obtained PCR products for this study were sequenced in both directions by the company Macrogen of South Korea. New sequences were aligned with a pre-existing dataset from Oliver *et al.* (2007b) using Se-al (version 1.0µ1; Rambaut, 1996).

Maximum Parsimony (MP) analyses were performed using PAUP (Version 4; Swofford 2000). We used the heuristic search algorithm with 100 random additions to trees. A bootstrap analysis with 500 heuristic pseudoreplicates was carried out to assess the robustness nodes in the MP tree. Bayesian analyses were performed using MrBayes V3.0 (Ronquist and Huelsenbeck 2003). A model of molecular evolution appropriate to our data was determined using MrModeltest (Nylander 2004). Monte Carlo Markov Chain sampling was run for 1,000,000 generations sampling every 100 generations. The burnin was set at 100,000 generations after plotting generation number against likelihood scores indicated that stationarity had been reached well inside this point.

### Morphometrics

Table 1 lists the characters and their abbreviations we measured for all species in the analysis. We also calculated the following ratios: TrunkL/SVL, HeadL/SVL, HeadW/SVL, HeadH/SVL, ArmL/SVL and LegL/SVL and also TailL as a percentage of SVL (TailL/SVL). As body size differed among taxa and sex (see Results), we carried out 2-way ANCOVAs on TrunkL, ArmL, LegL, HeadL, HeadW, HeadH, NoIO and NoSC with SVL as a covariate. In addition, we obtained radiographs of four individuals of *D. mitchelli* from the Pilbara (WAM R14823, R84458, R113618, R113642) and the

**Table 1** Meristic characters and their abbreviations used in this study.

SVL	Snout-vent length
TL	Tail length
TrunkL	Trunk length from axilla to groin
TailW	Tail width at widest point on original tails
ArmL	Foreleg length from elbow to tip of 4 <sup>th</sup> finger
LegL	Tibia length from upper surface of knee to tip of 4 <sup>th</sup> toe
HeadL	Head length from tip of snout to retroarticular process
HeadW	Head width at widest point
HeadH	Head height at highest point
OrbL	Orbit length – maximum
NarEye	Distance from nare to anterior corner of eye
SnEye	Distance from snout to anterior corner of eye
EyeEar	Distance from posterior edge of eye to anterior margin of ear
INar	Internarial distance
IO	Interorbital width at centre of eyes
SupLab	Number of supralabial scales
InfLab	Number of infralabial scales
Rcrease?	Whether the rostral was smooth or creased at all
CreaseL	Proportional length of the crease
IntNar	Number of internarial scales
NoIO	Number of scales between center of orbits
NoSC	Number of subcaudal scales from fracture plane to tip
PostNas	Number of postnasal scales
RelLab	Relative height of 1 <sup>st</sup> and 2 <sup>nd</sup> labial scales: 1 – 1 <sup>st</sup> > 2 <sup>nd</sup> ; 2 – 1 <sup>st</sup> >= 2 <sup>nd</sup> ; 3 – 1 <sup>st</sup> = 2 <sup>nd</sup> ; 4 – 1 <sup>st</sup> <= 2 <sup>nd</sup> ; 5 – 1 <sup>st</sup> < 2 <sup>nd</sup>
CSpurs	Average number of enlarged cloacal spurs
4FL	4 <sup>th</sup> finger length from base to tip
4FW	4 <sup>th</sup> finger width near distal joint
4FscanW	Width of scansor of 4 <sup>th</sup> finger
4FLam1	Number of undivided lamellae on 4 <sup>th</sup> finger
4FLam2	Total number of lamellae on 4 <sup>th</sup> finger
4TL	4 <sup>th</sup> toe length from base to tip
4TW	4 <sup>th</sup> toe width near distal joint
4TscanW	Width of scansor of 4 <sup>th</sup> toe
4TLam1	Number of undivided lamellae on 4 <sup>th</sup> toe
4TLam2	Total number of lamellae on 4 <sup>th</sup> toe
MenL/W	Ratio of length/width of mental scale

Northwest Cape (WAM R81328, R102843, R132466, R132467) for vertebrae counts.

## RESULTS

### Allozyme electrophoresis

The final allozyme dataset comprised genotypes for 36 animals at 38 putative loci. An initial PCoA based on all specimens (Figure 2A) revealed the presence of three primary genetic groups, corresponding to *D. ornatus*, *D. mitchelli*, and the *D. granariensis* complex. The five *D.* 'NW Cape' specimens fell unequivocally into the latter group, demonstrating that their principal genetic affinities lie with *D. granariensis* rather than *D. mitchelli*. Follow-up PCoAs on all three primary genetic groups found no evidence for distinctive subgroups within *D. ornatus* or *D. mitchelli* (analyses not

shown), but did reveal clearly defined subgroups within the *D. granariensis* complex (Figure 2B). These subgroups correspond to 'NW Cape' (which was separated from true *D. granariensis* by the first dimension), and the two subspecies *D. g. rex* and *D. g. granariensis*. A final PCoA involving only individuals of *D. granariensis* (analysis not shown) provided additional support for the observation in Figure 2B of a primary genetic dichotomy within *D. granariensis* which concords with the currently-recognized subspecies.

In summary, stepwise PCoA unreservedly placed each individual into one of five diagnosable units – the four taxa already described plus the distinctive 'NW Cape' form. Allele frequencies at all polymorphic loci and pairwise genetic distances for these five taxa are presented in Tables 2 and 3, respectively. The three described species are diagnosable from one another by a minimum of

**Table 2** Allozyme frequencies for the five taxa under investigation. For polymorphic loci, the frequencies of all but the rarer/rarest alleles are expressed as percentages and shown as superscripts (allowing the frequency of each rare allele to be calculated by subtraction from 100%). Alleles joined without being separated by a comma all shared the frequency indicated. A dash indicates no genotypes assignable at this locus. Taxon codes as per Figure 1. The maximum number of haploid genomes sampled for each taxon in shown in brackets. Invariant loci: *Ak*, *Mdh*, *Ndpk*, and *Srdh*.

Locus	ORN (8)	MITCH (14)	CAPE (10)	REX (20)	GRAN (20)
<i>Acon-1</i>	a	a <sup>57</sup> ,d	d	d <sup>50</sup> ,b <sup>15</sup> ,f	b <sup>70</sup> ,a <sup>15</sup> ,cde <sup>5</sup>
<i>Acon-2</i>	a <sup>75</sup> ,b <sup>13</sup> ,d	b <sup>57</sup> ,d	d	d <sup>15</sup> ,c <sup>35</sup> ,e	e <sup>15</sup> ,d <sup>15</sup> ,bcfg <sup>5</sup>
<i>Acp</i>	a <sup>88</sup> ,b	a	a	a	a
<i>Acyc</i>	c <sup>62</sup> ,a	a	a	a	a <sup>95</sup> ,b
<i>Adh-2</i>	b	b	b	b <sup>90</sup> ,a	b
<i>Dia</i>	c <sup>88</sup> ,d	a <sup>86</sup> ,c	a	a	a <sup>95</sup> ,b
<i>Enol</i>	b	b	b	b <sup>50</sup> ,a <sup>15</sup> ,c	b
<i>Est</i>	b <sup>87</sup> ,a	d <sup>86</sup> ,c	c	c	c <sup>90</sup> ,b
<i>Fdp</i>	b	b <sup>93</sup> ,a	b	b	b
<i>Fum</i>	b	b <sup>86</sup> ,a	b	b <sup>60</sup> ,a	b <sup>90</sup> ,a
<i>G6pd</i>	a	b	b	b <sup>85</sup> ,a <sup>15</sup>	b
<i>Gda</i>	b <sup>87</sup> ,a	a	a	a	a
<i>Glo</i>	b <sup>87</sup> ,a	b	b	b	b
<i>Got-1</i>	b <sup>87</sup> ,a	b	b	b	b
<i>Got-2</i>	b	b	a <sup>70</sup> ,b	b <sup>95</sup> ,c	b
<i>Gpi</i>	b <sup>88</sup> ,c	b	b	b	b <sup>95</sup> ,a
<i>Guk</i>	b	b	d <sup>90</sup> ,b	b	b <sup>90</sup> ,a <sup>5</sup> ,c
<i>Hbdh</i>	-	a	b	c <sup>60</sup> ,b <sup>40</sup>	b <sup>90</sup> ,d <sup>10</sup>
<i>Idh-1</i>	b <sup>87</sup> ,a	b	b	b	b
<i>Idh-2</i>	a	b	a <sup>90</sup> ,b	a <sup>95</sup> ,b	a <sup>65</sup> ,b
<i>Lap</i>	c <sup>67</sup> ,b <sup>17</sup> ,d	c	c <sup>67</sup> ,a	c	c <sup>95</sup> ,b
<i>Ldh-1</i>	b	b	b	b <sup>95</sup> ,a	b
<i>Ldh-2</i>	b	a	a	a	a
<i>Me-1</i>	b <sup>75</sup> ,d	c	b <sup>50</sup> ,d <sup>40</sup> ,e	b <sup>50</sup> ,a <sup>45</sup> ,d	b <sup>65</sup> ,d
<i>Me-2</i>	c <sup>75</sup> ,a	c	b	cd <sup>45</sup> ,ab <sup>5</sup>	c <sup>35</sup> ,d <sup>25</sup> ,ab <sup>20</sup>
<i>Mpi</i>	b	b	b	b <sup>90</sup> ,ac <sup>5</sup>	b <sup>95</sup> ,a
<i>PepA-1</i>	b	a	c	c <sup>90</sup> ,ad <sup>5</sup>	a <sup>70</sup> ,c
<i>PepB</i>	e	d	d	h <sup>65</sup> ,d <sup>30</sup> ,a	f <sup>30</sup> ,b <sup>25</sup> ,dg <sup>15</sup> ,c <sup>10</sup> ,a
<i>Pgam</i>	a	b <sup>93</sup> ,a	b	b <sup>90</sup> ,a	a <sup>50</sup> ,b
<i>6Pgd</i>	c <sup>75</sup> ,e	a	c	c <sup>90</sup> ,d	c <sup>90</sup> ,bd <sup>5</sup>
<i>Pgm-1</i>	f <sup>50</sup> ,g <sup>25</sup> ,b <sup>13</sup> ,d	g <sup>79</sup> ,h <sup>14</sup> ,f	f <sup>90</sup> ,d	f <sup>75</sup> ,d <sup>15</sup> ,ag <sup>5</sup>	f <sup>45</sup> ,b <sup>20</sup> ,eg <sup>10</sup> ,acd <sup>5</sup>
<i>Pgm-2</i>	a	b	b	b	b <sup>95</sup> ,c
<i>Sod</i>	a <sup>73</sup> ,c	b	a	a	a
<i>Tpi</i>	b	a	a	a	a

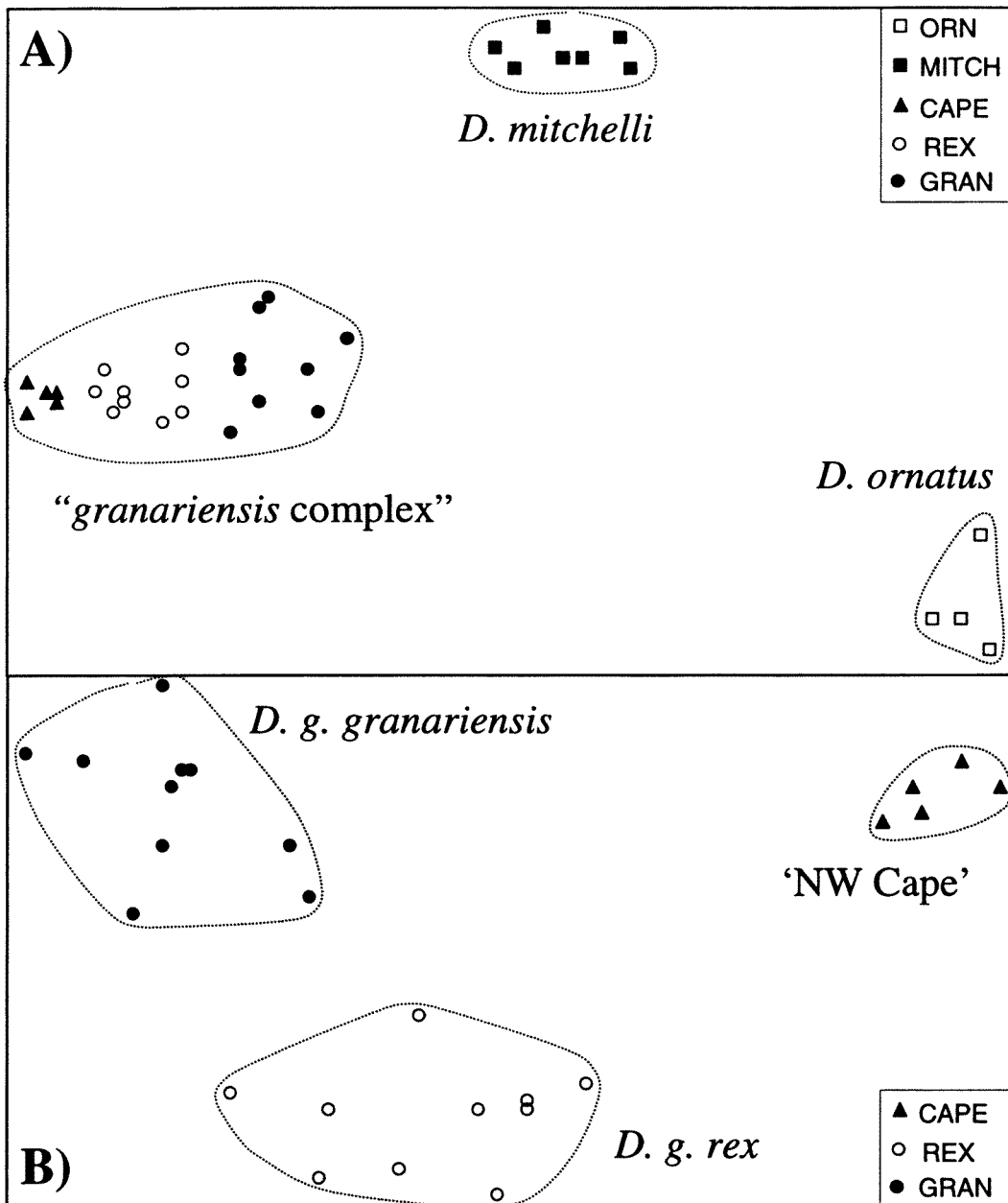
**Table 3** Pairwise genetic distances among the five taxa. Lower triangle = %FD (allowing a 10% tolerance for shared alleles, see Oliver *et al.* [2007]); upper triangle = Nei Ds.

Taxon	ORN	MITCH	CAPE	REX	GRAN
ORN	-	0.53	0.54	0.43	0.36
MITCH	32	-	0.32	0.26	0.21
CAPRE	32	24	-	0.11	0.12
REX	24	16	5	-	0.07
GRAN	22	11	5	0	-

four and a maximum of 12 fixed differences (range 11–32 %FD, Table 2), whereas the two subspecies of *D. granariensis* displayed no fixed differences between each other and only a modest Nei D of 0.07. The 'NW Cape' taxon, while clearly allied genetically with *D. granariensis* to the exclusion of

*D. mitchelli*, nevertheless displays two fixed differences (5%FD, Table 3) involving three loci (*Acon-1*, *Guk* and *Me-2*; Table 2) when compared to both *D. g. rex* and *D. g. granariensis*. A further three loci display major differences in allele frequency ( $p > 50\%$  for *Acon-2*, *Got-2*, and *PepB*); Table 2) between 'NW Cape' and both subspecies of *D. granariensis*.

Figure 3 contrasts the overall genetic similarities among the five taxa (as assessed by UPGMA analyses) with their comparative phylogenetic affinities, as assessed using the NJ approach). Although the 'NW Cape' taxon is genetically less similar to the two subspecies of *D. granariensis* than either is from the other (Figure 2B), the phylogenetic analyses suggest that its genetic affinities lie within *D. granariensis* in general and in particular with the geographically more proximate northern subspecies of *D. g. rex*.



**Figure 2** Summary of Stepwise PCoA of western *Diplodactylus*, demonstrating how individuals were assigned to taxa on genetic criteria. A) Initial PCoA on all 36 individuals. The relative PCoA scores have been plotted for the first (X-axis) and second (Y-axis) dimensions, which individually explained 24% and 22% respectively of the total multivariate variation. B) Follow-up PCoA on the 25 individuals comprising the *D. granariensis* complex of A). The first and second dimensions individually explained 22% and 17% respectively of the total multivariate variation. Taxon code: ORN = *D. ornatus*, MITCH = *D. mitchelli*, CAPE = ‘NW Cape’, REX = *D. g. rex*, GRAN = *D. g. granariensis*.

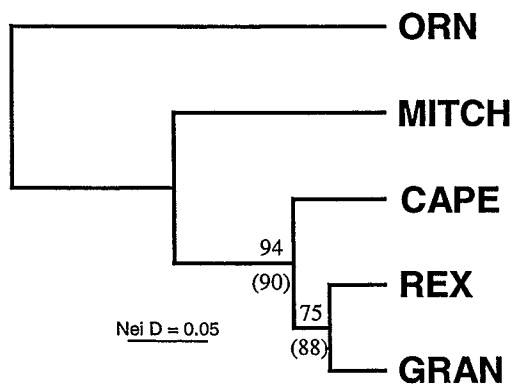
### Mitochondrial DNA

The final aligned sequence comprised 749 base pairs from within the coding region of the *ND2* gene. Of these sites, 474 were constant, 234 were variable and parsimony informative and 41 were variable and not parsimony informative. A single three base pair indel was present in all samples of *D. mitchelli*. MrModeltest indicated that the most appropriate model of molecular evolution for our dataset was GTR+I+G.

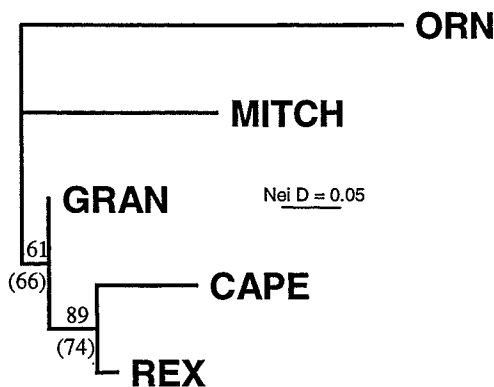
Both maximum parsimony and Bayesian analyses

identified three major lineages within the *Diplodactylus* populations of interest; these correspond to *D. mitchelli*, the Northwest Cape population and both subspecies of *D. granariensis* (Figure 4). In all analyses these three lineages formed a strongly supported clade exclusive to all outgroups. Relationships among the three lineages were less clearly resolved. However there was a tendency for *D. mitchelli* to be most divergent, and the Northwest Cape population and *D. g. granariensis* to be sister taxa.

## A) UPGMA



## B) NJ



**Figure 3** A comparison of the genetic and phylogenetic affinities of western *Diplodactylus*, based on Nei Distances. Analyses based on %FD values (not presented) displayed the same arrangement of nodes. Taxon codes as per Figure 2. Bootstrap values above 60% are shown for all nodes (bracketed values below the branch are those obtained using %FD). A) UPGMA dendrogram. B) NJ tree.

The Northwest Cape population showed very little intraclade genetic diversity, differing by a single change in one individual. Within *D. mitchelli*, one individual was notably divergent from the other three which were almost identical. Within *D. granariensis*, genetic divergences were discordant with the current subspecific taxonomy. This lineage was divided into two strongly supported clades, one is represented by only two animals from the western edge of the Darling Range near Perth (Bindoon), while the other occupies all of the species' distribution to the east of the Darling Range. Animals assigned to *D. g. rex* formed a very

shallow clade nested within deeper lineages assigned to *D. g. granariensis*.

## Morphometrics

Table 4 compares the four taxa for the morphological characters measured with the results of the statistical analyses. Sex had an effect on SVL, TrunkL, ArmL and LegL with females being significantly longer than males for these characters. There were no other sex differences for the other characters. However, SVL was a significant covariate for most of the morphological characters tested (Table 4). *Diplodactylus mitchelli* was the largest taxon, followed by *D. g. rex*, *D. 'NW Cape'* and *D. g. granariensis*. In contrast, *D. g. granariensis* had the relatively longest tail with the most supracaudal scales, followed by *D. 'NW Cape'*, *D. g. rex* and *D. mitchelli* with a very short tail with fewer, larger scales. Limb length was also significantly different among species with both *D. mitchelli* and *D. g. rex* with longer arms and legs than *D. 'NW Cape'* and *D. g. granariensis*, although limb length as a proportion of SVL showed no strong trends. *Diplodactylus g. rex* had a much more massive head for all of the measures for head size, whereas *D. mitchelli* had an elongate head that was dorsoventrally compressed. The number of interorbital scales also varied, with *D. mitchelli* having fewer (owing to large scale size) and *D. g. granariensis* having much more numerous (and smaller) scales.

Some scale characters also showed differences among taxa. Rostral scales were almost always slightly creased in *D. mitchelli* and *D. g. granariensis*, but rarely so for *D. 'NW Cape'* and *D. g. rex* (reflected also in the length of the crease). *Diplodactylus mitchelli* was also notable for having a greater number of cloacal spurs and wider scansors than the other taxa. There were some differences with subdigital lamellae, with *D. mitchelli* and *D. 'NW Cape'* having fewer but with a higher proportion of undivided lamellae than both subspecies of *D. granariensis*. There were no differences among the four taxa in labial scales, mental scale ratios or other characters commonly used as diagnostic traits in geckos (Table 4). Vertebral counts for *D. mitchelli* from the Pilbara were all 26 (N = 4) whereas for the Northwest Cape population they were all 25 (N = 4).

Colour and pattern of the four taxa also differed. The two subspecies of *D. granariensis* have a strong to slightly scalloped vertebral stripe, whereas both *D. mitchelli* and *D. 'NW Cape'* both have a more broken stripe with short transverse bars. The ground colour of *D. g. granariensis* is a dark brown to almost black, *D. g. rex* is much paler and *D. mitchelli* and *D. 'NW Cape'* have a ground colour imbued with a rich red.

**Table 4** Summaries of characters and ratios measured for *Diplodactylus*. Mean±S.D. (range). Sample sizes are listed in column headings, unless noted for individual characters below. See Table 1 for abbreviations. SVL was tested with a 2-way ANOVA. 2-way ANCOVAs (factors – species and sex, covariate – SVL) were carried out (see text for explanation) and reported in the last column. All species X sex interaction terms were not significant with alpha = 0.05. Key: NS – not significant: P > 0.10, \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001, \*\*\*\* P < 0.0001.

Character	<i>D. 'Cape Range'</i> N = 19	<i>D. mitchelli</i> N = 22	<i>D. g. granariensis</i> N = 32	<i>D. g. rex</i> N = 27	Statistics
SVL	Female (N = 9): 60.7±3.4 (56.0-66.5) Males (N = 10): 52.2±4.2 (43.0-57.5)	Female (N = 9): 65.5±7.5 (53.0-77.0) Males (N = 13): 63.3±5.7 (47.5-71.5)	Female (N = 12): 55.7±5.5 (47.0-62.0) Males (N = 20): 53.4±3.6 (44.0-61.0)	Female (N = 12): 63.4±7.9 (49.0-72.0) Males (N = 15): 58.9±4.9 (51.0-67.0)	Spp. – F <sub>3,95</sub> = 16.834**** Sex – F <sub>1,95</sub> = 13.497****
TrunkL	Female (N = 7): 27.2±3.4 (23.7-32.2) Males (N = 12): 23.1±1.8 (20.1-25.9)	Female (N = 9): 31.5±4.3 (23.4-38.4) Males (N = 13): 27.7±3.2 (18.6-31.0)	Female (N = 12): 25.0±2.8 (29.0-39.0) Males (N = 2): 22.7±2.9 (16.9-28.7)	Female (N = 12): 28.4±3.7 (20.8-32.5) Males (N = 15): 25.2±2.7 (20.9-30.3)	Spp. – F <sub>3,92</sub> = 1.704 <sup>NS</sup> Sex – F <sub>1,92</sub> = 11.410** SVL – F <sub>1,92</sub> = 185.573****
TailL	30.6±3.2 (25.0-34.0) N = 8	32.3±3.9 (25.0-38.0) N = 13	33.0±3.7 (22.0-39.0) N = 29	34.5±4.8 (24.0-42.0) N = 20	Spp. – F <sub>3,60</sub> = 15.699**** Sex – F <sub>1,60</sub> = 1.756 <sup>NS</sup> SVL – F <sub>1,60</sub> = 57.544****
ArmL	13.9±0.8 (11.5-14.9) N = 18	16.7±1.2 (13.8-18.5) N = 21	13.6±0.9 (11.9-15.0) N = 31	15.8±1.4 (12.7-17.7)	Spp. – F <sub>3,91</sub> = 24.043**** Sex – F <sub>1,91</sub> = 5.842* SVL – F <sub>1,91</sub> = 171.055****
LegL	17.0±0.9 (14.1-18.0) N = 16	20.5±1.6 (16.5-22.8) N = 21	16.5±1.1 (14.7-18.5) N = 30	19.1±1.7 (15.7-21.5) N = 26	Spp. – F <sub>3,87</sub> = 16.740**** Sex – F <sub>1,87</sub> = 6.320* SVL – F <sub>1,87</sub> = 91.514****
HeadL	15.7±1.2 (12.2-17.3)	17.2±1.3 (14.1-19.3)	15.0±0.8 (13.3-16.4)	17.3±1.7 (14.3-20.0)	Spp. – F <sub>3,94</sub> = 13.385**** Sex – F <sub>1,94</sub> = 0.092 <sup>NS</sup> SVL – F <sub>1,94</sub> = 337.651****
HeadW	10.5±1.0 (8.3-12.3) N = 18	11.7±1.1 (9.0-13.4) N = 21	10.7±0.8 (8.9-12.3)	12.7±1.4 (10.0-15.7)	Spp. – F <sub>3,92</sub> = 23.915**** Sex – F <sub>1,92</sub> = 2.890 <sup>NS</sup> SVL – F <sub>1,92</sub> = 128.543****
HeadH	7.1±0.6 (5.1-8.1) N = 18	7.6±0.7 (6.0-8.8) N = 21	6.8±0.6 (5.1-7.8)	8.4±0.9 (7.0-10.4)	Spp. – F <sub>3,92</sub> = 21.324**** Sex – F <sub>1,92</sub> = 0.579 <sup>NS</sup> SVL – F <sub>1,92</sub> = 55.967****



NoIO	35±2 (32-38) N = 18	32±2 (29-39) N = 10	39±2 (35-44)	38±2 (34-45)	Spp. - $F_{3,92} = 41.241^{****}$ Sex - $F_{1,92} = 0.200^{NS}$ SVL - $F_{1,92} = 0.152^{NS}$
NoSC	59±3 (54-63) N = 11	38±4 (31-46) N = 13	74±6 (63-84) N = 25	60±3 (55-67) N = 20	
TailW	6.2±1.1 (4.6-8.0) N = 10	9.4±1.2 (6.7-11.3) N = 12	6.4±1.0 (4.6-8.0) N = 10	7.6±1.0 (5.8-9.5) N = 21	
OrbL	4.3±0.3 (3.7-4.9) N = 18	4.6±0.4 (3.4-5.2)	4.2±0.4 (3.6-4.9) N = 31	4.5±0.5 (3.8-5.8)	
NarEye	4.4±0.4 (3.7-5.0) N = 18	5.0±0.4 (4.2-5.5)	4.4±0.4 (3.9-5.6)	5.0±0.5 (3.9-6.5)	
SnEye	6.1±0.5 (4.9-6.8) N = 18	6.8±0.5 (5.9-7.9)	5.9±0.4 (5.0-6.6)	6.6±0.6 (5.3-7.9)	
EyeEar	5.9±0.6 (4.6-6.8) N = 18	6.3±0.8 (4.7-8.3)	5.4±0.4 (4.5-6.2)	6.4±0.8 (5.0-8.0)	
INar	1.9±0.1 (1.6-2.1)	2.1±0.2 (1.8-2.3)	1.9±0.1 (1.7-2.1)	2.0±0.2 (1.6-2.3)	
IO	5.3±0.5 (4.1-6.0) N = 18	5.9±0.4 (5.1-6.5)	5.4±0.4 (4.7-6.2) N = 27	6.0±0.6 (4.9-6.8) N = 25	
SupLab	11.0±0.7 (10-12)	11.4±0.8 (10-13)	11.9±0.9 (10-15)	11.7±0.9 (10-13)	
InfLab	10.6±1.0 (10-12)	11.3±0.9 (10-13)	11.9±0.9 (10-15)	11.3±0.9 (10-13)	
Rcrease?	3/19	10/10	32/32	4/27	
CreaseL	0.03±0.08 (0-0.25)	0.25±0.16 (0-0.5)	0.32±0.10 (0.125-0.5)	0.06±0.13 (0-0.5)	

Table 4 (cont.)

Character	<i>D. 'Cape Range'</i> N = 19	<i>D. mitchelli</i> N = 22	<i>D. g. granariensis</i> N = 32	<i>D. g. rex</i> N = 27	Statistics
IntNar	3/19	6/22	4/32	3/27	
PostNas	2.82±0.51 (2-4)	2.48±0.50 (2-3)	3.05±0.32 (2-3)	3.06±0.63 (1-4)	
RelLab	4.26±0.87 (3-5)	3.05±1.46 (1-5)	3.44±1.01 (1-5)	2.89±1.05 (1-5)	
CSpurs	5.2±0.4 (5-6) N = 10	7.3±1.0 (5.5-9.5) N = 13	5.3±0.9 (3-7) N = 20	5.1±1.3 (3.5-8.5) N = 15	
4FL	3.8±0.2 (3.6-4.1) N = 13	4.5±0.5 (3.6-5.3) N = 20	3.6±0.3 (3.1-4.2) N = 24	4.1±0.4 (3.4-4.7) N = 16	
4FW	0.7±0.1 (0.5-0.9) N = 13	0.9±0.1 (0.7-1.1) N = 21	0.7±0.1 (0.6-0.9) N = 25	0.8±0.1 (0.6-0.9) N = 18	
4FscanW	1.2±0.1 (1.1-1.4) N = 12	1.5±0.2 (1.1-1.8) N = 21	1.1±0.1 (0.9-1.3) N = 25	1.1±0.1 (0.8-1.3) N = 17	
4FLam1	6.1±0.3 (6-7) N = 13	6.0±0.5 (5-7) N = 21	4.9±1.2 (3-7) N = 27	4.6±0.8 (4-6) N = 19	
4FLam2	6.2±0.4 (6-7) N = 13	6.5±0.6 (5-7) N = 21	7.0±0.7 (6-8) N = 27	7.2±0.6 (6-8) N = 19	
4TL	4.3±0.1 (4.1-4.4) N = 9	5.3±0.5 (4.5-6.2) N = 19	4.4±0.3 (3.9-5.0) N = 20	4.9±0.5 (4.1-5.5) N = 11	
4TW	0.8±0.1 (0.6-0.9) N = 11	0.9±0.1 (0.7-1.2) N = 21	0.8±0.1 (0.6-0.9) N = 22	0.9±0.1 (0.6-1.1) N = 16	

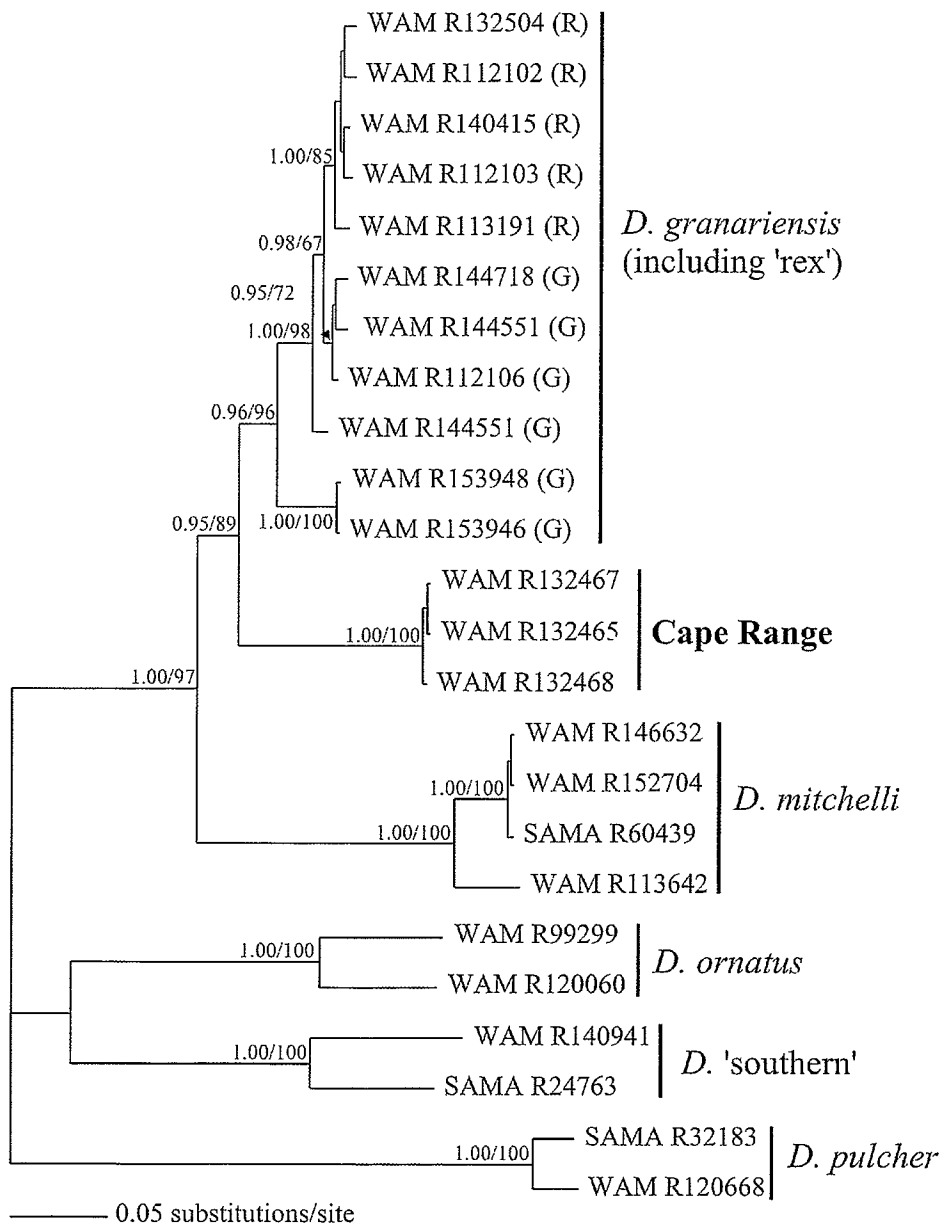
4TscanW	1.4±0.1 (1.2-1.6) N = 11	1.7±0.2 (1.3-2.0) N = 21	1.2±0.2 (1.0-1.4) N = 22	1.3±0.2 (0.9-1.6) N = 18
4TLam1	7.2±0.9 (6-9) N = 13	6.8±1.5 (3-8) N = 21	5.0±1.5 (3-9) N = 27	5.2±1.0 (3-8) N = 18
4TLam2	7.9±0.7 (7-9) N = 13	7.9±0.6 (7-9) N = 21	8.7±0.9 (7-11) N = 27	8.9±0.6 (8-10) N = 18
MenL/W	1.2±0.1 (1.1-1.4)	1.3±0.2 (1.1-1.7) N = 10	1.1±0.2 (0.8-1.8) N = 31	1.3±0.2 (0.9-1.8)
TrunkL/SVL	0.44±0.03 (0.40-0.49) N = 17	0.45±0.03 (0.39-0.53)	0.43±0.04 (0.36-0.52)	0.44±0.03 (0.37-0.50)
HeadL/SVL	0.28±0.01 (0.26-0.30) N = 19	0.27±0.03 (0.25-0.30)	0.28±0.02 (0.25-0.32)	0.28±0.01 (0.26-0.31)
HeadW/SVL	0.19±0.01 (0.16-0.20) N = 18	0.18±0.01 (0.16-0.19) N = 21	0.20±0.01 (0.17-0.23)	0.21±0.02 (0.18-0.24)
HeadH/SVL	0.13±0.01 (0.11-0.14) N = 18	0.12±0.01 (0.10-0.14) N = 21	0.13±0.01 (0.09-0.16)	0.14±0.01 (0.11-0.16)
ArmL/SVL	0.25±0.02 (0.22-0.29) N = 18	0.26±0.02 (0.25-0.30) N = 21	0.25±0.02 (0.23-0.32) N = 31	0.26±0.01 (0.24-0.29)
LegL/SVL	0.30±0.02 (0.26-0.33) N = 16	0.32±0.02 (0.28-0.36) N = 21	0.31±0.03 (0.27-0.38) N = 30	0.31±0.02 (0.27-0.36) N = 26
Tail%SVL	56.6±2.2 (52.4-60.0) N = 8	49.4±3.9 (43.9-56.7) N = 13	63.9±4.4 (55.7-71.0) N = 24	58.1±6.1 (45.2-70.2) N = 21

**DISCUSSION**

Our molecular and morphological results were not always consistent with current taxonomic arrangements, specifically not strongly supporting the subspecies within *D. granariensis* and supporting the Northwest Cape taxon as distinct from *D. mitchelli* and *D. granariensis*. We review all of the evidence below to arrive at our taxonomic conclusions.

Despite consistent morphological differences and allozyme profiles, there was only weak support for *D. g. rex* as a valid subspecies within *D. granariensis* with mtDNA data which indicated very recent divergence. Neither molecular dataset provided diagnostic markers which could unequivocally identify animals as belonging to one

or the other subspecies or a hybrid between the two. Moreover, the two different molecular techniques presented a different picture of where the most significant phylogeographic split occurs, with allozymes indicating a split to distinguish northern versus southern populations (i.e., generally concordant with the subspecific taxonomy; Figure 2B), whereas mtDNA placed it across either side of the Darling Range (Figure 4), with a further divide separating wheatbelt *D. g. granariensis* from northern *D. g. rex*. Although the allozyme data mirrored the morphological differences, the mtDNA patterns indicated that *D. g. rex* populations were more closely related to *D. g. granariensis* from the wheatbelt; furthermore, the Darling Range (near Perth) population of *D. g.*



**Figure 4** Bayesian consensus tree of inferred phylogenetic relationships of northwestern *Diploactylus* based on 749 bp of the mitochondrial *ND2* gene. Posterior probabilities above 95% and bootstrap support values above 50% are shown for major nodes.

*granariensis* formed the sister taxon to wheatbelt *D. g. granariensis* and *D. g. rex*. All branches were very shallow relative to other species in our analysis.

The subspecies *D. g. rex* was named by Storr (1988) based on a combination of unusual characters possessed by the populations to the north of typical *D. g. granariensis* (Figure 1). These characters include large body size, increased rostral scale and more bold vertebral stripe with little pattern on the sides. The relatively low level of mtDNA differentiation between populations of *D. g. rex* and *D. g. granariensis* contrasts strikingly with significant morphological differentiation. Further work on this interesting problem is continuing, as this may be an instance of active speciation. The evolution of the massive head in *D. g. rex* suggests that the maximum prey size that is able to be taken may be a factor, although other hypotheses such as phenotypic plasticity, allometry and character displacement could play a role.

Our second finding was that the Northwest Cape population of *D. 'mitchelli'* was distinct from *D. mitchelli* from the Pilbara. The genetic data strongly supported a closer relationship with *D. granariensis* than with *D. mitchelli*, although the morphological data was ambiguous as to their affinities. We describe the Northwest Cape population as a new species below.

## SYSTEMATICS

### Reptilia

### Squamata

### Family Diplodactylidae Underwood, 1954

### 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 preanal pores, numerous (> 5) cloacal spurs, two pairs of cloacal bones and anteriorly enlarged jugal bone entering floor of lacrimal foramen (Oliver *et al.* 2007a).

#### *Diplodactylus capensis* sp. nov.

Cape Range Stone Gecko

Figures 5, 6

#### Material examined

##### Holotype

WAM R154901 in the collection of the Western

Australian Museum, Perth. An adult male collected at Shothole Canyon, Northwest Cape, Western Australia (22°03'12"S, 114°01'11"E) by P. Doughty on 13 April 2004. Liver sample stored at -75°C at WAM.

##### Paratypes

WAM R81328 (F) 6 km S of Exmouth (21°58'S, 114°06'E); WAM R81342 (M) Shothole Canyon (22°05'S, 114°02'E); WAM R102843 (M) Cape Range N.P. (22°04'17"S, 114°00'23"E); WAM R102900 (F) Cape Range N.P. (22°09'01"S, 113°59'52"E); WAM R117870 (F) Shothole Canyon (22°02'S, 114°02'E); WAM R132465 and WAM R132466 (both F) Shothole Canyon (22°03'00"S, 114°01'01"E); WAM R141700 (M) Learmonth (22°14'31"S, 114°02'02"E); WAM R154902 (M) 9 km S of Exmouth (22°01'18"S, 114°06'39"E).

#### Diagnosis

A medium-large member of *Diplodactylus* characterised by stout head with tall labial scales, mental similar size to infralabials, elongate tail, wide scansors with a row of discrete unbroken lamellae along digit, medium-sized dorsal scales, 25 vertebrae and by light reddish brown dorsal colouration with pale continuous dorsal stripe with transverse bars.

#### Measurements

##### Holotype (mm)

SVL – 57.5; TrunkL – 25.9; TailL – 32.5; ArmL – 13.7; LegL – 17.2; HeadL – 15.8; HeadW – 11.0; HeadH – 7.0; Orbl – 4.4; NarEye – 4.6; SnEye – 6.3; EyeEar – 6.7; INar – 1.9; IO – 5.4; SupLab – 11; InfLab – 12; CreaseL – 0.1 of height; IntNar – 0; NoIO – 35; NoSC – 55; PostNas – 3; RelLab – 3 (equal); CSpurs – 5; 4FL – 3.7; 4FW – 0.8; 4FscanW – 1.2; 4FLam1 – 6; 4FLam2 – 6; 4TL – 4.2; 4TW – 0.8; 4TscanW – 1.5; 4TLasm1 – 7; 4TLam2 – 8; MenL/W – 1.2; TrunkL/SVL – 0.45; HeadL/SVL – 0.28; Head/SVL – 0.19; HeadH/SVL – 0.12; ArmL/SVL – 0.24; LegL/SVL – 0.30; Tail%SVL – 56.5%.

#### Description

A large *Diplodactylus* with a slight to medium build and medium-large head. Arms and legs slender and of moderate length. Tail moderately thick and short, covered by scales much larger than on dorsum. Head moderately wide and deep. Snout triangular when viewed dorsally but rounded in profile at tip. Adductor muscles of jaw large. Eyes moderately large with straight brow ridge above eye and eyes only slightly protruding above top of head. Eyelid margin begins at anterior-ventral edge of eye, then extends dorsally and anteriorly before extending posteriorly to form a protruding ridge above eye. There are 2–7 spinose scales towards the





Figure 5 Male (A) and female (B) of *Diplodactylus capensis* sp. nov. from the Cape Range. Photographs by B. Maryan.

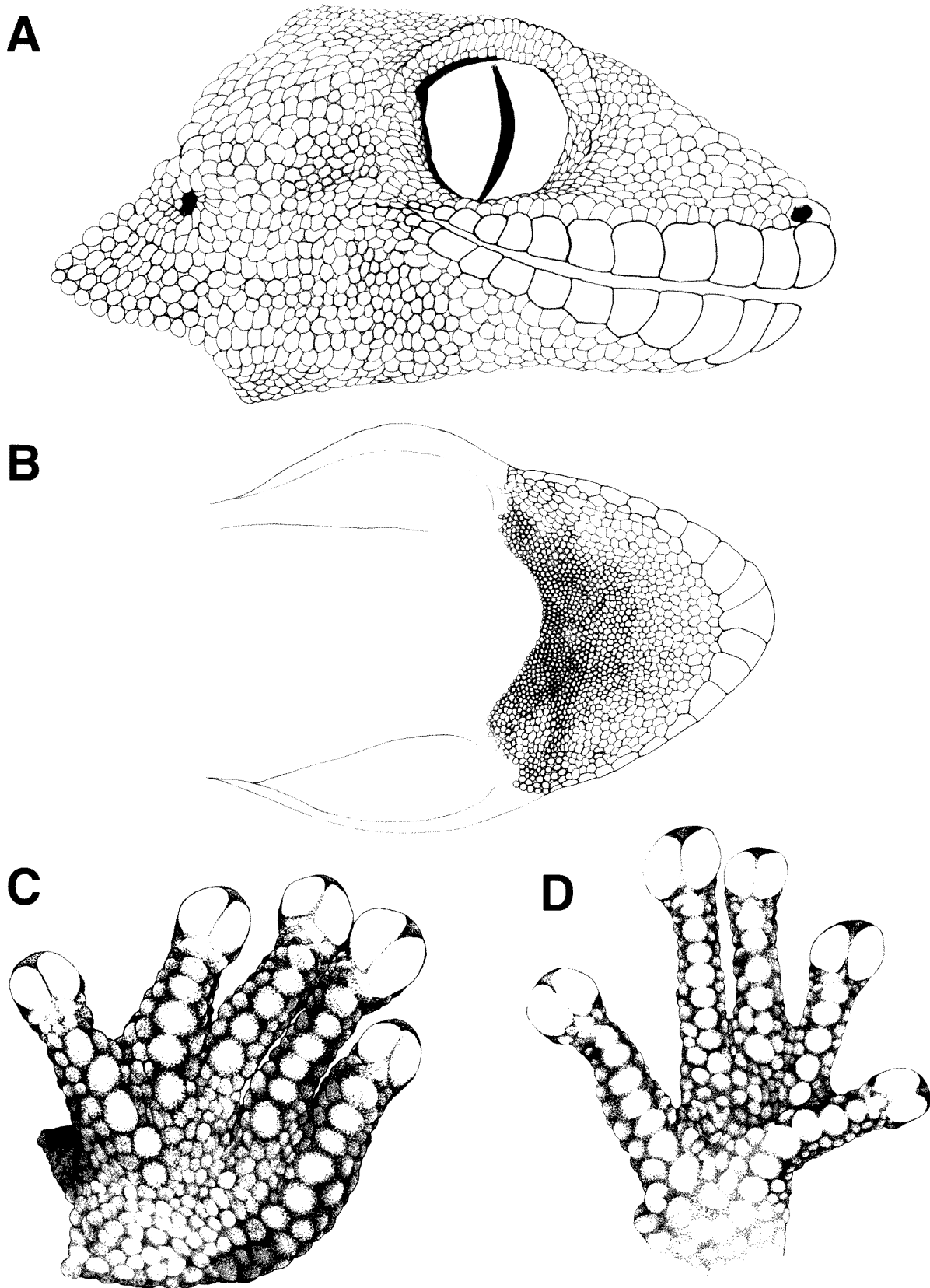
posterior fold of the eyelid margin. Ridge at posterior edge of eye extends anteriorly and ventrally so that the posterior ventral portion of eye socket is covered.

Usually 11 (10–12) upper and lower labial scales. Nostril surrounded by rostral, 2 supranasals, 2–4 postnasals and first labial. Second labial not lower than first. Rostral scale usually undivided ( $N = 16$ ) or at most with a small dorsal notch (3). Nostrils separated by 2 lower supranasals and usually 4 or 5 upper supranasals. Mental scale sharply triangular or lanceolate, only slightly longer than wide.

Postmentals gradually decrease in size posteriorly over 5–8 scale rows that gradually reduce to the size of the granular scales under the chin.

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 than dorsal scales and chin covered with small granular scales. Limbs with small granular scales. Male cloacal spurs consist of 5–6 spinose scales arranged in 2–3 transverse rows; females have 3–10 enlarged scales (rarely spinose) where the male spurs occur. The tail is short and





**Figure 6** Holotype (WAM R154901) of *Diplodactylus capensis* sp. nov. Lateral (A) and ventral (B) views of head; ventral surface of hand (C) and foot (D). Drawings by C. Stevenson.

round to slightly oblong in cross-section with a slight constriction near base. Fine granular scales cover plantar surface of manus and pes. Two enlarged terminal pads to either side of claw. The shape of the subdigital lamellae is circular, rarely transversely oblong. Usually six unbroken subdigital lamellae on 4<sup>th</sup> finger and eight under 4<sup>th</sup> toe. There are 25 presacral vertebrae in the four specimens examined.

#### Colouration

In life the dorsal pattern consists of a light reddish-brown background which extends half-way down the flanks. The top of the head is paler than the body, with a wide pale streak extending forward from the vertebral stripe through the dorsal portion of the eye. Below this streak and above the pale upper labials is a reddish temporal streak through the ventral portion of eye. There is a cream-coloured irregular vertebral stripe with 5–8 short transverse bars to either side of midline. These transverse bars are aligned in some animals but not in others producing an irregular serrated pattern. The stripe and transverse bars have a reddish-chocolate border, but this fades on the transverse sections towards the flanks. The ventral surface and half way up the flanks is a creamy white. On original tails the dorsal vertebral stripe and transverse bar pattern continues as far as half the length of the tail before breaking up in to blotches or fading to creamy white. Regenerated tails are darker on the dorsal surface and lack the original patterns and blotches of original tails.

In very old specimens (preserved > 50 y), the pattern is very faint but the reddish hues and longitudinal pattern persist. In more recently preserved specimens, the rich red hues and dark borders are lost.

#### Reproduction and ecology

A gravid female had two eggs, one of which was 13.1 x 7.5 mm (the other was damaged). Very little else is known of this species, other than its apparent preference for hard stony surfaces. Most known specimens were collected from limestone massif itself, which is extensively vegetated by hummock grass with low shrubs and trees.

#### Etymology

Named for the Northwest Cape of Western Australia, the region to which it is restricted.

#### Distribution

*Diplodactylus capensis* is restricted to the northern end of the Northwest Cape in Western Australia (Figure 1). Within the peninsula, it occurs on the hard rocky substrate of the limestone massif itself. There are also two records from the eastern plain near the towns of Exmouth and Learmonth.

#### Morphological comparisons with other species

*Diplodactylus capensis* differs from *D. conspicillatus*, *D. ornatus* and *D. polyophthalmus* by reddish background colour, and from *D. conspicillatus*, *D. pulcher* and *D. klugei* by large labial scales, longer tail, mental not longer than infralabials and rostral in contact with nostril. From *D. mitchelli* by dorsals approximately the same size as ventrals, smaller adult body size, more robust appearance (*D. mitchelli* has a dorsoventrally compressed head and long limbs that are unique in *Diplodactylus*), fewer vertebrae, fewer cloacal spurs, lighter colour and unincreased rostral. It is distinguished from *D. g. granariensis* by greater SVL, large scale size (as measured by NoIO), unincreased rostral scale, shorter tail, fewer subdigital lamellae, reddish ground colour and presence of poorly defined transverse bars on dorsum. It is distinguished from *D. g. rex* by smaller SVL and head, fewer subdigital lamellae, reddish ground colour and presence of poorly defined transverse bars on dorsum.

We found a consistent count of 25 presacral vertebrae in *D. capensis* compared to 26 in *D. mitchelli*. This is interesting given that the modal gekkotan count is 26, with a range of 23 to 29 (see Bauer *et al.* 1996). As only two taxa were sampled, it is not possible to determine whether the difference represents a loss or a gain, although the body shape and limb proportions of *D. mitchelli* are considerably more elongate relative to other stone geckos. Further taxon sampling of vertebral counts within the Diplodactylidae is necessary to resolve the polarity issue and to explore trends within this group.

#### Conservation

*Diplodactylus capensis* has one of the smallest distributions of an Australian gecko, although some species are only known from a single remote location (e.g., *D. fulleri* Storr 1978) or restricted to mountains (e.g., leaf-tailed geckos along the Great Dividing Range; Wilson and Swan 2003).

The description of *D. capensis* raises the number of reptile species endemic to the Cape Range to three. The others endemics are the blindsnake *Rhamphotyphlops splendidus* Aplin 1998 and the pygopod *Delma tealei* Maryan, Aplin and Adams 2007. In addition there are a number further reptile taxa that have isolated allopatric populations on the Cape Range (see Wilson and Swan 2003). These patterns, in addition the high levels of endemism shown by other faunal groups, underline the biogeographical uniqueness and conservation significance of the Northwest Cape. Much of the Cape Range is currently protected within the Cape Range National Park. However, the entire Northwest Cape is currently subject to degradation by large numbers of feral goats, including the



national park. Conservation of *D. capensis* and other significant fauna on the Northwest Cape (e.g., Maryan *et al.* 2007) would be best achieved by increasing the size of the conservation reserve to include the entire peninsula (which is also fringed by the Ningaloo reef) and eradicating feral goats.

#### ACKNOWLEDGEMENTS

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## APPENDIX 1

Specimens of *Diplodactylus* examined morphologically.

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*Diplodactylus capensis* (non type-series material)

Males

WAM R52906, WAM R61277, WAM R81327, WAM R102844, WAM R132467.

Females

WAM R52920, WAM R52928, WAM R52929, WAM R61276.

*Diplodactylus mitchelli*

Males

WAM R110136, WAM R110152, WAM R113642, WAM R140406, WAM R146604, WAM R152704, WAM R154975, WAM R158095, WAM R158098, WAM R158137, WAM R170674, WAM R170686, WAM R170718.

Females

SAM R60439, WAM R84458, WAM R113618, WAM R145754, WAM R146630, WAM R146631, WAM R146632, WAM R158104, WAM R170689.

*Diplodactylus granariensis granariensis*

Males

WAM R72278, WAM R72361, WAM R74347, WAM R76042, WAM R84452, WAM R96573, WAM R110779, WAM R127572, WAM R134044, WAM R134106, WAM R135210, WAM R137776, WAM R144170, WAM R144551, WAM R151675, WAM R153946, WAM R153947, WAM R153948, WAM R153949, WAM R153950.

Females

WAM R136581, WAM R72718, WAM R93462, WAM R74518, WAM R72602, WAM R161181, WAM R144780, WAM R134816, WAM R132023, WAM R132278, WAM R103846, WAM R103857.

*Diplodactylus granariensis rex*

Males

WAM R97289, WAM R113191, WAM R132504, WAM R140415, WAM R141120, WAM R141121, WAM R144718, WAM R154934, WAM R154944, WAM R154955, WAM R154957, WAM R161164, WAM R167476, WAM R167485.

Females

WAM R100350, WAM R110702, WAM R112102, WAM R112106, WAM R136593, WAM R136619, WAM R136802, WAM R141122, WAM R145285, WAM R145448, WAM R151421, WAM R154956, WAM R167490.

## APPENDIX 2

Material of *Diplodactylus* examined genetically.

Taxon	Specimen Number	Locality	State	Allozymes	mtDNA	Genbank Accession
NW Cape	WAMR132465	Cape Range NP	WA	Y	Y	EF532862
NW Cape	WAMR132466	Cape Range NP	WA	Y	N	NA
NW Cape	WAMR132467	Cape Range NP	WA	Y	Y	NA
NW Cape	WAMR132468	Cape Range NP	WA	Y	Y	NA
NW Cape	WAMR117870	Shothole Canyon	WA	Y	N	NA
<i>D. granariensis</i>	WAMR153949	Bindoon Military Training Area	WA	Y	N	NA
<i>D. granariensis</i>	WAMR153946	Bindoon Military Training Area	WA	Y	Y	EF532869
<i>D. granariensis</i>	WAMR153947	Bindoon Military Training Area	WA	Y	N	NA
<i>D. granariensis</i>	WAMR153948	Bindoon Military Training Area	WA	Y	Y	NA
<i>D. granariensis</i>	WAMR153950	Bindoon Military Training Area	WA	Y	N	NA
<i>D. granariensis</i>	WAMR132023	4km W. of Dryandra Settlement	WA	Y	Y	NA
<i>D. granariensis</i>	WAMR112106	20km S.W Paynes Find	WA	Y	Y	EF532867
<i>D. granariensis</i>	WAMR144551	Mt Jackson	WA	Y	Y	EF532870
<i>D. granariensis</i>	WAMR112102	86km north of Meekatharra	WA	Y	Y	EF532865
<i>D. granariensis</i>	WAMR112103	86km north of Meekatharra	WA	Y	Y	EF532863
<i>D. granariensis</i>	WAMR113191	35 km S of Kumarina	WA	Y	Y	EF532866
<i>D. granariensis</i>	WAMR145285	Hill 50 Mine, Mount Magnet	WA	Y	N	NA
<i>D. granariensis</i>	WAMR144718	Bungalbin	WA	Y	Y	NA
<i>D. granariensis</i>	WAMR140415	3km S. of Vivien Mine	WA	Y	Y	EF532868
<i>D. granariensis</i>	WAMR132504	Jundee	WA	Y	Y	NA
<i>D. granariensis</i>	WAMR141120	15km ENE Wildara Pinnacle	WA	Y	N	NA
<i>D. granariensis</i>	WAMR141121	15km ENE Wildara Pinnacle	WA	Y	N	NA
<i>D. granariensis</i>	WAMR141122	15km ENE Wildara Pinnacle	WA	Y	N	NA
<i>D. granariensis</i>	WAMR127572	Goongarrie	WA	Y	Y	EF532871
<i>D. granariensis</i>	WAMR145448	Lorna Glen Station	WA	Y	N	NA
'Southern'	WAMR140941	27.5 km SSE Peak Eleanora	WA	Y	Y	EF532882
'Southern'	SAMAR24763	Stenhouse Bay	SA	Y	Y	EF532874
<i>D. mitchelli</i>	WAMR146604	198km S. Port Hedland	WA	Y	N	NA
<i>D. mitchelli</i>	WAMR146630	198km S. Port Hedland	WA	Y	N	NA
<i>D. mitchelli</i>	WAMR146631	198km S. Port Hedland	WA	Y	N	NA
<i>D. mitchelli</i>	WAMR146632	198km S. Port Hedland	WA	Y	Y	EF532857
<i>D. mitchelli</i>	WAMR152704	Chichester Range	WA	Y	Y	EF532858
<i>D. mitchelli</i>	WAMR113618	Not available	WA	Y	N	NA
<i>D. mitchelli</i>	WAMR113642	37km NNE Auski Roadhouse	WA	Y	Y	EF532857
<i>D. mitchelli</i>	SAMA R60439	Roy Hill area	WA	N	Y	NA
<i>D. ornatus</i>	WAMR120060	3km E. of Greenough River Mouth	WA	Y	Y	EF532859
<i>D. ornatus</i>	WAMR99299	False Entrance Tank	WA	Y	Y	EF532860
<i>D. ornatus</i>	WAM100000	False Entrance Tank	WA	Y	N	NA
<i>D. ornatus</i>	WAMR119295	Wicherina Dam	WA	Y	N	NA
<i>D. pulcher</i>	SAMAR32183	47km N Muckera Roadhouse	SA	Y	Y	EF532840
<i>D. pulcher</i>	WAMR120668	Carnarvon Basin Survey	WA	N	Y	EF681789
<i>D. pulcher</i>	SAMA R26383	Near Cook	SA	Y	N	EF532839