

# Revision of *Lucasium stenodactylus* (Boulenger, 1896; Squamata: Diplodactylidae), with the resurrection of *L. woodwardi* (Fry, 1914) and the description of a new species from south-central Australia

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**ABSTRACT** – The past two decades have seen an increase in the documentation of reptile diversity in the Australian arid zone through a combination of genetic and morphological analyses based on widespread collections. Especially common are descriptions of new species of geckos, mostly from rocky refugia, but also widespread terrestrial species as well. Here we focus on outstanding taxonomic issues with the widely distributed diplodactylid *Lucasium stenodactylus* (Boulenger). We analysed published and newly generated genetic sequences, especially from South Australia, to resolve previous indications from morphology and molecular data that at least two other species may exist within the current definition of *L. stenodactylus*. We found strong support for a Pilbara region species, to which the name *Diplodactylus woodwardi* Fry applies, and for a new species occurring mostly in South Australia, *Lucasium microplax* sp. nov. The Pilbara and South Australian lineages are distinguished on numerous distinctive scalation and pattern characteristics and show deep genetic divergences. The redescription of *L. woodwardi* adds yet another gecko species to the highly diverse Pilbara region reptile fauna, and the description of the South Australian lineage as a separate species from *L. stenodactylus* adds another widespread arid-adapted species to its reptile fauna.

**KEYWORDS:** Australian arid zone, gecko, molecular genetics, ND2, South Australia

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## INTRODUCTION

The Australian arid zone (AAZ) is now recognised as a major area for the generation of diversity (Byrne et al. 2008; Anderson et al. 2016) and especially reptile diversity (Brennan and Oliver 2017). The AAZ harbours the most diverse lizard fauna in the world (Pianka 1986; Powney et al. 2010) and has become a model area for the study of diversification and large-scale evolutionary radiations (Rabosky et al. 2007). Although already noted for its very high species richness, descriptions of species from the AAZ are ongoing at a relatively high rate. Almost all new lizard species descriptions from the AAZ in the past 20 years have involved a combination of

morphological and molecular data, with recent additions to the fauna coming from across the range of major squamate taxa that inhabit the region, including agamids (Melville et al. 2019), skinks (Rabosky et al. 2017) and snakes (Ellis et al. 2017; Maryan et al. 2020).

Geckos (Carphodactylidae, Diplodactylidae, Gekkonidae and Pygopodidae) are particularly diverse in the AAZ and knowledge of their diversity and the potential drivers of its evolution has advanced rapidly in recent years (Pepper et al. 2013; Nielsen et al. 2016; Ashman et al. 2018). Most new species of geckos have been described from rocky refugia within the AAZ, especially the Pilbara and Central Ranges (e.g. Oliver

et al. 2010; Pepper et al. 2013; Doughty et al. 2018a), but new species also continue to be revealed in the superficially more homogeneous sandy desert regions (e.g. Maryan et al. 2007; Oliver et al. 2014; Oliver and Doughty 2016).

An early taxonomic synthesis on AAZ geckos was Kluge's landmark 1967 monograph on *Diplodactylus* Gray, 1832 which included a diverse subgroup of largely or completely terrestrial species (excluding the largely arboreal *Strophurus* Fitzinger, 1843) with significant variation across the AAZ (Storr et al. 1990). Since then this terrestrial subgroup has become better understood as a clade of diplodactylid geckos belonging to three genera: *Diplodactylus*, *Lucasium* Wermuth, 1965 and *Rhynchoedura* Günther, 1867 (Oliver et al. 2007). Among these, the genus *Lucasium* is a group of small to medium sized terrestrial geckos, inhabiting much of arid and semiarid Australia, excluded only from the humid south-western, eastern and south-eastern forests. Currently, *Lucasium* includes 12 species (Uetz et al. 2020; Vanderduys et al. 2020), but there is still evidence for unrecognised diversity in the genus.

Within the very wide-ranging *L. stenodactylus* (Boulenger, 1896), morphological evidence from as far back as Kluge's (1967) monograph and more recent molecular data (Pepper et al. 2006) point to the existence of cryptic species in this complex. Kluge's (1967) *Diplodactylus stenodactylus* 'population A' comprised specimens from the western deserts, which included the type locality of *Diplodactylus stenodactylus*, Roebuck Bay, Broome, Western Australia in the north-west of its distribution. Kluge depicted the colour pattern of this population as having small to moderately large pale spots distributed over light reddish-brown dorsal surfaces and limbs, and possessing a vertebral stripe. Other significant morphological features were small apical plates, a reduction from 5 to 4 in the phalanges of the fourth finger and nostril excluded from contact with the rostral scale. In his description of 'population A' from Western Australia, Kluge also included the holotype of *Diplodactylus woodwardi* Fry, 1914 although it was in very poor condition making assessment difficult (Kluge 1963). However, he explicitly excluded specimens of *stenodactylus* collected from the Warburton area, near the border of South Australia and the Northern Territory. He referred these to his 'population B', with the specimens possessing a wide and distinct vertebral stripe and bordered by dark red or brown colouration with large pale spots on the dorsal and lateral surfaces of the body and limbs. Morphologically, these specimens possessed apical plates that were small ('rarely wider than the proximal portion of digit'; p. 1049; illustrated in figure 3I), retained the plesiomorphic count of five phalanges in the fourth finger and the nostril was not in contact with rostral in ~3/4 of specimens.

*Lucasium stenodactylus* was the subject of a detailed molecular study by Pepper et al. (2006; see also Pepper et al. 2008). They found significant genetic variation in populations from Western Australia, with dense

sampling from the Pilbara region and sparser sampling across the state. The Pilbara and Gascoyne regions to the south were a cohesive lineage in the analysis (which they called 'Pilbara'), and to which the name *D. woodwardi* could apply. The three other lineages recovered were 'non-Pilbara' which referred to western desert populations, 'sp. 1' which corresponded to specimens from the Western Australia-South Australia border and 'sp. 2' whose distribution was to the south of the other three lineages. Pepper et al.'s 'sp. 2' was later described as *L. bungabinna* Doughty & Hutchinson, 2008 based on a combination of morphological analysis, the genetic results of Pepper et al. (2006) and an unpublished allozyme study (M. Adams and S. Donnellan, pers. comm.). Although the description of *L. bungabinna* reduced some of the taxonomic ambiguity within *L. stenodactylus*, there remain two major lineages from Pepper et al. (2006), i.e. 'Pilbara' and 'sp. 1', as well as Kluge's 'population A' and 'population B' that require resolution.

Here, we investigate these unresolved populations to further stabilise the taxonomy of *L. stenodactylus*. We sequenced 45 more individuals of the Pepper et al. (2006) 'sp. 1' population from South Australia and 12 more individuals of 'non-Pilbara' *L. stenodactylus*, and provide a morphological analysis of the three main groups considered here: i) true *L. stenodactylus* from the western deserts, ii) the Pilbara region population, for which the name *Diplodactylus woodwardi* potentially applies, and iii) Kluge's 'population B' and Pepper et al.'s 'sp. 1' that occurs widely within arid South Australia and bordering states, which we describe herein as a new species. Although there was some genetic structure among some of the samples from the Australian monsoonal tropics from Pepper et al. (2006), the available samples are insufficient to resolve the wide variation in morphology observed in this region, hence our focus here is largely on the three major arid zone populations of what are currently regarded as *L. stenodactylus*.

## MATERIALS AND METHODS

### DNA AMPLIFICATION AND SEQUENCING

We collected new NADH Dehydrogenase Subunit 2 (ND2) sequence data for 47 individuals and these were added to data generated in Pepper et al. (2006) and Pepper et al. (2008) (see Appendix for specimen information and GenBank accession numbers). We included multiple additional taxa in order to put the putative new taxon in genetic context with the other members of the genus *Lucasium*. Detailed information on DNA extraction and sequencing protocols for all three loci used in this study are outlined elsewhere (Pepper et al. 2006). In brief, DNA from new samples was obtained using the EDNA HiSpEx tissue kit (Chaga) following the manufacturers protocol. The ND2 region was amplified and sequenced in three overlapping fragments, using the forward primer L4437 (5'-AAGCTTTTCGGGGCCCATAACC-3';

Macey et al. 1998) and the reverse primer tRNA Asn (5'-CTAAAATRTTRCGGGATCGAGGCC-3'; Read et al. 2001). A modified version of L4882 (5'-CAACCTGACAAAAAHTHGCMC-3'; Macey et al. 2000) was used as an internal sequencing primer. PCR products were amplified for 37 cycles at an annealing temperature of 60°C. Purified PCR products were run on an ABI 3100 auto-sequencer. All genes were sequenced from both 3' and 5' ends separately.

#### ANALYSIS OF SEQUENCE DATA

New ND2 sequences generated in this study were aligned with data presented in Pepper et al. (2006) and Pepper et al. (2008) in Geneious Prime 2020 1.1. We translated nucleotide data into amino acid sequences and checked the alignment for internal stop codons and frame-shift mutations. In addition to ND2, we also collated data from the aforementioned studies that included a portion of the 16S ribosomal RNA and a portion of the protein-coding locus RAG1. Following the removal of ambiguously aligned nucleotide sites, the final ND2 dataset consisted of 1051 base-pairs (bp), 16S consisted of 484 bp and RAG1 consisted of 834 bp, totalling 2369 bps for the concatenated dataset. Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian methods. For the likelihood analysis we concatenated the data and partitioned the combined dataset by gene. We used the RAxML plugin in Geneious, implemented the general time-reversible substitution model with gamma-distributed rates among sites (GTR + G). We used *Diplodactylus fulleri* Storr, 1978 to root the phylogenetic tree. Bootstrap support was determined using 1000 replicates. Bootstrap values above 80 are considered as providing strong nodal support.

In addition to our concatenated ML approach, we used the hierarchical model implemented in starBEAST2 v. 2.6.3 (Ogilvie et al. 2017). The phylogenetic signal was limited in the 16S and RAG1 loci (visible in figure 3 of Pepper et al. [2006], and also corroborated in RAxML analyses of individual loci in our study, not shown) so we used the concatenated dataset for this analysis as well, using the HKY substitution model, employing a strict clock, and using a Yule tree prior. We conducted two separate runs, with samples drawn every 10,000 steps over a total of 100,000,000 steps, with the first 10% discarded as burn-in. Acceptable convergence to the stationary distribution was checked by inspecting the posterior samples using the diagnostic software Tracer v1.5 (Rambaut and Drummond 2007). Effective sample sizes were well above 200 for all parameters. Both runs produced the same topology with very similar posterior probabilities, so we combined runs to generate a single consensus tree. Posterior probabilities above 90 were considered as providing strong nodal support.

#### MORPHOLOGY

We examined specimens, including type material, held at the Western Australian Museum, Perth (WAM), Northern Territory Museum, Darwin (NTM) and the

South Australian Museum, Adelaide (SAMA). Type specimens were examined from WAM, Natural History Museum, London (NHMUK, formerly BMNH) and Zoolgisk Museum, Universitetets Oslo, Oslo, Norway (UZMO). Specimens measured are listed and denoted as such in the Appendix.

For the morphological measurements, we sorted specimens based on the genetic results of Pepper et al. (2006) and original sequences presented here. We chose a subset of well-preserved adult specimens for measuring with most specimens genotyped. Several smaller specimens were measured (<43 mm snout-vent length), but these were excluded from statistical summaries except for scalation counts. Colouration was determined from photographs of live individuals or recently collected specimens.

The following measurements were recorded to the nearest 0.1 mm using digital callipers and dissecting microscope: snout-vent length (SVL), from tip of snout to anterior edge of vent; trunk length (TrunkL), from axilla to groin; tail length of original and regenerated tails (TailL), from cloaca to tail tip; tail width (TailW) from widest point of tail; forearm length (ArmL), from elbow to tip of 4<sup>th</sup> finger; foreleg length (LegL), from upper surface of knee to tip of 4<sup>th</sup> toe; head length (HeadL), from tip of snout to posterior margin of the retroarticular process, measured at an oblique angle; head width (HeadW), at widest point; head depth (HeadD) at largest point on crown; orbit length (OrbL), from lower anterior to upper posterior edges of bony socket; naris to eye (NarEye), from naris to anterior corner of eye; snout to eye (SnEye), from tip of snout to inner anterior edge of eye socket; eye to ear (EyeEar), from inside the posterior edge of bony eye socket to anterior margin of ear; internarial distance (INar), from naris to naris; interorbital width (IO), interorbital width at centre of eyes; mental length (MenL), from mouth to posterior edge; mental ratio (MenL/W), ratio of mental length/width; rostral crease length (CreaseL), proportional length of crease from dorsal edge of rostral scale.

The following scalation data were recorded and scored under a dissecting microscope: supralabial scales (SupLab), infralabial scales (InfLab), anterior supranasals (AntSup) and precloacal pores (Pores). Sex was determined by the presence of enlarged cloacal spurs, cloacal bulge and/or everted hemipenes (males) or by follicles and eggs (females).

## RESULTS

#### MOLECULAR GENETICS

Our RAxML phylogeny (Figure 1) includes all the Western Australian members of the genus *Lucasium*, as well as the two Western Australian *Rhynchoedura* species and *Diplodactylus fulleri*. Within *Lucasium*, two main clades were recovered. A well-supported clade with taxa distributed largely in southern Western

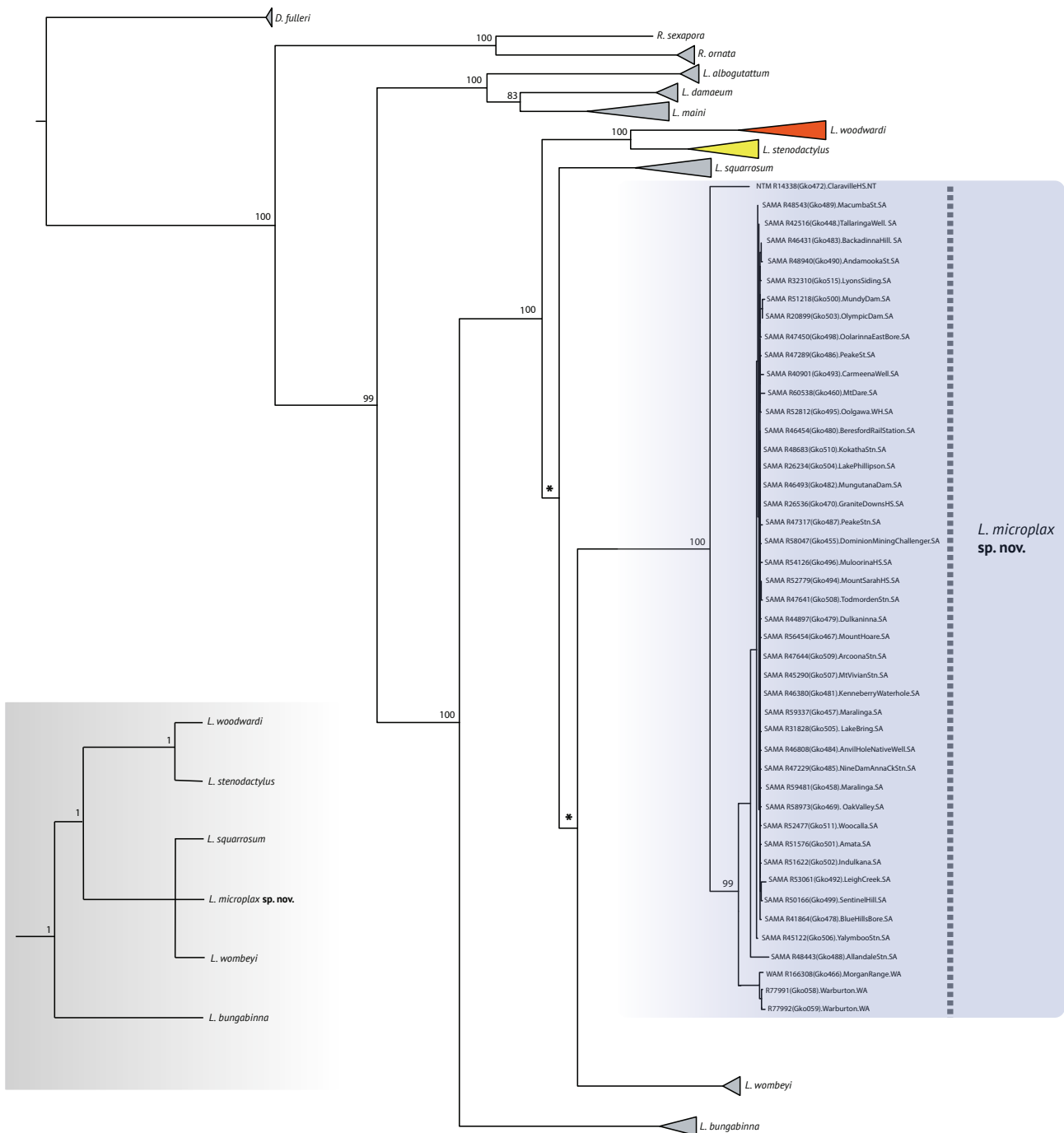


FIGURE 1 Phylogram of major lineages of *Lucasium* in the western arid zone. Names for lineages within the *L. stenodactylus* species complex referred to in the text: *L. stenodactylus*, northern lineage; *L. woodwardi*, Pilbara lineage; *L. microplax* sp. nov., South Australian lineage. \* = BP support <50.

Australia comprises *L. alboguttatum* (Werner, 1910) and the sister taxa *L. damaeum* and *L. maini*. The second clade included the more northerly distributed species; however, within this clade, relationships among *L. stenodactylus*, the Pilbara lineage of *L. stenodactylus* (i.e. *L. woodwardi* in Figure 1), the South Australian lineage of *L. stenodactylus* (i.e. *L. microplax* sp. nov. in Figure 1), *L. squarrosum* (Kluge, 1962) and *L. wombeyi* (Storr, 1978) are largely unresolved (Figure 1). Our Bayesian analysis implemented in starBEAST2 also

failed to resolve the relationships within this group (see Figure 1, inset). Our analyses expanded on those presented in Pepper et al. (2006) by sequencing tissues from more specimens, especially from South Australia. These additional South Australian individuals grouped together with those labelled ‘sp. 1’ in Pepper et al. (2006), along with three individuals from Western Australia (WAM R77991, WAM R77992, WAM R166308) and a single individual from the southern Northern Territory (NTM R14338). The ‘sp. 1’ lineage

is distributed predominantly in South Australia (Figure 2). Uncorrected P-distances calculated in PAUP\* v. 4.0a (Swofford 2002) between this South Australian clade (*L. microplax* sp. nov.) and *L. squarrosum* and *L. wombeyi* range from 15–18%, and are between 15–19% between the South Australian clade and *L. stenodactylus*. A deep phylogenetic split (bootstrap 100) separates populations of *L. stenodactylus* from the Pilbara region from those in the western deserts, with uncorrected P-distances between these clades at 11–15%.

In summary, we found that the specimens currently assigned to *L. stenodactylus* fell into three well-supported and potentially species-level clades. One clade ('Northern') includes specimens from near the type locality of *L. stenodactylus* and includes populations extending across much of the northern and central arid areas of Western Australia and east into the Northern

Territory (Figure 2). The second ('Pilbara') clade is centred on the arid ranges of the Pilbara and Gascoyne regions of the central west of Western Australia. These two clades are recovered as sister lineages. The third ('South Australian') clade comprises specimens from central and northern South Australia, eastern Western Australia and southern Northern Territory. Although previously included with *L. stenodactylus*, this clade is phylogenetically closer to *L. squarrosum* from the southern inland of Western Australia and *L. wombeyi* from the eastern Pilbara.

#### MORPHOLOGICAL ASSESSMENT

Table 1 summarises the morphological measurements among the three groups of *L. stenodactylus* considered here. A mensural character that was noticeably different among forms was the shorter original tails of the South

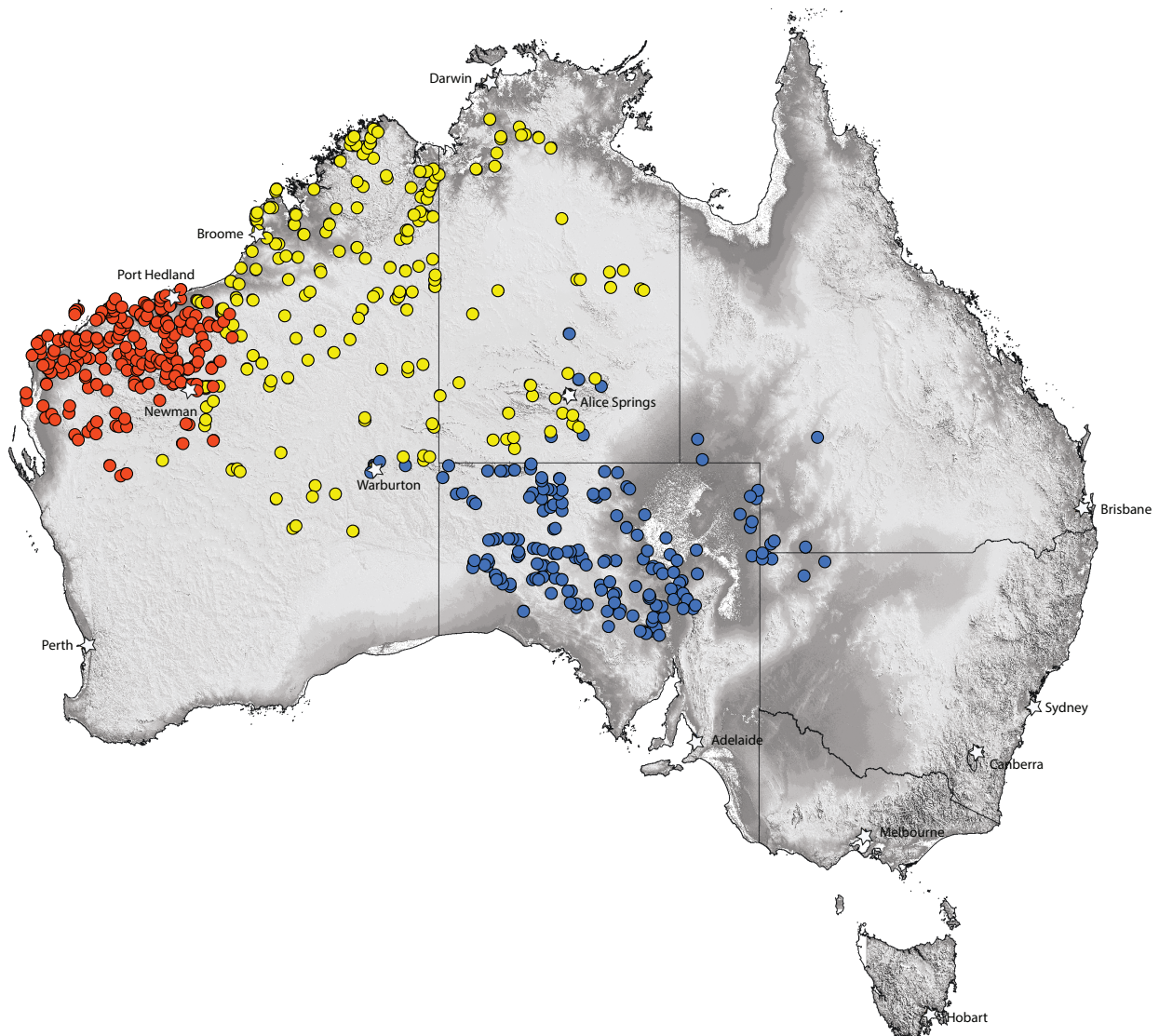


FIGURE 2 Distribution of the *Lucasium stenodactylus* species complex clades in the Australian arid zone. Key: yellow = Northern lineage (*L. stenodactylus*); red = Pilbara lineage (*L. woodwardi*); blue = South Australian lineage (*L. microplax* sp. nov.; Kluge [1967]'s 'population B'; Pepper et al. [2006]'s 'sp. 1').

Australia individuals: the average TailL%SVL was around 80% for Northern and Pilbara populations, but only 70% for South Australian populations. Features of scalation that are informative in separating the three clades include terminal apical plate (scansor) size and shape, rostral scale arrangement, infralabial size and preloacal pores. Northern specimens have small apical plates that were nearly as wide as the digit (Figure 3A). In contrast, Pilbara specimens have expanded apical plates that were wider than the width of the digit (Figure 3B) and visible in dorsal view. Populations from South Australia have very small apical plates that do not exceed the width of the digit and usually fail to contact the base of the claw (Figure 3C). Differences in finger width were also apparent for South Australia populations, with the distal phalanx noticeably narrowing in width (Figure 3C) compared to the other two taxa (Figures 3A, B). The rostral scale is separated from the nostril in the Northern and Pilbara populations (Figure 4A); in contrast, in South Australian populations the rostral is either in point contact with the nostril or only narrowly separated from it (Figure 4B).

The mental and infralabial scales in Northern specimens are smaller than the other two lineages, with these scales not extending far onto the gular region (Figure 5A). In contrast, the mental and infralabial scales of specimens from the South Australia clade are relatively large, extending much further on to the gular region (Figure 5C). Pilbara populations are intermediate between these two extremes (Figure 5B).

Precloacal pores also differed among lineages. In Northern and Pilbara clades, there was a range of 2–6 pores, whereas in the South Australia clade there was a consistent pattern of only two pores, the typical configuration in *Lucasium*. There was sexual dimorphism in pore expression as well. In Northern adult males and females, the pattern was typically two pores per side, but occasional three on a side and sometimes zero. Pilbara males also shared this pattern, but interestingly females usually had no pores, or occasionally one or two. In South Australian populations, both males and females almost always had a single pore on each side.

**TABLE 1** Summaries of characters and ratios measured for *Lucasium stenodactylus*, *L. woodwardi* and *L. microplax* sp. nov. Mean±S.D. (range). Sample sizes of adults are listed in column headings (with juveniles in parentheses — not used in meristic calculations), and for males and females separately for SVL and TrunkL. Only original tails measured. Samples sizes also provided when they deviate from total N.

Character	<i>L. stenodactylus</i> N = 16 (19)	<i>L. woodwardi</i> N = 25 (27)	<i>L. microplax</i> sp. nov. N = 22 (23)
SVL	Female (N = 8): 49.9±4.1 (44.0–55.0) Male (N = 8): 51.0±3.9 (44.0–56.5)	Female (N = 9): 48.6±1.3 (47.0–50.5) Male (N = 16): 47.4±2.5 (44.0–50.5)	Female (N = 11): 49.0±3.1 (44.0–55.5) Male (N = 11): 47.7±1.2 (40.0–51.5)
TrunkL	Female: 25.9±3.0 (19.3–30.4) Male: 26.2±2.2 (23.2–30.7)	Female: 23.6±1.0 (22.0–24.8) Male: 22.8±1.4 (20.2–25.2)	Female: 24.4±1.8 (21.5–27.5) Male: 22.7±1.9 (19.5–25.5)
TailL	41.4±5.6 (35.0–50.0) N = 13	36.6±2.9 (31.5–40.0) N = 18	33.7±2.3 (28.5–38.0) N = 18
TailW	3.8±0.5 (2.9–4.7) N = 13	3.6±0.5 (2.6–4.4) N = 18	3.7±0.5 (2.9–4.4) N = 19
ArmL	6.3±0.5 (5.4–6.9)	6.3±0.4 (5.4–7.2)	6.4±0.3 (5.7–6.9)
LegL	7.9±0.6 (7.0–8.8)	7.5±0.4 (6.6–8.8)	8.2±0.5 (6.8–8.9)

Character	<i>L. stenodactylus</i> N = 16 (19)	<i>L. woodwardi</i> N = 25 (27)	<i>L. microplox</i> sp. nov. N = 22 (23)
HeadL	13.2±1.1 (10.6–14.8)	12.7±0.8 (11.4–13.8)	12.7±0.8 (10.9–13.7)
HeadW	8.0±0.8 (6.8–9.3)	7.6±0.7 (6.8–9.2)	7.7±0.4 (6.8–8.4)
HeadH	5.5±0.8 (4.1–6.5)	5.3±0.5 (4.2–6.0)	5.6±0.3 (4.9–6.2)
OrbL	3.1±0.4 (2.4–3.9)	3.1±0.2 (2.5–3.3)	3.2±0.3 (2.6–3.5)
NarEye	4.1±0.4 (3.5–4.6)	3.7±0.2 (3.3–4.1)	4.2±0.4 (3.5–4.8)
SnEye	5.0±0.5 (4.0–5.5)	4.7±0.2 (4.4–5.0)	4.8±0.3 (3.9–5.3)
EyeEar	4.3±0.4 (3.4–4.9)	3.9±0.3 (3.4–4.3)	3.6±0.2 (3.0–3.9)
INar	1.6±0.3 (1.1–2.0)	1.3±0.1 (1.2–1.4)	1.3±0.2 (1.0–1.5)
IO	3.9±0.4 (3.1–4.3)	3.3±0.3 (2.9–3.9)	3.6±0.3 (3.0–4.0)
SupLab	9.4±1.1 (8–12)	9.3±0.6 (8–10)	9.3±0.9 (8–10)
InfLab	10.2±1.0 (9–12)	10.0±0.8 (9–12)	9.5±1.0 (8–12)
CreaseL	0.24±0.22 (0–0.60)	0.30±0.20 (0–0.75)	0.21±0.16 (0–0.50)
AntSup	5.3±0.6 (4–6) N = 17	4.6±0.6 (4–6)	4.6±0.8 (4–7)
MenL	1.14±0.17 (0.93–1.40)	1.12±0.16 (0.96–1.38)	1.27±0.16 (0.85–1.57)
MenL/W	1.13±0.16 (0.82–1.44)	1.24±0.15 (0.99–1.48)	1.20±0.18 (0.97–1.54)
Tail%SVL	0.81±0.4 (0.73–0.88) N = 13	0.77±0.04 (0.68–0.83) N = 18	0.70±0.03 (0.64–0.78) N = 18
HeadL/SVL	0.26±0.01 (0.23–0.27)	0.27±0.01 (0.24–0.30)	0.26±0.02 (0.23–0.30)
HeadW/SVL	0.16±0.01 (0.13–0.17)	0.16±0.01 (0.14–0.18)	0.16±0.01 (0.15–0.17)
HeadH/SVL	0.11±0.01 (0.09–0.13)	0.11±0.01 (0.09–0.13)	0.12±0.01 (0.10–0.12)

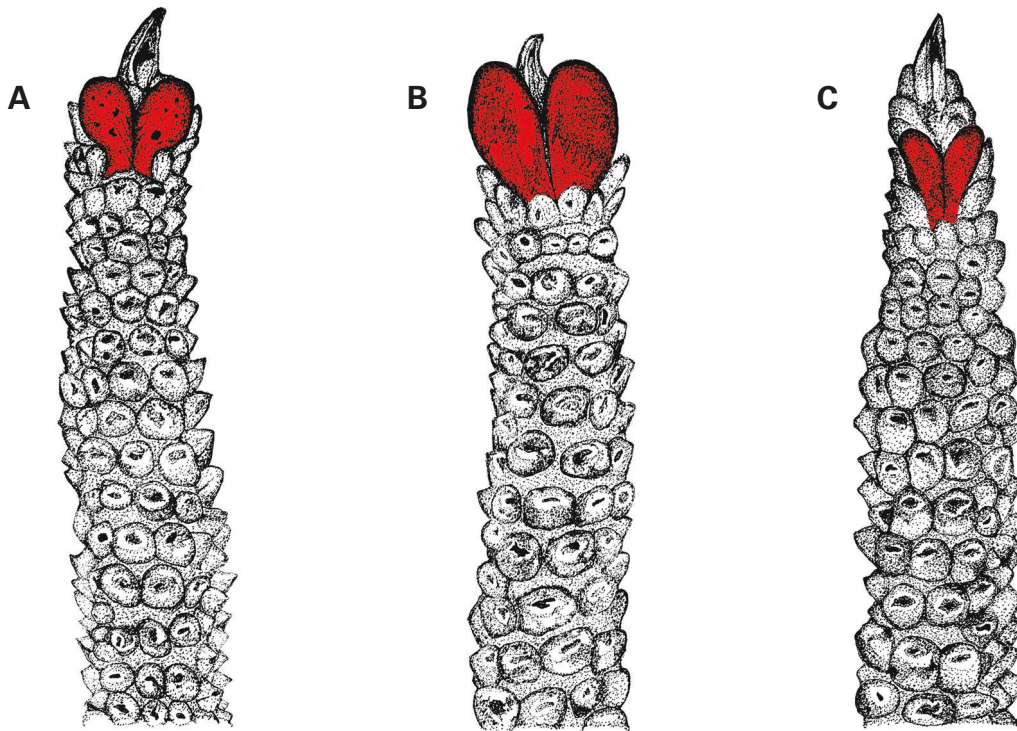


FIGURE 3 Ventral surfaces of the 4th toe of the *Lucasium stenodactylus* species complex. A) Northern lineage (specimen NTM R6299); B) Pilbara lineage (WAM R127703); C) South Australian lineage (SAMA R53061). Terminal plates highlighted in red to show relative differences in size. (Illustrations J. Eastwood.)



FIGURE 4 Two different scale configurations on the surface of the snout tip of *Lucasium stenodactylus* species complex members. A) Northern (illustrated specimen, WAM R84551) and Pilbara lineages; B) South Australian lineage (SAMA R53061). Rostral scale highlighted in green to show separation (A) or point contact (B) with nostril. (Illustrations J. Eastwood.)

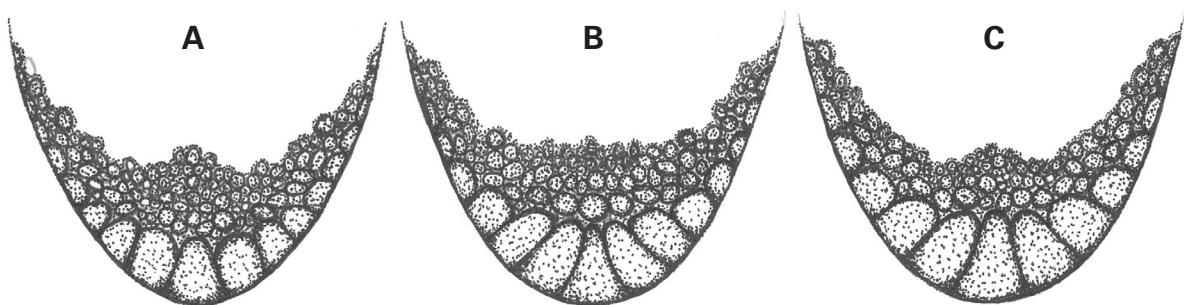


FIGURE 5 Chin of *Lucasium stenodactylus* species complex lineages, showing the relatively small mental and infralabial scale sizes typical of *L. stenodactylus*. A) Northern lineage (WAM R157948); B) Pilbara lineage (WAM R113591); C) South Australian lineage (holotype, SAMA R48940). (Illustrations J. Eastwood.)



Dorsal pattern and colouration differed consistently among all three lineages, although there was wide variation within taxa and moderate overlap among them. The basic pattern, common to all three clades considered here, was a red to brown background colour with usually a narrow pale vertebral stripe with small to moderate spots or blotches on the sides (Figures 6–7). The Northern lineage had a lighter overall appearance, with the vertebral stripe always present and with dark variegations overlain on the background pattern; spots were typically small but frequently joined together, especially towards the forebody (Figures 6A–B, 7A). In the Pilbara lineage the background colour was a rich reddish-brown; the vertebral stripe was variably expressed, including completely absent, and the

small spots tended to be discrete (Figures 6C–D, 7B). In the South Australia lineage, the appearance was also darker, with a more solid brown background colour; the vertebral stripe was always present and clearly defined with black margins; spots tended to be larger and often connected with the vertebral stripe (Figures 6E–F, 7C).

#### TAXONOMIC CONCLUSIONS

We found minor morphological differences among lineages, and strong genetic and distributional evidence that indicates there are three lineages that are currently combined as *Lucasium stenodactylus*. The type of *Diplodactylus stenodactylus* was collected by K. Dahl during the Mjöberg Expedition from Roebuck Bay (Broome), Western Australia. Specimens from this area



**FIGURE 6** Photographs in life of members of the *Lucasium stenodactylus* species complex. A) Northern lineage, Lake Disappointment, Western Australia; B) Northern lineage, Empress Springs, Western Australia; C) Pilbara lineage, Upper Carawine Gorge, Western Australia; D) Pilbara lineage, Balla Balla, Western Australia; E) South Australian lineage, Stuart Creek, South Australia; F) South Australian lineage, Owen Springs, Northern Territory. (Images A–B: B. Maryan; C–D: R.J. Ellis; E: M.N. Hutchinson; F: A. Fenner.)

are part of the Northern lineage genetically (Figures 1–2). The type specimen UZMO 2001 (Figure 8), a subadult male, also corresponded morphologically with specimens from the western deserts (cf. Figures. 7 vs. 8). Therefore, we regard the Northern form as true *L. stenodactylus*.

Ellis et al. (2018) presented a photograph of the holotype of *Diplodactylus woodwardi* Fry, 1914 (WAM R14370; formerly 9876) and provided an account of its collection by J.B. Cleland from the Strelley River in the north-western Pilbara region in 1907. We have sequenced specimens from the Strelley River crossing near Port Hedland (e.g. WAM R102053, WAM R145566; see Pepper et al. [2008]) and all belong to the Pilbara clade. The holotype is a juvenile in extremely poor condition, but we can discern some of the diagnostic morphological features discussed above such as dorsals and ventrals of similar size, enlarged labial scales, narrow toes and overall resemblance in head, body and limb proportions, all of which are consistent with the morphology of the Pilbara clade. Hence, the Pilbara region lineage should be regarded as *L. woodwardi*.

For the South Australian lineage of *L. stenodactylus*, there is no available name. Therefore, we describe this lineage as a new species below.

## SYSTEMATICS

### Family Diplodactylidae Underwood, 1954

#### Genus *Lucasium* Wermuth, 1965

*Lucasium* Kinghorn, 1929: 77 (junior homonym of *Lucasium* Kinahan, 1859 and *Lucasium* Dours, 1872).

*Lucasium* Wermuth, 1965: 100.

#### TYPE SPECIES

*Ceramodactylus damaeus* Lucas & Frost, 1896, by monotypy (as *Lucasium damaeum* Wermuth, 1965)

#### REMARKS

We follow the expanded concept of *Lucasium* outlined in Oliver et al. (2007) as a genus of the Diplodactylidae (sensu Han et al. 2004) distinguished from all Australian diplodactylids except for *Diplodactylus* and *Rhynchoedura* by having both lateral and medial pairs of cloacal bones. It is distinguished from *Diplodactylus* and *Rhynchoedura* by the reduced or vestigial jugal and medial expansion of the suborbital portion of the maxilla. Further distinguished from *Diplodactylus*, by low numbers of precloacal spinose scales (generally 2–5), presence of precloacal pores (usually one left and one right) in males (absent in *L. byrnei* (Lucas & Frost, 1896), *L. maini* (Kluge, 1962), *L. occultum* (King, Braithwaite & Wombey, 1982) and *L. steindachneri* [Boulenger, 1885]) and by more gracile, elongate proportions of the body, limbs and tail; fourth toe of hind foot approximately seven times as long as wide,

tail narrow and moderate to long (70% to 110% of SVL). Further distinguished from *Rhynchoedura* by lower presacral vertebral count (mode 26 versus mode 27), more robust skull, absence of beak-like projecting mental and rostral scales, moderately large labial scales and absence of large precloacal pores (Greer 1989).

Some remarks on the generic and specific endings of names are warranted here. The genus *Lucasium* began as *Lucasius* (Kinghorn 1929), coined for naturalist Arthur H. S. Lucas, one of the describers of the type species (and at the time only species), *Ceramodactylus damaeus* (Lucas & Frost 1896). Owing to *Lucasius* being a junior homonym twice over (see synonymy above), Wermuth (1965) emended the ending to *Lucasium*. As proposed the name *Lucasius* would have been masculine in gender, but the emendation to *Lucasium* changed this to a neuter ending. The endings of several species in *Lucasium* that were transferred from *Diplodactylus* by Oliver et al. (2007) were emended to agree with the neuter gender of *Lucasium*. For the species *L. alboguttatum*, *L. damaeum*, *L. immaculatum*, *L. occultum* and *L. squarrosus*, the specific names can all be interpreted as adjectives and so the endings have been emended correctly. Oliver et al. (2007) also emended the spelling of *stenodactylus* to *stenodactylum*. Boulenger (1896), in describing *Diplodactylus stenodactylus*, did not indicate whether he considered his specific name to be an adjective or a noun. The name translates as ‘narrow finger’ (noun) rather than ‘narrow-fingered’ (adjective; e.g. *stenodactylatus*), and so we suggest that the emendation by Oliver et al. (2007) was unnecessary as a noun does not have to agree in gender with the generic name. Accordingly, under Article 31.2.2 under the ICZN Code, we regard *stenodactylus* as a noun in apposition and conserve the original spelling; hence — *Lucasium stenodactylus*.

### *Lucasium stenodactylus* (Boulenger, 1896)

Western sandplain gecko

Figures 3–8

#### SYNONYMY

*Diplodactylus woodwardi* Fry, 1914: 175 (fide Kluge 1963)

*Diplodactylus stenodactylus stenodactylus* Underwood 1954

*Lucasium stenodactylum* Oliver et al. 2007

*Lucasium stenodactylus* Swan et al. 2017; this work

#### MATERIAL EXAMINED

##### Holotype

**Australia: Western Australia:** UZMO K2001, subadult male, collected from Roebuck Bay (Broome), by K. Dahl.

See Appendix for additional material examined.

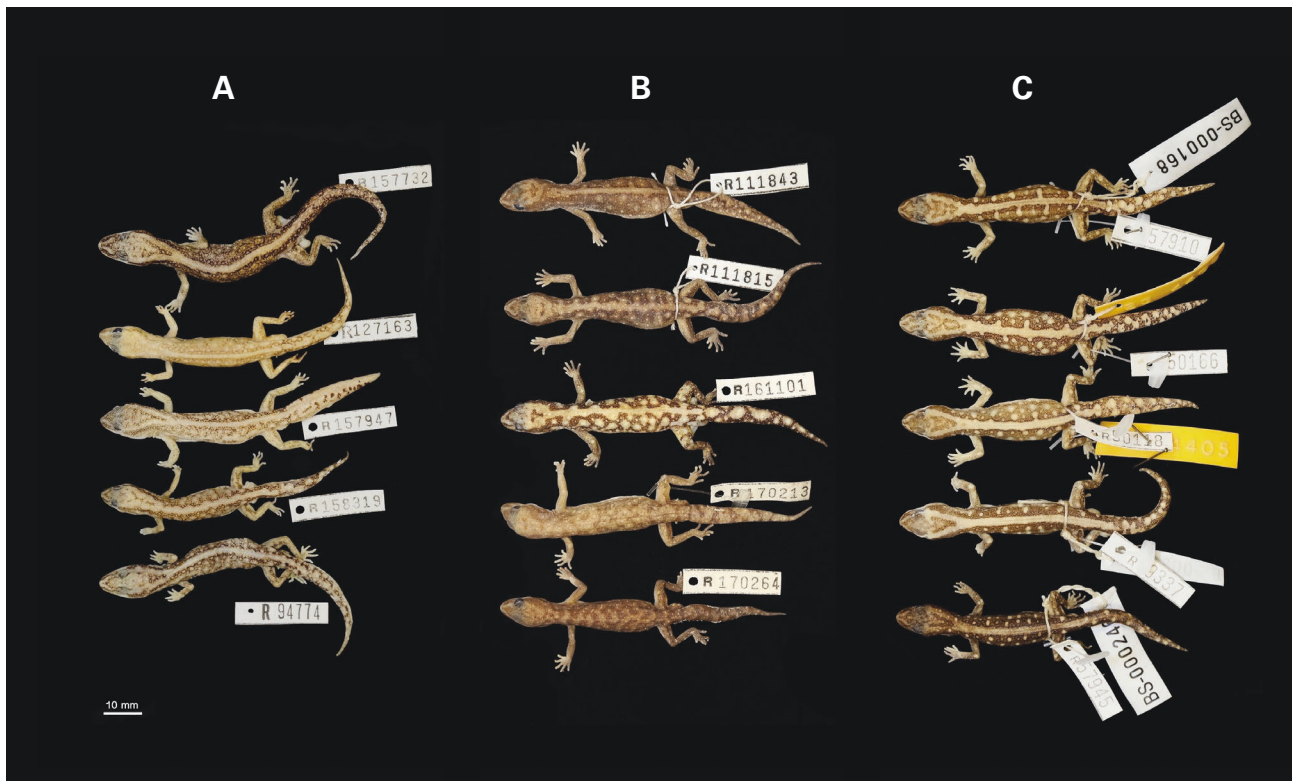


FIGURE 7 Dorsal view of series of preserved specimens of the *Lucasium stenodactylus* species complex. A) Northern lineage; B) Pilbara lineage; C) South Australian lineage.



FIGURE 8 Photographs of the holotype of *Diplodactylus stenodactylus* Boulenger (ZMO 2001) from dorsal, ventral, lateral head and fourth toe tip. The tag with the specimen also shown. (Images A.-H. Rønning, K. Sund and Øystein Wiig, UZMO.)

## DIAGNOSIS

A *Lucasium* distinguished from other members of the genus by rostral excluded from nostril, rostral crease present, terminal apical plates approximately the same width as digits, tail moderately long (TailL%SVL ~0.81), males and females with 2–5 precloacal pores and males with a single enlarged cloacal spur. Background colour light reddish brown, overlain by dark variegations, small pale spots tending to join together on forebody and pale vertebral stripe that forks strongly on the nape.

## DESCRIPTION

Table 1 presents a morphological summary. Body cylindrical with flat venter; head triangular, narrowing to rounded snout tip; eyes large; loreal region concave; moderate adductor muscles; ear opening small and circular; limbs gracile; five fingers and toes; tail long and tapering to fine point.

Rostral rectangular with crease extending from dorsal edge; rostral separated from nostril; two enlarged supranasals with rounded edges in narrow contact or separated by an internasal; enlarged upper and lower labials, approximately twice as wide as high; first supralabial twice the height of second; scales on snout slightly enlarged; posterior edge of eyelid with short row of spinose scales; mental squarish and flanked by three moderately large infralabials on each side, decreasing in size posteriorly (Figure 5A); gular scales decreasing in size, becoming granular on throat.

Scales on body juxtaposed, rounded with apex posteriorly; scales on venter juxtaposed and slightly rounded; single enlarged cloacal spur on each side of tail; precloacal pores usually 3–6; scales on tail square and flattened, occurring in regular rows; digits covered in fine scales, subdigital scales slightly enlarged; digits only slightly narrowing towards claw; paired terminal apical plates approximately similar width as digit.

*Pattern and colour.* In life (Figures 6A–B), background colour light reddish brown, overlain with dark complex reticulated variegations extending to limbs; pale cream vertebral stripe with straight to slightly wavy well-defined edges; background with small scattered pale spots, often darkly edged; vertebral stripe forks at neck, continuing anteriorly above and through eye and continuing along canthus as pale streak to tip of snout; top of head with irregular diffuse pale blotches often forming a pale cap; margins of eyelid highlighted with sulphur or yellow pigmentation; on lateral surfaces of body, a series of larger pale spots, surrounded by a halo of bordering pigmentation; larger blotches irregular, often joining adjacent blotches; blotches tending to form a lateral line anteriorly, often extending to below ear, connecting with gular region; dorsal region of tail either a continuation of straight-edged vertebral line or a series of pale blotches; ventral surfaces pale cream. Kimberley specimens tend to have a more amoeboid pattern of irregular blotches, with the vertebral stripe less defined. In preservative, the reddish hues are lost, becoming brown (Figure 7A). Older specimens can be quite faded.

## HABITAT

Occurs largely on sandplains with spinifex, but also other open areas such as red sandy loams, rocky and alluvial plains and claypans. In the Kimberley region, occurs in woodlands with lateritic or sandstone surfaces, and also sandy and clayey substrates that are more typical of desert populations.

## DISTRIBUTION

Most confirmed specimens of this species are from the western deserts in Western Australia, from the type location in the western Kimberley near Broome and extending north into the Dampier Peninsula in the eastern Kimberley, extending south to the east of the Pilbara to near Meekatharra and inland of Shark Bay, then east to near north-eastern South Australia and north again to the Tanami and Kimberley region (Figure 2). Appears to be widespread in the Northern Territory but does not extend into South Australia, Queensland or New South Wales.

## COMPARISON WITH OTHER SPECIES

True *L. stenodactylus* can be separated from its congeners based on several morphological characters. It has dorsal scales of similar size as on the venter (vs. dorsals larger on *L. squarrosus*) with dorsal scales uniform (vs. scattered raised tubercles on *L. byrnei*). It differs by possessing small apical plates (vs. absent in *L. damaeum*). For precloacal pores, *L. stenodactylus* typically has 4–6 (occasionally 0–3), *L. woodwardi* 0–5, whereas *L. byrnei*, *L. maini*, *L. occultum* and *L. steindachneri* have none, with the other species typically having two. The rostral does not contact the nostril in *L. stenodactylus* as well as in *L. byrnei*, *L. immaculatum* (Storr, 1988), *L. steindachneri* and *L. woodwardi*, and is variable in *L. occultum* and *L. squarrosus* and in contact in the other species. In *L. stenodactylus* and other congeners the terminal apical plates are approximately as wide as the width of the finger, except the plates are much larger in *L. bungabinna*, *L. byrnei*, *L. occultum*, *L. wombeyi* and *L. woodwardi*, and much smaller in *L. maini* and *L. microplax* sp. nov. and absent in *L. damaeum*.

In addition to these morphological characters, *L. stenodactylus* has a strong vertebral stripe, shared also by *L. bungabinna*, *L. immaculatum* and *L. microplax* sp. nov, whereas the other species tend to have irregular blotches on the dorsum. In contrast to the species with strong vertebral stripes, *L. stenodactylus* possesses a complex pattern of small to medium-sized spots on the side, whereas the other species tend to have a plainer background pattern with the spots in higher relief.

*Lucasium stenodactylus* is most closely related to *L. woodwardi*, and this is reflected in their resemblance. The most reliable way to distinguish between these species is size of the apical plates. In *L. stenodactylus*, the plates are relatively small and are only in contact proximally, giving a butterfly-like appearance. In contrast, in *L. woodwardi* the paired terminal plates are larger, protruding past the digit and in longer contact with each other where they join (Figure 3). Pattern also

differs, with *L. stenodactylus* usually having a strong vertebral stripe, although this is more variably expressed in the Kimberley region. In addition, *L. woodwardi* can also possess a vertebral stripe, but it is usually less well-defined (Figures 6–7).

#### REMARKS

Although *L. stenodactylus* has a relatively uniform appearance in the arid zone, specimens from the Kimberley of Western Australia and Top End of the Northern Territory tend to have a more complex pattern with a more weakly-defined vertebral stripe. Pepper et al. (2006) presented evidence of more complex genetic structure of the ‘non-Pilbara’ (= true *stenodactylus*) populations compared to the ‘Pilbara’ (= *woodwardi*) populations, suggesting the more uniform habitats of the arid zone have promoted greater genetic homogeneity compared to the Pilbara. Further sampling of *L. stenodactylus* across its range may reveal more complexity in the northern regions, but genetic sampling is not sufficient at present to evaluate this hypothesis.

The revised distribution of this species confines it to only Western Australia and the Northern Territory. *Lucasium stenodactylus* is not known to occur in South Australia, south-western Queensland or north-western New South Wales where it is replaced by the new species. In addition, records of *L. stenodactylus* from north-western Queensland have been reidentified to other *Lucasium* species (unpublished data; see also Vanderduys et al. [2020]).

#### ***Lucasium woodwardi* (Fry, 1914)**

Pilbara ground gecko

Figures 3–7

#### SYNONYMY

*Diplodactylus polyophthalmus* Gunther, 1867 (partim)

*Diplodactylus stenodactylus* Loveridge, 1934

*Diplodactylus woodwardi* Glauert, 1956

*Diplodactylus stenodactylus* Wermuth, 1965

*Lucasium stenodactylum* Oliver et al., 2007

#### MATERIAL EXAMINED

[*Diplodactylus polyophthalmus* (part.)] Günther, A. (1867). Paralectotype – unnumbered specimen in the collection of NHMUK from Nickol Bay (Karratha), Western Australia.

#### *Holotype*

**Australia: Western Australia:** WAM R14370 (juvenile), from Strelley River, Pilbara Division, Western Australia, collected by J.B. Cleland, probably August–October 1907; previously registered as 9876 on 27 March 1909 (see Ellis et al. 2018). The juvenile specimen is in very poor condition (Figure 1 in Ellis et al. [2018]).

See Appendix for additional material examined.

#### DIAGNOSIS

A *Lucasium* distinguished from other members of the genus by rostral excluded from nostril, rostral crease present, terminal apical plates slightly wider than width of the digits, tail moderately long (TailL%SVL ~0.77), males with 2–5 precloacal pores and females with 0–2 pores (usually none) and males with an enlarged cloacal spur typically flanked by a second smaller spur. Background colour rich reddish-brown, overlain by a network of dark variegations, small to medium pale yellowish spots scattered over dorsum; pale vertebral stripe typically absent, but if present usually poorly-defined.

#### DESCRIPTION

Body cylindrical with flat venter; head triangular, narrowing to rounded snout tip; eyes large; loreal region concave; moderate adductor muscles; ear opening small and circular; limbs gracile; five fingers and toes; tail long and tapering to fine point.

Rostral rectangular with crease extending from dorsal edge; rostral separated from nostril; two enlarged supranasals with rounded edges in narrow contact or separated by an internasal; enlarged upper and lower labials, approximately twice as wide as high; first supralabial approximately twice the height of second; scales on snout slightly enlarged; a small row of supraciliary spines in posterodorsal corner of the eye; mental with concave sides, flanked by three relatively large infralabials to each side, decreasing in size posteriorly (Figure 5B); gular scales decreasing in size, becoming granular on throat.

Scales on dorsum juxtaposed, rounded and slightly raised posteriorly; scales on venter juxtaposed and slightly rounded; scales on tail square and flattened, occurring in regular rows; in males a single large cloacal spur usually flanked by a second spur half to equal the size of the larger one on each side of tail base; precloacal pores dimorphic: 2–5 in mature males, typically 0 in females but occasionally up to 2; digits covered in fine scales, subdigital scales slightly enlarged; digits only slightly narrowing towards claw; paired terminal apical plates comparatively very wide, extending past margins of digit.

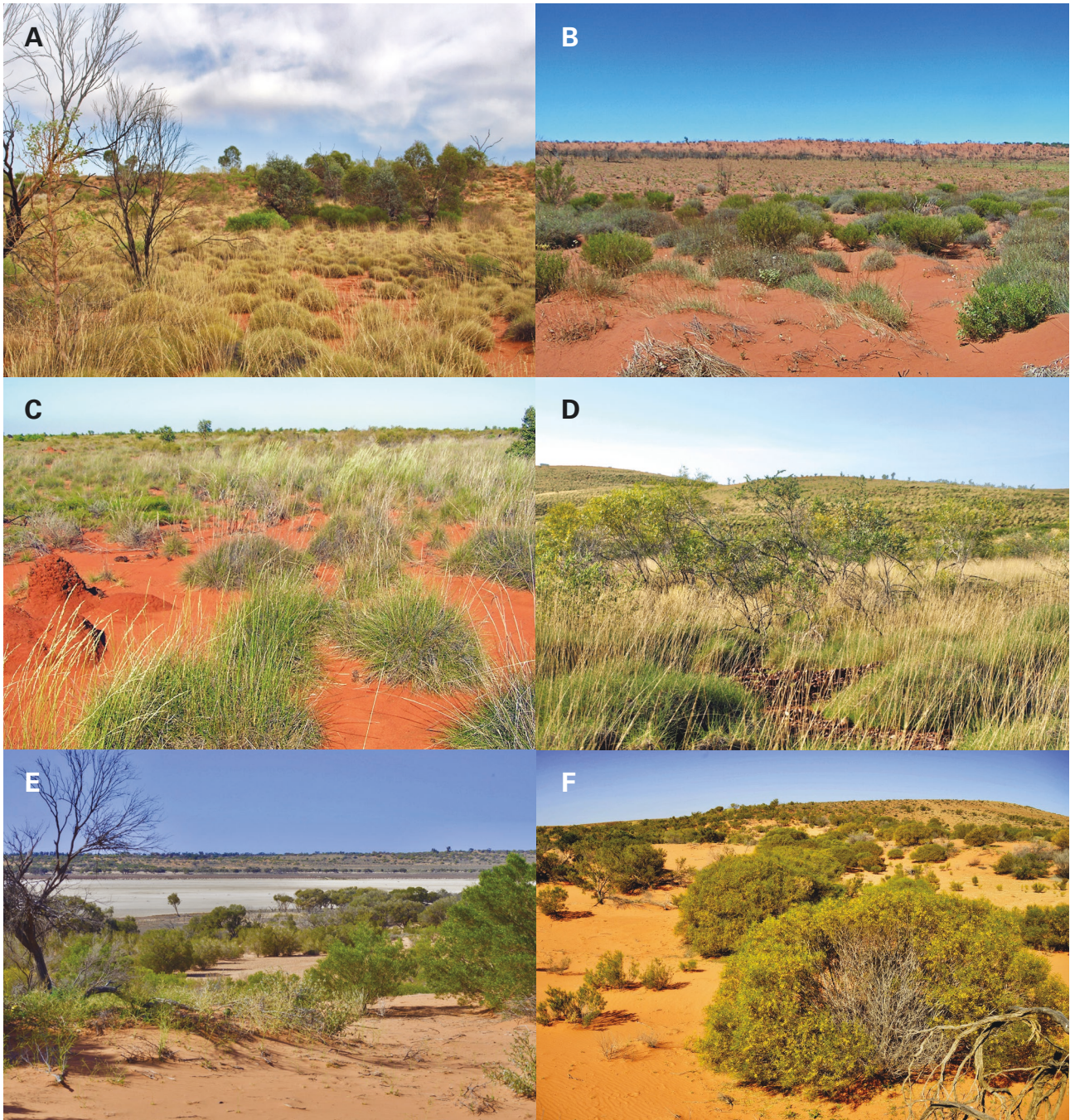
*Pattern and colour.* In life (Figures 6C, D), background colour rich reddish brown, with dark variegations tending to form a diffuse network; vertebral stripe variably present, formed by connection of blotches or with wavy edges, stripe frequently completely absent; small to medium pale yellow spots scattered across dorsum; a more diffuse yellow colouration frequently encloses several small spots to form larger irregularly-shaped blotches; top of head with irregular diffuse pale blotches; pale canthal stripe present, ventral edge with dark border; margins of eyelid highlighted with sulphur or yellow; tail pattern a continuation of body pattern, breaking into blotches distally. In preservative, specimens fade to a reddish-brown with most of the yellow hues lost (cf. Figures 6 vs. 7).

## HABITAT

Occurs on a range of substrates, including red sandhills, loamy soils, stony ground, creek lines, gibber plains and claypans (see Figures 9C, D). In the Pilbara Biodiversity Survey, habitat variables associated with this species indicated an affiliation with sandy and loamy surfaces, and rugged surfaces at the lower edges of slopes (Doughty et al. 2011). Vegetation includes spinifex, acacia and eucalyptus. Shelters under low rocks, fallen logs and recorded from spider burrows.

## DISTRIBUTION

This species is largely confined to the Pilbara region in Western Australia. It extends south along the coast to the North West Cape to the Gascoyne region as far as inland of Shark Bay and south-east to Kumarina (Figure 2). It is known from Barrow Island and the South Murion islands. In the sandy deserts to the north and east it is replaced by *L. stenodactylus*, and to the south-east by *L. bungabinna*.



**FIGURE 9** Habitats of lineages of the *Lucasium stenodactylus* species complex. A) Northern lineage, 30km W. Ilkurlka, Western Australia; B) Northern lineage, near Plumridge Lakes, Western Australia; C) Pilbara lineage, 50km E. Port Hedland, Western Australia; D) Pilbara lineage, 60km S. Karratha, Western Australia; E) South Australian lineage, near Lake Mary, South Australia; F) South Australian lineage, near Roxby Downs, South Australia. (Images A–D: B. Bush; E–F: M. Newton.)

## COMPARISON WITH OTHER SPECIES

This species is most similar to *L. stenodactylus*, its sister species (Figure 1). Accordingly, many of the characters that separate *L. stenodactylus* from other *Lucasium* also separate *L. woodwardi* from them (see account above). These characters include homogeneous dorsal scales of similar size to those on venter, nostril separated from rostral and multiple precloacal pores.

The main morphological character that reliably separates *L. woodwardi* from *L. stenodactylus* is the size and shape of the terminal apical plates. These pads are larger in *L. woodwardi* and have greater medial contact proximally before angling outwards past the edge of the digit. In contrast, the pads in *L. stenodactylus* are much smaller and do not typically protrude past the digit, the pads are in narrow contact proximally before angling outwards to form a butterfly shape (see Figure 3).

Pattern and colouration also separate these two species, but there is some degree of overlap. *Lucasium woodwardi* has a much richer reddish-brown background colouration compared to *L. stenodactylus*, which has a much lighter appearance (Figure 6). Presence of a vertebral stripe is variable in *L. woodwardi*, but when present it typically has irregular or wavy edges. In contrast, *L. stenodactylus* from the western deserts has a strongly-defined straight-edged vertebral stripe. Where these two species meet at the edge of the northern and eastern Pilbara the contrast between them is strong. However, Kimberley and some Northern Territory *L. stenodactylus* have a tendency to have a less pronounced vertebral stripe and the more amoeboid pattern of irregular blotches that is more common in *L. woodwardi*, making identification of museum specimens of unknown locality difficult on pattern alone.

## REMARKS

The close phenotypic resemblance of *L. woodwardi* and *L. stenodactylus* was reflected in the genetic results of Pepper et al. (2006, 2008) who found them to be sister taxa that diverged from each other ~5 mya. In his revision, Kluge (1967) barely commented on *L. woodwardi*, believing it to be *L. stenodactylus*. Not helping matters was the particularly poor state of the type specimen of *L. woodwardi*, a highly desiccated subadult, and the widely distributed '*D. stenodactylus* group' specimens that he examined over many years that were collected over a massive area of Australia (including those of the South Australian clade, his 'population B'). Owing to their ephemeral colours and often poor state of preservation in museum collections, the task of sorting large series of specimens into meaningful groups on the basis of colour pattern can be difficult, a problem that would have been more pronounced in the 1960s before specimens were preserved with the limbs and digits laid out and digital photographs taken.

Within the Pilbara, Pepper et al. (2008) found evidence for several major lineages within *L. woodwardi* that diverged from each other ~3–4.5 mya. They

hypothesised that lineages may be adapted to different substrates within the region, but this has yet to be tested against a non-adaptive biogeographic diffusion hypothesis.

***Lucasium microplax* sp. nov.**

Southern sandplain gecko

Figures 3–7, 10

urn:lsid:zoobank.org:act:5A1388B2-86B6-4059-8209-3C697DE04AB4

## MATERIAL EXAMINED

*Holotype*

**Australia: South Australia:** SAMA R48940, male, collected by G. Medlin and H. Ehmann from 6.4 km south-east of Stonewall Dam, Andamooka Station (30.7411°S, 137.3411°E) on 11 November 1996.

*Paratypes*

**Australia: South Australia:** SAMA R47644, male, Arcoona Station (31.074°S, 137.07°E); SAMA R50285, male, 3 km E Gap Well, Beltana Station (30.7844°S, 138.1547°E); SAMA R57229, male, Lake Bevis Paddock, Oakden Hills Station (31.5997°S, 136.7886°E); SAMA R57910, female, 59 km west-north-west of Emu (28.5367°S, 131.6067°E); SAMA R59337, male, 41 km north-north-west of Maralinga (29.8964°S, 131.2792°E).

**Australia: Western Australia:** WAM R166307, female, 16.8 km east-north-east of Blackstone (25.935°S, 128.438°E).

**Australia: Northern Territory:** NTM R25650, male, 10 km south of Kulgera (25°55'S, 133°12'E).

See Appendix for additional material examined.

## DIAGNOSIS

A *Lucasium* distinguished from other members of the genus by rostral in point contact with nostril, rostral crease present, terminal apical plates very small, not extending past digits, tail relatively short (TailL%SVL ~0.70), males and females with two precloacal pores and males with two enlarged cloacal spurs. Background colour a plain dark reddish-brown, isolated small to medium pale yellowish spots on sides that may be connected to well-defined vertebral stripe narrowly outlined by black.

## DESCRIPTION

Body cylindrical with flat venter; head triangular, narrowing to rounded snout tip; eyes large; loreal region concave; moderate adductor muscles; ear opening small and oval shaped; limbs gracile; five fingers and toes; tail long and tapering to fine point.

Rostral rectangular with crease extending to 1/3 into scale from dorsal edge; rostral usually in point contact

with nostril, at most, narrowly excluded from nostril; two enlarged supranasals with rounded edges always in narrow to moderate contact; enlarged upper and lower labials, approximately twice as wide as high; first supralabial 1.5 times the height of second; scales on snout slightly enlarged; several spinose scales on posterior edge of eyebrow; mental elongate, over twice the length as width, flanked by three large infralabials on each side, decreasing in size posteriorly, all infralabials relatively elongate (Figure 5C); gular scales decreasing in size, becoming granular on throat.

Scales on body juxtaposed, rounded and slightly raised posteriorly; scales on venter juxtaposed and slightly rounded; two enlarged cloacal spurs on each side of tail; precloacal pores in males and females 2, rarely 0; scales on tail square and flattened, occurring in regular rows; digits covered in fine scales, subdigital scales slightly enlarged; digits noticeably narrowing towards claw on distal phalanx; paired terminal apical plates very small, not extending past edges of digit.

*Pattern and colour.* In life, background colour dark reddish brown; pale beige vertebral stripe with straight well-defined edges; vertebral stripe forks at neck, continuing anteriorly above and through eye, continuing along canthus as pale streak to tip; top of head with irregular diffuse pale blotches; margins of eyelid highlighted with sulphur or yellow pigmentation; on lateral surfaces of body, a simple pattern of moderately large pale yellow spots contrasting with background colouration; yellow spots variably connected to vertebral

stripe or neighbouring spots; blotches occasionally forming a lateral line on forebody, extending below ear and connecting with gular region; dorsal surface of digits whitish; dorsal region of tail with a series of pale blotches; ventral surfaces drab white. In preservative, background colour becomes dark brown and yellow hues entirely lost.

*Measurements of holotype* (in mm). SVL – 51.5; TrunkL – 25.4; TailL – 31.5 (regenerated); TailW – 3.8; ArmL – 6.8; LegL – 8.6; HeadL – 13.6; HeadW – 8.4; HeadH – 5.6; OrbL – 3.5; NarEye – 4.7; SnEye – 5.3; EyeEar – 3.8; INar – 1.8; IO – 3.6; SupLab – 10; InfLab – 10; CreaseL – 15%; AntSup – 5; MenL – 1.4; MenL/W – 1.34; Pores – 2; Tail%SVL – 61.2 (regenerated); HeadL/SVL – 0.26; HeadW/SVL – 0.16; HeadH/SVL – 0.11.

#### HABITAT

This species occurs on a range of substrates, from compact sand, to coarse sand to sandy clay and stony country. In contrast, it is not known to occur on gibber, cracking clay or soft dune sand.

#### DISTRIBUTION

Most specimen records are from South Australia (Figure 2). In Western Australia, known from Blackstone and Warburton near the South Australia-Northern Territory border. Occurs in the central southern Northern Territory as far north as the Barrow Creek area. In Queensland it occurs in the Simpson



FIGURE 10 Holotype of *Lucasium microplax* sp. nov. in dorsal, ventral and lateral views. Scale bar = 1 cm.



desert in the south-west corner near the Northern Territory, as far east as Welford National Park and south to Bullo Downs. In New South Wales they occur in the extreme north-west of the state, with records from Sturt National Park, Milparinka and Thurloo Downs.

#### ETYMOLOGY

The specific name *microplax* means ‘small plate’ (Greek), in reference to the tiny apical plates in this species. Used as a noun in apposition.

#### COMPARISON WITH OTHER SPECIES

*Lucasium microplax* can be separated from its congeners on several scalation and pattern elements. It possesses homogeneous dorsal and ventral scales of approximately the same size compared to *L. byrnei* (heterogeneous dorsals) and *L. squarrosum* (enlarged dorsals). Males and females almost always have two precloacal pores (one on each side) in contrast to those species with more than two (*L. stenodactylus*, *L. woodwardi*) or zero (*L. byrnei*, *L. maini*, *L. occultum* and *L. steindachneri*). In *L. microplax*, the rostral is in point contact with the nostril most of the time (Figure 4B), although this varies occasionally with more extensive contact or narrow separation among individuals and is best used in combination with other characters.

Based on the presence of a strong vertebral stripe with straight edges, *L. microplax* resembles *L. stenodactylus*, *L. bungabinna* and *L. immaculatum* most, but differs in scalation and subtle elements of pattern and colouration. The new species possesses tiny apical plates, whereas *L. bungabinna* and *L. immaculatum* have much larger terminal lamellae. From *L. stenodactylus*, it differs by having the rostral and nostril in point contact, two precloacal pores, much smaller apical plates on a narrow terminal phalanx and a shorter tail. The pattern of the new species also has a more uniform dark brown background compared to the lighter *L. stenodactylus*, with the spots larger and in higher contrast.

#### REMARKS

After over 50 years since Kluge (1967) first posited that *L. microplax* (as his ‘population B’) could represent a new species, the molecular evidence of Pepper et al. (2006) and this study, coupled with a detailed examination of specimens from the WAM and SAMA collections have resolved the morphological variation sufficiently to confirm Kluge’s ‘population B’ as a new species.

The new species has an odd distribution, with its limits almost completely conforming to the borders of the state of South Australia. A detailed examination of specimens from across northern South Australia revealed no individuals of *L. stenodactylus*, while in south-western Northern Territory (Yulara, Curtin Springs) only *L. stenodactylus* has been recorded. Further field work in the states that adjoin northern South Australia would be useful in clarifying the

geographic extent of each species, habitat preferences and the degree to which the two species contact or overlap. There is an area of overlap between *L. microplax* and *L. stenodactylus* in south-central Northern Territory but at present no syntopic locations are known.

The unusual degree to which the distributions of *L. stenodactylus* and *L. microplax* align with state borders potentially explains why it took some time for the existence of two species to be recognised. Since each Australian state or territory has its own museum collection and research institute, it is possible that previous workers relegated one or two odd-looking ‘*L. stenodactylus*’ specimens in their collections to variation within that species. Only by drawing from specimens and tissue samples from several collections was it possible to demonstrate an abrupt and consistent change in both morphology and genetic data that has led to resolution of arid ‘*L. stenodactylus*’.

#### DISCUSSION

The taxonomy presented here further resolves ambiguity across the widespread *L. stenodactylus* species complex. The new species from South Australia had been suspected as early as the 1960s by Kluge (1967), but the species concepts employed then and with collections from the AAZ in their infancy, he simply denoted the Western Australian and South Australian populations in his monograph and did not formally describe them as separate species. Interestingly, he saw little evidence for recognising *L. woodwardi* from the Pilbara as a separate species from the western desert *L. stenodactylus* at the time. Again, this may have been due to critical lack of specimens available to him in the 1960s when collections had not yet grown owing to the development of the resource industry in the Pilbara. Equally, the introduction of molecular genetic methods has allowed us to overcome the problems posed by the extremely poor condition of the type of *Diplodactylus woodwardi*. By demonstrating the Strelley River type locality is occupied by a species that is distinct from *L. stenodactylus*, it has been possible to re-examine the type of *L. woodwardi* and to interpret its morphology with more confidence.

An unexpected insight of this study was that although long associated with *L. stenodactylus*, *L. microplax* is less closely related to that species than it is to some other *Lucasium*. Morphology within *Lucasium* appears to be an indifferent predictor of phylogenetic relationships, with morphologically distinctive species scattered among more conservatively patterned and structured species. Across *Lucasium*, there is a consistent colour pattern that is present in most species, comprising a reddish-brown dorsum patterned with numerous small pale spots and a vertebral stripe (sometimes broken into large semi-confluent blotches) that forks on the nape to terminate behind each eye, usually continuing as a canthal streak to the nostrils. Most species have adhesive terminal toe pads that are small to very small and

dorsal scales that are homogeneous and small. Species that diverge from one or more of these generalisations include *L. byrnei*, *L. wombeyi* and *L. alboguttatum* (colour pattern), *L. byrnei* and *L. squarrosus* (dorsal scalation), with the members of each of these subgroups not closely related to one another, and the padless *L. damaeum* is the sister of *L. alboguttatum* (toe pads moderately large) and *L. maini* (toe pads minute), not the very small-padded *L. squarrosus* or *L. microplax*.

Adaptive explanations of these morphological variations within *Lucasium* are hard to find. Most species are terrestrial and only climb, if at all, on very low vegetation (e.g. Oliver et al. 2008). The only rock-associated species, *L. wombeyi*, is perhaps the most divergent member of the genus in its slender, long-legged body form and relatively large adhesive pads, both consistent with moving over bare rock surfaces. However, the remaining species do not present much obvious adaptive correlation with substrate or habits. Large, small or no toe pads are found in desert sand-dwelling species, while moderate to small toe pads are found on species living on arid loamy or clayey terrain. Further study of the species when they are active at night may help clarify the degree to which their foraging behaviour and choice of microhabitat might correlate with the degree of toe pad development.

Based on a rough but commonly used mean rate of 2% pairwise sequence divergence per million years for the ND2 locus (Zamudio and Greene 1997; Oliver et al. 2010), divergences between the members of *Lucasium* treated here (~11–19%) indicate speciation largely occurred during the late Miocene, roughly 5.5–9.5 mya. This timing is concordant with a deepening of aridity across the AAZ, and is consistent with major radiations within other gekkonid species groups (e.g. Pepper et al. 2011; Oliver et al. 2014; Brennan et al. 2016; Laver et al. 2017).

Much of the recent taxonomic and population genetic work on *Lucasium* has been a progressive increase in our understanding of what constitutes inter- and intraspecific variation, which has been marked by a steady reduction in the set of populations that should be included within '*L. stenodactylus*' as additional species are recognised. Our restriction of *L. stenodactylus* is a further step, but this problem is still a work in progress. The Australian monsoonal tropics, the west of Queensland and New South Wales, the southern limits of the Northern Territory and eastern Great Victoria Desert in Western Australia remain poorly sampled for members of this genus. Given the variation which exists within our restricted concept of *L. stenodactylus*, future studies may be necessary to complete the revision of this species.

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APPENDIX Specimens of *Lucasium* used in this study. 'Morphology' — used in morphological assessment; 'Genotyped' — used in genetic analyses (x - this study; P06 - Pepper et al. [2006]).

Taxon	Collection	Specimen number	Location	Latdec	Londec	Morphology	Genotyped	GenBank
Northern	NTM	R6299	8KM S. Katherine, NT	-14.4833	132.3333	x		
Northern	SAMA	R29878	25.4km NNW. Curtin Springs Homestead, NT	-25.1917	131.6167		x	MW324003
Northern	SAMA	R36111	Yulara Township, NT	-25.2333	131.0167		x	MW324007
Northern	WAM	R108382	Sunrise Hill, WA	-20.5000	120.0800	x		
Northern	WAM	R108803	19km NE. Sandfire Roadhouse, WA	-19.7000	121.2333	x		
Northern	WAM	R110591	Tanami Desert, WA	-19.8986	128.8658	x	P06	
Northern	WAM	R110615	Tanami Desert, WA	-19.8997	128.8270	x		
Northern	WAM	R110766	Jimblebar East, WA	-23.3861	120.2353	x		
Northern	WAM	R127163	Nifty Mine, WA	-21.6666	121.5833	x		
Northern	WAM	R157732	Tanami Desert, WA	-19.5794	128.8681	x		
Northern	WAM	R157733	Tanami Desert, WA	-19.5794	128.8681	x		
Northern	WAM	R157946	Lake Disappointment, WA	-23.2983	122.7017	x		
Northern	WAM	R157947	Lake Disappointment, north-western lake edge, WA	-23.2341	122.7014	x		
Northern	WAM	R157949	Lake Disappointment, WA	-23.2983	122.7017	x		
Northern	WAM	R166309	22.6km NE. Blackstone, WA	-25.8572	128.4456		x	MW324006
Northern	WAM	R166325	5.3km SSE. Pungkulpirri Waterhole, WA	-24.7072	128.7603		x	MW324005
Northern	WAM	R175154	Kiwirrkurra Remote Community, WA	-22.8123	127.8313	x		
Northern	WAM	R21407	4mi E. Tennant Ck, NT	-19.6500	134.2500	x		
Northern	WAM	R84551	15km NE. Mt Aloysius, WA	-25.8000	128.6000	x		
Northern	WAM	R94774	~80km S. Telfer, WA	-22.3247	122.0756	x		
Northern	WAM	R94775	~80km S. Telfer, WA	-22.3280	122.0842	x		
Pilbara	WAM	R102053	De Grey River, WA	-20.3166	119.2500	x	P06	
Pilbara	WAM	R106155	31.5km SSW. Turee Ck Homestead, WA	-23.8666	118.5667	x	P06	
Pilbara	WAM	R108835	Kumarina Roadhouse, WA	-24.7000	119.6000	x	P06	
Pilbara	WAM	R110130	8km S. Coolawanyah (PBS-PE02), WA	-21.8822	117.7950	x	P06	

Taxon	Collection	Specimen number	Location	Latdec	Londec	Morphology	Genotyped	GenBank
Pilbara	WAM	R111806	16.8km SW. Pannawonica (PBS-BDRS02), WA	-21.7594	116.2275	x		
Pilbara	WAM	R111815	36km E. Wheelarra Hill (PBS-BDRS02), WA	-23.3831	120.4790	x		
Pilbara	WAM	R111843	14km SE. Wheelarra Hill (PBS-BDRS10), WA	-23.4711	120.2150	x		
Pilbara	WAM	R111858	22km SE. Wheelarra Hill (PBS-BDRS11), WA	-23.4986	120.2910	x		
Pilbara	WAM	R113031	Lesley Salt Works, WA	-20.2472	118.8472	x	P06	
Pilbara	WAM	R113591	42km NNE. Auski Roadhouse, WA	-21.9233	118.8333	x	P06	
Pilbara	WAM	R114920	6km E. Marble Bar, WA	-21.1666	119.8167	x	P06	
Pilbara	WAM	R115245	South Muiron Islands, WA	-21.6333	114.3833	x	P06	
Pilbara	WAM	R127703	5km S. Mt Tom Price, WA	-22.7991	117.7764	x	P06	
Pilbara	WAM	R132239	Urala Station, WA	-21.7777	114.8706	x	P06	
Pilbara	WAM	R154560	Wheelarra Hill, WA	-23.3791	120.1053	x	P06	
Pilbara	WAM	R156157	Waldburg Station, WA	-24.7811	116.9589	x	P06	
Pilbara	WAM	R158319	3.8km N. Giralia Homestead, WA	-22.6577	114.3919	x	P06	
Pilbara	WAM	R161075	7km SE. Marda Pool (PBS-DRW09), WA	-21.0699	116.2070	x	P06	
Pilbara	WAM	R161101	7.7km SW. Yanyare River Mouth (PBS-DRW03), WA	-20.8514	116.3770	x		
Pilbara	WAM	R161152	14km WSW. Roy Hill Station (PBS-RHNE05), WA	-22.6757	119.8410	x		
Pilbara	WAM	R170180	46km WSW. Tom Price (PBS-TCMBW01), WA	-22.8261	117.3710	x		
Pilbara	WAM	R170184	46km WSW. Tom Price (PBS-TCMBW01), WA	-22.8261	117.3710	x		
Pilbara	WAM	R170213	45km WSW. Tom Price (PBS-TCMBW02), WA	-22.8347	117.3820	x		
Pilbara	WAM	R170253	31km SE. Paraburdoo (PBS-TCMBC07), WA	-23.4164	117.8690	x		
Pilbara	WAM	R170264	51km ESE. Paraburdoo (PBS-TCMBC12), WA	-23.2925	118.1560	x		
Pilbara	WAM	R170272	19km SSW. Paraburdoo (PBS-TCMBC01), WA	-23.3644	117.6250	x		
Pilbara	WAM	R90635	Woodstock Station, WA	-21.6094	118.9744	x		
Pilbara	WAM	R90671	Woodstock Station, WA	-21.6094	118.9744	x		
SA	NTM	R14338	6km SSW. Claraville, NT	-23.4170	134.7340		x	MW323969
SA	NTM	R25650	10km S. Kulgera, NT	-25.9167	133.2000	x		
SA	SAMA	R20899	Olympic Dam, Roxby Downs, SA	-30.3800	136.8800		x	MW323993

Taxon	Collection	Specimen number	Location	Latdec	Londec	Morphology	Genotyped	GenBank
SA	SAMA	R26234	10km N. Lake Phillipson	-29.3583	134.4700		x	MW323994
SA	SAMA	R26536	Granite Downs Station, SA	-26.9500	133.5700		x	MW323968
SA	SAMA	R31828	23km SE. Lake Bring, SA	-30.3186	133.2161		x	MW323995
SA	SAMA	R32310	Lyons Siding, SA	-30.6300	133.9300		x	MW324002
SA	SAMA	R40901	Carmeena Well area, SA	-27.1331	132.4239		x	MW323984
SA	SAMA	R41864	6.8km S. Blue Hills Bore, SA	-27.1944	132.8686		x	MW323970
SA	SAMA	R42516	2km SE. Tallaringa Well, SA	-29.0500	133.3200		x	MW323960
SA	SAMA	R44897	1.5km ENE. Dulkaninna, SA	-28.9350	138.6178		x	MW323971
SA	SAMA	R45122	Yalymboo Paddock, Yalymboo Station, SA	-31.5422	136.6764		x	MW323996
SA	SAMA	R45290	Mt Vivian Station, 1.35km SE Crows Nest Bore, SA	-30.8422	135.7400		x	MW323997
SA	SAMA	R46380	2.4km E. Kenneberry Waterhole, SA	-29.6381	137.8078		x	MW323973
SA	SAMA	R46431	18.3km SW. Backadinna Hill, SA	-29.2889	135.1833		x	MW323975
SA	SAMA	R46454	3.5km NW. Beresford Rail Station, SA	-29.2164	136.6308		x	MW323972
SA	SAMA	R46493	7.6km NW. Mungutana Dam, SA	-29.2714	135.6328		x	MW323974
SA	SAMA	R46808	3.2km N. Anvil Hole Native Well, Witjira, SA	-26.3292	135.7053		x	MW323976
SA	SAMA	R47229	6.3km SSW. Ninety Nine Dam, Anna Ck Station, SA	-28.9508	136.7819		x	MW323977
SA	SAMA	R47289	8.4km NE. Mussel W/H, Peake Station, SA	-28.4156	136.4464		x	MW323978
SA	SAMA	R47317	6.5km ESE. Coppertop Hill, Peake Station, SA	-28.1453	136.0281		x	MW323979
SA	SAMA	R47450	1.2km SSW. Oolarinna East Bore, SA	-27.6250	132.9119		x	MW323988
SA	SAMA	R47641	Near Sangsters Bore, Todmorden Station, SA	-27.0700	134.8200		x	MW323998
SA	SAMA	R47644	Arcoona Station, SA	-31.0700	137.0700	x	x	MW323999
SA	SAMA	R48443	2.4km W. Little Cadna-owie Spring, Allandale Station, SA	-27.7861	135.6592		x	MW323980
SA	SAMA	R48543	1km SE. Muntree Kullana Bore, Macumba Station, SA	-27.7458	136.6994		x	MW323981
SA	SAMA	R48683	Kokatha Station, SA	-31.4092	135.3514		x	MW324000
SA	SAMA	R48940	6.4km SE. Stonewall Dam, Andamooka Station, SA	-30.7411	137.3411	x	x	MW323982
SA	SAMA	R50118	2.7km WSW. Sentinel Hill, SA	-26.1019	132.4353	x	x	
SA	SAMA	R50166	3.2km WNW. Sentinel Hill, SA	-26.0728	132.4192	x	x	MW323989

Taxon	Collection	Specimen number	Location	Latdec	Londec	Morphology	Genotyped	GenBank
SA	SAMA	R50285	3km E. Gap Well, Beltana Station, SA	-30.7844	138.1547	x		
SA	SAMA	R50286	3km E. Gap Well, Beltana Station, SA	-30.7844	138.1547	x		
SA	SAMA	R51218	22.9km WSW. Mundy Dam, SA	-26.5544	132.8672	x	x	MW323990
SA	SAMA	R51576	35km ESE. Amata, SA	-26.2769	131.4606	x	x	MW323991
SA	SAMA	R51620	29.2km ENE. Mimili, SA	-26.8975	132.9753	x		
SA	SAMA	R51622	29.7km WNW. Indulkana, SA	-26.8744	133.0272	x	x	MW323992
SA	SAMA	R52477	5km E. Woocalla, south of Pernatty Lagoon, SA	-31.6903	137.2442		x	MW324001
SA	SAMA	R52779	11.7km SSW. Mount Sarah homestead, SA	-27.0256	135.2211		x	MW323985
SA	SAMA	R52812	19.4km ESE. Oolgaawa W/H, SA	-26.8347	136.0717		x	MW323986
SA	SAMA	R53061	20km SE. Leigh Creek Town, SA	-30.4681	138.2808	x	x	MW323983
SA	SAMA	R54126	28.8km NW. Muloorina homestead, SA	-29.0786	137.6714		x	MW323987
SA	SAMA	R56454	5.6km W. Mt Hoare, SA	-27.0575	129.6439	x	x	MW323966
SA	SAMA	R57229	28km E. Vokes Hill Corner, SA	-28.5619	131.0014	x		
SA	SAMA	R57910	59km WNW. Emu, SA	-28.5367	131.6067	x		
SA	SAMA	R57911	59km WNW. Emu, SA	-28.5367	131.6067	x		
SA	SAMA	R57931	44.7km ESE. Emu, SA	-28.8525	132.5858	x		
SA	SAMA	R57945	51.1km ESE. Emu, SA	-28.8628	132.6556	x		
SA	SAMA	R58047	25km NE. Half Moon Lake, SA	-29.8761	133.6181		x	MW323961
SA	SAMA	R58973	47.4km W. Oak Valley, SA	-29.5086	130.2550	x	x	MW323967
SA	SAMA	R59337	41km NNW. Maralinga, SA	-29.8963	131.2791	x	x	MW323962
SA	SAMA	R59481	67.1km NNW. Maralinga, SA	-29.7325	131.0858	x	x	MW323963
SA	SAMA	R59484	67.1km NNW. Maralinga, SA	-29.7325	131.0858	x		
SA	SAMA	R60538	26.8km SSW. Mt Dare, SA	-26.3022	135.1783		x	MW323964
SA	WAM	R166307	16.8km ENE. Blackstone, WA	-25.9352	128.4378	x		
SA	WAM	R166308	16.8km ENE. Blackstone, WA	-25.9352	128.4378		x	MW323965
SA	WAM	R77991	23km NE. Warburton, WA	-26.0000	126.7500		P06	
SA	WAM	R77992	23km NE. Warburton, WA	-26.0000	126.7500		P06	