

RESEARCH ARTICLE

# Independent Transitions between Monsoonal and Arid Biomes Revealed by Systematic Revision of a Complex of Australian Geckos (*Diplodactylus*; Diplodactylidae)

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**Data Availability Statement:** All relevant data are within the paper and its Supporting Information files. Sequence data has been uploaded to GenBank and the accession numbers can be found in [Table 1](#).

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## Abstract

How the widespread expansion and intensification of aridity through the Neogene has shaped the Austral biota is a major question in Antipodean biogeography. Lineages distributed across wide aridity gradients provide opportunities to examine the timing, frequency, and direction of transitions between arid and mesic regions. Here, we use molecular genetics and morphological data to investigate the systematics and biogeography of a nominal Australian gecko species (*Diplodactylus conspicillatus sensu lato*) with a wide distribution spanning most of the Australian Arid Zone (AAZ) and Monsoonal Tropics (AMT). Our data support a minimum of seven genetically distinct and morphologically diagnosable taxa; we thus redefine the type species, resurrect three names from synonymy, and describe three new species. Our inferred phylogeny suggests the history and diversification of lineages in the AAZ and AMT are intimately linked, with evidence of multiple independent interchanges since the late Miocene. However, despite this shared history, related lineages in these two regions also show evidence of broadly contrasting intra-regional responses to aridification; vicariance and speciation in older and increasingly attenuated mesic regions, versus a more dynamic history including independent colonisations and recent range expansions in the younger AAZ.

## Introduction

The extent and intensity of arid conditions in the Southern Hemisphere has increased through the late Neogene, and expansive deserts are now a prominent feature of most southern continents (Africa, Australia and South America) [1–4]. These generally young arid zones are characterised by low, unpredictable rainfall and strong seasonal variation in temperature, and this major climatic shift has had profound biological implications; some lineages have adapted to

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aridity, while many others have retreated into shrinking mesic refugia or simply gone extinct [5–10].

In the face of expanding and intensifying aridification, comparatively mesic environments adjacent to arid areas serve a number of important functions. Over longer timescales, peripheral semi-arid or seasonally arid areas may provide zones in which lineages can accumulate preadaptations that mediate subsequent successful colonisation of more arid zones [11,12]. Over shorter timescales (for instance the Pleistocene glacial oscillations over the last 2.5 million years) peripheral habitats may also function as refugia during peaks of aridity, and subsequently a source of populations able to recolonize the arid zone when conditions ameliorate [13,14]. Radiations which now comprise multiple taxa widely distributed across arid and mesic areas provide powerful opportunities to compare lineage diversity across regions, and test the ideas about when, from where, and how, lineages colonised (or recolonised) nascent arid biomes [6,12,14–16].

The Australian Arid Zone (AAZ) and Australian Monsoonal Tropics (AMT) are two of the largest Australian biomes, and share a long border that spans most of northern Australia [9,17]. Many lineages occur across both regions, suggesting there has been significant evolutionary interchange, however only a small number of studies have examined the diversification of taxa spanning these two areas [14,18]. This work has generally supported the hypothesis that lineages in the AMT are characterised by higher taxonomic or genetic diversity and more narrow distributions (indicative of persistence and localised diversification), while the AAZ is inhabited by a smaller number of derived and often relatively widespread lineages (indicative of colonisation and range expansion) [14,16,18]. However the total number of studies remains few, and broader insight into how often, and when lineages diversified across these two biomes requires examination of additional lineages.

Squamates (lizards and snakes) are arguably the most successful vertebrate group in Australia [19,20] and are playing a key role in an emerging research program to understand how aridification has shaped patterns of evolution [12,21]. However, while the problem of cryptic diversity within Australian squamates was flagged over two decades ago [22], ongoing research and new methods continue to reveal high levels of unrecognised evolutionary diversity (e.g. [23,24]). Therefore it is not surprising that systematic work over the last two decades has also revealed numerous instances where overly conservative taxonomy has obscured macroevolutionary patterns such as long-term persistence, micro-endemism, inter-regional dispersal events, and morphological stasis (e.g. [6–8,14,15,25–27]).

*Diplodactylus conspicillatus* Lucas & Frost 1897 [28] is a small (svl < 65mm), terrestrial Australian gecko with a distinctive short plump tail (commonly referred to as the Fat-tailed Gecko). As currently defined this species has one of the widest distributions of any Australian lizard, and occurs across most of the AAZ and AMT in a diverse range of habitats, including desert, low open shrubland, low shrubland, low open woodland, low woodland, woodland and tall shrubland, and on a wide range of substrates [29]. A published overview of phylogenetic diversity in the genus *Diplodactylus* based on mitochondrial DNA, allozymes and karyotypes revealed nine divergent clades within the *D. conspicillatus* complex [30]. Although many of these were represented by few samples, each was recognised as a ‘candidate species’, pending further morphological and molecular work. Pepper *et al.* [24] subsequently presented a more comprehensive sampling of *D. conspicillatus sensu lato* in Western Australia, and also found evidence of deep divergences, including two near parapatric lineages in the Pilbara region.

Here we use an expanded mitochondrial dataset along with detailed morphological examination to assess how lineages of the *D. conspicillatus* complex have diversified across the AAZ and AMT. Specifically we a) contrast genetic diversity in the two regions, and b) use simple ancestral state reconstruction to assess the frequency and trajectory of shifts between biomes.

Based on these data we also present a revised taxonomy, formally recognizing seven of the lineages identified by Oliver et al. [29] as species (redefined *Diplodactylus conspicillatus sensu stricto*, resurrected *Diplodactylus hillii*, *D. laevis* and *D. platyurus* and three newly described species) and thereby add six further species to the diverse Australian lizard fauna.

## Methods

### Material examined

This study utilised specimens and tissues held in the Australian Museum (AMS), National Museum of Victoria (NMV), Northern Territory Museum and Art Gallery (NTM), Queensland Museum (QM), South Australian Museum (SAMA) and Western Australian Museum (WAM). Where possible, specimens included in genetic analyses were also included in morphological analyses. Tissue samples from nominated holotypes for all three newly described taxa were included in assessments of genetic diversity.

Morphological characterisation of the types of *D. conspicillatus* and its synonyms (as listed in Cogger et al., 1983), *D. hillii*, *Gymnodactylus laevis* and *D. platyurus*, was made by direct examination (*D. conspicillatus* [NMV] and *D. hillii* [QM]) or using photographic images generously provided by Dr H.G. Cogger (*Gymnodactylus laevis* [Naturmuseum Senckenberg, Frankfurt] and *D. platyurus* [British Museum of Natural History, London]).

### Genetic data

Genetic analyses included mitochondrial data from 169 specimens of *Diplodactylus conspicillatus sensu lato* (see Table 1 for specimen and locality information). DNA extraction and sequencing protocols for most samples are detailed elsewhere [25,31]. DNA from new samples was extracted using a Qiagen high throughput extraction robot at Museum Victoria. A ~1200 base pair (bp) region of the *ND2* gene and surrounding tRNAs was amplified using one of the following two combinations of primers: 1) AAG CTT TCG GGG CCC ATA CC (L4437) [32] and CTA AAA TRT TRC GGG ATC GAG GCC (Asn-tRNA) [33]; or 2) GCC CAT ACC CCG AAA ATS TTG and TTA GGGTRG TTA TTT GHG AYA TKC G [25]. PCR products were amplified for 40 cycles at an annealing temperature of 55°C. Unpurified PCR products were sent to a genetic services company (Macrogen, Korea) and sequenced in both directions using Sanger sequencing technologies.

New sequences generated in this study were aligned with data presented by Oliver et al. [30] and Pepper et al. [24]. Alignment of sequences was first performed automatically using the software MUSCLE [34], then refined by eye in Se-Al [35]. We translated nucleotide data into amino acid sequences and checked the alignment for internal stop codons and frame-shift mutations. Our final edited alignment included up to 1054 characters. We used the unlinked branch lengths and BIC settings in PartitionFinder [36] to determine the best partitioning strategy and model of nucleotide substitution (GTR+I+G, with all codon positions considered together in a single partition).

### Phylogenetic analyses

Phylogenetic relationships were estimated using standard Maximum Likelihood (RAxML v7.2.8) [37] and Bayesian techniques (BEAST v1.8.0) [38]. All unique samples were included in initial analyses (S1 Fig.), however for subsequent phylogenetic analyses we focused on a reduced subset of data from which a number of identical or near identical sequences for the two most extensively sampled major clades were removed. Maximum Likelihood analyses were run using the default settings for RAxML on the CIPRES portal; the GTR+G model of sequence

**Table 1. Museum Voucher and locality details of all specimens included in phylogenetic analyses.**

| Museum Number | Species               | Locality                               | Latitude (dec.) | Longitude (dec.) | Genbank # |
|---------------|-----------------------|--|-----------------|------------------|-----------|
| WAMR157640    | <i>conspicillatus</i> | Newman, WA                             | -23.3097        | 119.7569         | KM267082  |
| SAMAR20884    | <i>conspicillatus</i> | Olympic Dam area, Roxby Downs, SA      | -30.3833        | 136.8833         | FJ665543  |
| SAMAR45256    | <i>conspicillatus</i> | Salt Ck Cross E L Gairdner, SA         | -31.5500        | 136.3500         | FJ665541  |
| SAMAR51587    | <i>conspicillatus</i> | Amata, SA                              | -26.2828        | 131.4867         | FJ665542  |
| WAMR110770    | <i>conspicillatus</i> | Jimblebar East, WA                     | -23.4406        | 120.3333         | JX946871  |
| WAMR110769    | <i>conspicillatus</i> | Jimblebar East, WA                     | -23.3656        | 120.3211         | JX946870  |
| WAMR110762    | <i>conspicillatus</i> | Jimblebar East, WA                     | -23.3947        | 120.3097         | JX946873  |
| WAMR110767    | <i>conspicillatus</i> | Jimblebar East, WA                     | -23.3961        | 120.3100         | JX946874  |
| SAMAR46981    | <i>conspicillatus</i> | Mosquito Camp Dam, SA                  | -26.1578        | 134.5136         | FJ665547  |
| SAMAR26512    | <i>conspicillatus</i> | Granite Downs Station, WA              | -26.9500        | 133.5667         | FJ665545  |
| SAMAR26513    | <i>conspicillatus</i> | Granite Downs Station, WA              | -26.9500        | 133.5667         | FJ665544  |
| SAMAR51514    | <i>conspicillatus</i> | 3.3k SW Indulkana, SA                  | -26.9800        | 133.2700         | FJ665546  |
| WAMR136643    | <i>conspicillatus</i> | Lake Mason Station, WA                 | -27.6975        | 119.2800         | KM267080  |
| WAMR136647    | <i>conspicillatus</i> | Lake Mason Station, WA                 | -27.7141        | 119.5311         | KM267081  |
| WAMR97324     | <i>conspicillatus</i> | Mount Windarra, WA                     | -28.4583        | 122.2417         | JX946799  |
| WAMR144640    | <i>conspicillatus</i> | Kalgoorlie, WA                         | -30.2014        | 120.9742         | JX946847  |
| SAMAR42574    | <i>conspicillatus</i> | 168 km NE of Emu, SA                   | -28.2333        | 133.3333         | FJ665539  |
| SAMAR32133    | <i>conspicillatus</i> | Maralinga, SA                          | -30.2503        | 131.5458         | FJ665538  |
| SAMAR62135    | <i>conspicillatus</i> | 18.4k NE Blackstone, WA                | -25.8917        | 128.4269         | FJ665520  |
| SAMAR62106    | <i>conspicillatus</i> | Morgan Range, 16.8k ENE Blackstone, WA | -25.9353        | 128.4378         | FJ665523  |
| SAMAR62107    | <i>conspicillatus</i> | Morgan Range, 16.8k ENE Blackstone, WA | -25.9353        | 128.4378         | FJ665522  |
| WAMR166299    | <i>conspicillatus</i> | Morgan Range, 16.8k ENE Blackstone, WA | -25.9353        | 128.4378         | FJ665540  |
| QMJ92288      | <i>conspicillatus</i> | Mt Isa, QLD                            | -21.1300        | 139.2500         | FJ665534  |
| AMSR125042    | <i>conspicillatus</i> | Cunnamulla, QLD                        | -28.0667        | 145.6833         | FJ665533  |
| NTMR15362     | <i>conspicillatus</i> | Lawrence Gorge Waterhouse Range, NT    | -24.0200        | 133.4000         | FJ665535  |
| SAMAR38849    | <i>conspicillatus</i> | Namatjira/Larapinta Drive Junction, SA | -26.7667        | 133.4500         | FJ665536  |
| NTMR35949     | <i>conspicillatus</i> | 120km East of Argadargada, NT          | -21.2928        | 137.4100         | KM267074  |
| SAMAR38782    | <i>conspicillatus</i> | Tennant Creek, NT                      | -19.6667        | 134.2333         | FJ665537  |
| SAMARR38819   | <i>conspicillatus</i> | Three Ways, NT                         | -19.4333        | 134.2167         | EF681786  |
| NTMR24076     | <i>conspicillatus</i> | Arafura Swamp Arnhem Land, NT          | -12.5300        | 134.9000         | FJ665532  |
| WAMR110769    | <i>conspicillatus</i> | Jimblebar East, WA                     | -23.3656        | 120.3211         | KM267078  |
| WAMR110770    | <i>conspicillatus</i> | Jimblebar East, WA                     | -23.4406        | 120.3333         | KM267079  |
| WAMR110762    | <i>conspicillatus</i> | Jimblebar East, WA                     | -23.3947        | 120.3097         | KM267076  |
| WAMR110767    | <i>conspicillatus</i> | Jimblebar East, WA                     | -23.3961        | 120.3100         | KM267077  |
| WAMR97324     | <i>conspicillatus</i> | Mount Windarra, WA                     | -28.4583        | 122.2417         | KM267075  |
| WAMR144640    | <i>conspicillatus</i> | Kalgoorlie, WA                         | -30.2014        | 120.9742         | KM267083  |
| NTMR21395     | <i>barraganae</i>     | Mussellbrook, QLD                      | -18.6083        | 137.9883         | FJ665515  |
| NTMR17871     | <i>hillii</i>         | Corroboree Taven, NT                   | -12.7500        | 131.4833         | EF681785  |
| WAMR162453    | <i>custos</i>         | West Kununurra, WA                     | -15.7700        | 128.6700         | JX946794  |
| WAMR172853    | <i>custos</i>         | Ellenbrae Station, WA                  | -15.9839        | 127.0539         | KM267051  |
| WAMR164780    | <i>custos</i>         | The Grotto, WA                         | -15.7178        | 128.2597         | KM267049  |
| WAMR132713    | <i>custos</i>         | Wyndham, WA                            | -15.7119        | 128.2656         | JX946822  |
| WAMR172916    | <i>custos</i>         | Doongan Station, WA                    | 15.2290         | 125.2084         | KM267052  |
| WAMR172675    | <i>custos</i>         | Irvine Island, WA                      | 16.3353         | 124.0528         | KM267050  |
| CM1800        | <i>custos</i>         | Adcock Gorge, WA                       | -16.9267        | 125.7795         | KM267048  |
| AMSR143914?   | <i>platyurus</i>      | 16.6km W Georgetown on Croydon Rd, QLD | -18.2925        | 143.4014         | FJ665514  |

(Continued)

Table 1. (Continued)

| Museum Number | Species          | Locality                                    | Latitude (dec.) | Longitude (dec.) | Genbank # |
|---------------|------------------|---|-----------------|------------------|-----------|
| AMSR143909    | <i>platyurus</i> | 9.3km W Normanton P.O via Cloncurry Rd, QLD | -17.7300        | 141.0300         | FJ665512  |
| AMSR143911    | <i>platyurus</i> | 8.2km W Normanton P.O via Cloncurry Rd, QLD | -17.7300        | 141.0300         | FJ665511  |
| AMSR143916    | <i>platyurus</i> | 8.4km W of Georgetown on Croydon Rd, QLD    | -18.2800        | 143.4700         | FJ665513  |
| QMJ92887      | <i>platyurus</i> | Winton, QLD                                 | -22.4700        | 142.9200         | FJ665530  |
| SAMAR63336    | <i>platyurus</i> | Winton, QLD                                 | -22.4500        | 142.9500         | FJ665531  |
| ABTC31900     | <i>platyurus</i> | Noonbah Station, QLD                        | -24.1200        | 143.1800         | FJ665528  |
| AMSR143856    | <i>platyurus</i> | Stonehenge area, QLD                        | -24.3700        | 143.3200         | FJ665527  |
| AMSR158426    | <i>platyurus</i> | Sturt National Park, NSW                    | -29.3700        | 142.0300         | FJ66552   |
| QMJ92287      | <i>platyurus</i> | Mingella, QLD                               | -19.8700        | 146.6300         | FJ665526  |
| SAMAR63337    | <i>platyurus</i> | Mingella, QLD                               | -19.8700        | 146.6300         | FJ665525  |
| WAMR135321    | <i>bilybara</i>  | Cape Lambert, WA                            | -20.7544        | 117.0811         | JX946823  |
| WAMR140334    | <i>bilybara</i>  | Millstream-Chichester National Park, WA     | -21.4619        | 117.1625         | JX946838  |
| WAMR132531    | <i>bilybara</i>  | Burrup Peninsula, WA                        | -20.6767        | 116.7522         | JX946814  |
| WAMR132529    | <i>bilybara</i>  | Burrup Peninsula, WA                        | -20.6803        | 116.7436         | JX946813  |
| WAMR112197    | <i>bilybara</i>  | Onslow Area, WA                             | -21.6758        | 115.1458         | KM267032  |
| WAMR102917    | <i>bilybara</i>  | Cane River, WA                              | -22.1992        | 115.5486         | JX946835  |
| WAMR174500    | <i>bilybara</i>  | Barradale, WA                               | -22.9167        | 114.7667         | FJ665517  |
| WAMR158333    | <i>bilybara</i>  | Giralia Homestead, WA                       | -22.6939        | 114.3911         | JX946861  |
| WAMR157275    | <i>bilybara</i>  | Yanrey Station, WA                          | -22.2675        | 114.5228         | JX946865  |
| WAMR157302    | <i>bilybara</i>  | Yanrey Station, WA                          | -22.1578        | 114.5286         | JX946867  |
| WAMR126821    | <i>bilybara</i>  | Bush Bay, WA                                | -25.1258        | 113.8228         | KM267035  |
| WAMR120671    | <i>bilybara</i>  | Mardathuna Homestead, WA                    | -24.4069        | 114.4731         | JX946795  |
| WAMR127701    | <i>bilybara</i>  | Mount Tom Price Mine, WA                    | -22.8111        | 117.7675         | JX946796  |
| WAMR157533    | <i>bilybara</i>  | Robe River, WA                              | -21.7478        | 116.0753         | JX946856  |
| WAMR119206    | <i>bilybara</i>  | Carey Downs Homestead, WA                   | -25.5333        | 115.4667         | JX946787  |
| WAMR165713    | <i>bilybara</i>  | Jack Hills, WA                              | -26.0567        | 117.2161         | JX946876  |
| WAMR141359    | <i>bilybara</i>  | Cape Preston Area, WA                       | -21.0164        | 116.1956         | JX946843  |
| WAMR145193    | <i>bilybara</i>  | Learmonth Airstrip, WA                      | -22.2431        | 114.0347         | JX946848  |
| WAMR102503    | <i>bilybara</i>  | Barlee Range Nature Reserve, WA             | -23.1017        | 116.0078         | JX946784  |
| WAMR126769    | <i>bilybara</i>  | Mardathuna Homestead, WA                    | -24.5114        | 114.6367         | JX946773  |
| WAMR126770    | <i>bilybara</i>  | Boolathana Homestead, WA                    | -24.4131        | 113.6631         | JX946774  |
| WAMR126821    | <i>bilybara</i>  | Bush Bay, WA                                | -25.1258        | 113.8228         | JX946775  |
| WAMR126827    | <i>bilybara</i>  | Boolathana Homestead, WA                    | -24.4131        | 113.7067         | JX946776  |
| WAMR158331    | <i>bilybara</i>  | Giralia Homestead, WA                       | -22.6939        | 114.3911         | JX946860  |
| WAMR158333    | <i>bilybara</i>  | Giralia Homestead, WA                       | -22.6939        | 114.3911         | KM267045  |
| WAMR158335    | <i>bilybara</i>  | Giralia Homestead, WA                       | -22.6939        | 114.3911         | JX946862  |
| WAMR158349    | <i>bilybara</i>  | Giralia Station, WA                         | -22.7844        | 114.2792         | JX946863  |
| WAMR157275    | <i>bilybara</i>  | Yanrey Station, WA                          | -22.2675        | 114.5228         | KM267042  |
| WAMR157276    | <i>bilybara</i>  | Yanrey Station, WA                          | -22.2997        | 114.5931         | JX946866  |
| WAMR157302    | <i>bilybara</i>  | Yanrey Station, WA                          | -22.1578        | 114.5286         | KM267043  |
| WAMR126859    | <i>bilybara</i>  | Bush Bay, WA                                | -25.1258        | 113.8228         | JX946777  |
| WAMR156243    | <i>bilybara</i>  | Onslow Area, WA                             | -21.6886        | 115.0925         | JX946872  |
| WAMR151061    | <i>bilybara</i>  | Carnarvon, WA                               | -24.8833        | 113.7667         | JX946875  |
| WAMR165713    | <i>bilybara</i>  | Jack Hills, WA                              | -26.0567        | 117.2161         | KM267046  |
| WAMR102477    | <i>bilybara</i>  | Barlee Range Nature Reserve, WA             | -23.0447        | 115.7872         | JX946781  |
| WAMR102478    | <i>bilybara</i>  | Barlee Range Nature Reserve, WA             | -23.0447        | 115.7872         | JX946782  |
| WAMR102480    | <i>bilybara</i>  | Barlee Range Nature Reserve, WA             | -23.0447        | 115.7872         | JX946783  |

(Continued)

Table 1. (Continued)

| Museum Number | Species         | Locality  | Latitude (dec.) | Longitude (dec.) | Genbank # |
|---------------|-----------------|---|-----------------|------------------|-----------|
| WAMR102503    | <i>bilybara</i> | Barlee Range Nature Reserve, WA                       | -23.1017        | 116.0078         | KM267030  |
| WAMR123119    | <i>bilybara</i> | Bush Bay, WA  | -25.1258        | 113.8228         | JX946785  |
| WAMR122888    | <i>bilybara</i> | Mardathuna Homestead, WA                              | -24.4069        | 114.4731         | JX946786  |
| WAMR119206    | <i>bilybara</i> | Carey Downs Homestead, WA                             | -25.5333        | 115.4667         | KM267033  |
| WAMR127498    | <i>bilybara</i> | Onslow, WA  | -21.7333        | 115.0833         | JX946788  |
| WAMR127520    | <i>bilybara</i> | Onslow, WA  | -21.7333        | 115.0833         | JX946789  |
| WAMR120700    | <i>bilybara</i> | Boolathana Homestead, WA                              | -24.4131        | 113.7067         | JX946791  |
| WAMR120671    | <i>bilybara</i> | Mardathuna Homestead, WA                              | -24.4069        | 114.4731         | KM267034  |
| WAMR127701    | <i>bilybara</i> | Mount Tom Price Mine, WA                              | -22.8111        | 117.7675         | KM267036  |
| WAMR132529    | <i>bilybara</i> | Burrup Peninsula, WA                                  | -20.6803        | 116.7436         | KM267037  |
| WAMR132531    | <i>bilybara</i> | Burrup Peninsula, WA                                  | -20.6767        | 116.7522         | KM267038  |
| WAMR132532    | <i>bilybara</i> | Burrup Peninsula, WA                                  | -20.6767        | 116.7522         | JX946815  |
| WAMR135321    | <i>bilybara</i> | Cape Lambert, WA                                      | -20.7544        | 117.0811         | KM267039  |
| WAMR135378    | <i>bilybara</i> | Mt Brockman, WA                                       | -22.4197        | 117.4300         | JX946824  |
| WAMR135406    | <i>bilybara</i> | Mt Brockman, WA                                       | -22.3500        | 117.3500         | JX946825  |
| WAMR135408    | <i>bilybara</i> | Mt Brockman, WA                                       | -22.4197        | 117.4300         | JX946826  |
| WAMR135431    | <i>bilybara</i> | Mt Brockman, WA                                       | -22.4197        | 117.4300         | JX946827  |
| WAMR135455    | <i>bilybara</i> | Mount Brockman Area, WA                               | -22.4667        | 117.3000         | JX946828  |
| WAMR113620    | <i>bilybara</i> | Nanutarra, WA   | -22.4167        | 115.6167         | JX946830  |
| WAMR113621    | <i>bilybara</i> | Nanutarra, WA   | -22.4167        | 115.6167         | JX946831  |
| WAMR113635    | <i>bilybara</i> | Nanutarra, WA   | -22.4167        | 115.6167         | JX946832  |
| WAMR102917    | <i>bilybara</i> | Cane River, WA  | -22.1992        | 115.5486         | KM267031  |
| WAMR102945    | <i>bilybara</i> | Cane River, WA  | -22.1992        | 115.5486         | JX946836  |
| WAMR102946    | <i>bilybara</i> | Cane River, WA  | -22.1992        | 115.5486         | JX946837  |
| WAMR140334    | <i>bilybara</i> | Millstream-Chichester National Park, WA               | -21.4619        | 117.1625         | JX946838  |
| WAMR140980    | <i>bilybara</i> | Urala Station, WA                                     | -21.7767        | 114.8719         | JX946841  |
| WAMR141359    | <i>bilybara</i> | Cape Preston Area, WA                                 | -21.0164        | 116.1956         | KM267041  |
| WAMR139168    | <i>bilybara</i> | Burrup Peninsula, WA                                  | -20.6500        | 116.7667         | JX946844  |
| WAMR145193    | <i>bilybara</i> | Learmonth Airstrip, WA                                | -22.2431        | 114.0347         | KM267047  |
| WAMR112197    | <i>bilybara</i> | Onslow Area, WA                                       | -21.6758        | 115.1458         | JX946850  |
| WAMR157533    | <i>bilybara</i> | Robe River, WA  | -21.7478        | 116.0753         | KM267044  |
| WAMR158325    | <i>bilybara</i> | Giralia Homestead, WA                                 | -22.6939        | 114.3911         | JX946857  |
| WAMR158327    | <i>bilybara</i> | Giralia Homestead, WA                                 | -22.6939        | 114.3911         | JX946858  |
| WAMR158330    | <i>bilybara</i> | Giralia Homestead, WA                                 | -22.6939        | 114.3911         | JX946859  |
| SAMAR49077    | <i>laevis</i>   | 1.7k NE Candradecka Dam, SA                           | -27.2000        | 140.8700         | FJ665550  |
| SAMAR49081    | <i>laevis</i>   | 1.7k NE Candradecka Dam, SA                           | -27.2000        | 140.8700         | FJ665549  |
| SAMAR29936    | <i>laevis</i>   | Curtin Springs, NT                                    | -25.5200        | 131.8200         | FJ665544  |
| WAMR166303    | <i>laevis</i>   | 3.2k N Pungkulpirri Waterhole, Walter James Range, WA | -24.6286        | 128.7556         | FJ665551  |
| SAMAR36126    | <i>laevis</i>   | Yulara, NT  | -25.2300        | 131.0200         | FJ665553  |
| WAMR111703    | <i>laevis</i>   | Wheelara Hill, WA                                     | -23.3644        | 120.3450         | KM267059  |
| WAMR161577    | <i>laevis</i>   | Port Hedland, WA                                      | -20.3464        | 118.89301        | KM267069  |
| WAMR161601    | <i>laevis</i>   | Goldsworthy, WA                                       | -20.2419        | 119.5740         | KM267070  |
| WAMR157018    | <i>laevis</i>   | Fortescue Marsh, WA                                   | -22.4592        | 119.0364         | KM267067  |
| WAMR157131    | <i>laevis</i>   | Roy Hill, WA  | -22.6542        | 120.4097         | JX946864  |
| WAMR168480    | <i>laevis</i>   | Coulomb Point, WA                                     | -17.5736        | 122.1694         | KM267072  |
| WAMR132176    | <i>laevis</i>   | Nifty Mine, WA  | -21.6667        | 121.5833         | KM267062  |
| WAMR139264    | <i>laevis</i>   | Meentheena, WA  | -21.2869        | 120.4594         | JX946845  |

(Continued)

Table 1. (Continued)

| Museum Number | Species       | Locality                         | Latitude (dec.) | Longitude (dec.) | Genbank # |
|---------------|---------------|----------------------------------|-----------------|------------------|-----------|
| WAMR145516    | <i>laevis</i> | Port Hedland, WA                 | -21.0600        | 118.7500         | JX946849  |
| WAMR102048    | <i>laevis</i> | Strelley Homestead, WA           | -20.3667        | 119.0167         | JX946801  |
| WAMR104056    | <i>laevis</i> | Woodstock, WA                    | -21.6706        | 119.0417         | JX946807  |
| WAMR102054    | <i>laevis</i> | Mundabullangana, WA              | -20.7500        | 118.2500         | JX946802  |
| ABTC60729     | <i>laevis</i> | 30km SW Sangster's Bore, NT      | -21.0200        | 130.1300         | FJ665554  |
| WAMR114921    | <i>laevis</i> | Capricorn Roadhouse, WA          | -23.7167        | 119.7167         | JX946779  |
| WAMR166625    | <i>laevis</i> | Mons Cupri Mine, WA              | -20.8664        | 117.8219         | JX946877  |
| WAMR161868    | <i>laevis</i> | Marble Bar, WA                   | -21.4264        | 119.5530         | KM267071  |
| WAMR137010    | <i>laevis</i> | Wanjarri Nature Reserve, WA      | -27.3500        | 120.7667         | JX946833  |
| WAMR119777    | <i>laevis</i> | Tehan Rockface, WA               | -27.0333        | 124.7833         | JX946790  |
| WAMR110626    | <i>laevis</i> | Tanami Desert, WA                | -19.8944        | 128.8339         | JX946868  |
| WAMR94956     | <i>laevis</i> | Well 39, Canning Stock Route, WA | -21.7833        | 125.6500         | JX946798  |
| WAMR102637    | <i>laevis</i> | Little Sandy Desert, WA          | -24.0753        | 120.3606         | JX946780  |
| ABTC41350     | <i>laevis</i> | 134km ENE Laverton, WA           | -28.1700        | 123.6700         | FJ665547  |
| WAMR157131    | <i>laevis</i> | Roy Hill, WA                     | -22.6542        | 120.4097         | KM267068  |
| WAMR110626    | <i>laevis</i> | Tanami Desert, WA                | -19.8944        | 128.8339         | KM267058  |
| WAMR110758    | <i>laevis</i> | Jimblebar East, WA               | -23.3656        | 120.3303         | JX946869  |
| WAMR166625    | <i>laevis</i> | Mons Cupri Mine, WA              | -20.8664        | 117.8219         | KM267073  |
| WAMR166480    | <i>laevis</i> | Port Hedland, WA                 | -20.3697        | 119.6333         | JX946879  |
| WAMR113039    | <i>laevis</i> | Lesley Salt Works, WA            | -20.2833        | 118.8944         | JX946778  |
| WAMR114921    | <i>laevis</i> | Capricorn Roadhouse, WA          | -23.7167        | 119.7167         | KM267060  |
| WAMR102637    | <i>laevis</i> | Little Sandy Desert, WA          | -24.0753        | 120.3606         | KM267056  |
| WAMR119777    | <i>laevis</i> | Tehan Rockface, WA               | -27.0333        | 124.7833         | KM267061  |
| WAMR119956    | <i>laevis</i> | Woodie Woodie Mine, WA           | -21.6667        | 121.5833         | JX946792  |
| WAMR157395    | <i>laevis</i> | Tanami Desert, WA                | -19.6647        | 128.8858         | JX946793  |
| WAMR90895     | <i>laevis</i> | Woodstock, WA                    | -21.6117        | 118.9556         | JX946797  |
| WAMR94956     | <i>laevis</i> | Well 39, Canning Stock Route, WA | -21.7833        | 125.6500         | KM267053  |
| WAMR99143     | <i>laevis</i> | Woodstock Station, WA            | -21.6097        | 118.9622         | JX946800  |
| WAMR102048    | <i>laevis</i> | Strelley Homestead, WA           | -20.3667        | 119.0167         | KM267054  |
| WAMR102054    | <i>laevis</i> | Mundabullangana, WA              | -20.7500        | 118.2500         | KM267055  |
| WAMR104021    | <i>laevis</i> | Woodstock, WA                    | -21.6117        | 118.9556         | JX946803  |
| WAMR104047    | <i>laevis</i> | Woodstock, WA                    | -21.6117        | 118.9556         | JX946804  |
| WAMR104050    | <i>laevis</i> | Woodstock, WA                    | -21.6092        | 118.9742         | JX946805  |
| WAMR104051    | <i>laevis</i> | Woodstock, WA                    | -21.6092        | 118.9742         | JX946806  |
| WAMR104056    | <i>laevis</i> | Woodstock, WA                    | -21.6706        | 119.0417         | KM267057  |
| WAMR104061    | <i>laevis</i> | Woodstock, WA                    | -21.6092        | 118.9742         | JX946808  |
| WAMR104158    | <i>laevis</i> | Woodstock, WA                    | -21.6092        | 118.9742         | JX946809  |
| WAMR108856    | <i>laevis</i> | Mount Spinifex, WA               | -20.7833        | 118.1167         | JX946810  |
| WAMR113068    | <i>laevis</i> | Lesley Salt Works, WA            | -20.3194        | 118.9000         | JX946811  |
| WAMR104059    | <i>laevis</i> | Woodstock, WA                    | -21.6094        | 118.9619         | JX946812  |
| WAMR132546    | <i>laevis</i> | Degrey River Station, WA         | -20.2803        | 119.2019         | JX946816  |
| WAMR132175    | <i>laevis</i> | Nifty Mine, WA                   | -21.6667        | 121.5833         | JX946817  |
| WAMR132176    | <i>laevis</i> | Nifty Mine, WA                   | -21.6667        | 121.5833         | JX946818  |
| WAMR132177    | <i>laevis</i> | Nifty Mine, WA                   | -21.6667        | 121.5833         | JX946819  |
| WAMR132178    | <i>laevis</i> | Nifty Mine, WA                   | -21.6667        | 121.5833         | JX946820  |
| WAMR132689    | <i>laevis</i> | Shay Gap, WA                     | -20.5778        | 120.3331         | JX946821  |
| WAMR113612    | <i>laevis</i> | Newman, WA                       | -23.0175        | 119.8906         | JX946829  |

(Continued)

Table 1. (Continued)

| Museum Number | Species       | Locality                    | Latitude (dec.) | Longitude (dec.) | Genbank # |
|---------------|---------------|-----------------------------|-----------------|------------------|-----------|
| WAMR137010    | <i>laevis</i> | Wanjarri Nature Reserve, WA | -27.3500        | 120.7667         | KM267064  |
| WAMR138110    | <i>laevis</i> | Nifty Copper Mine, WA       | -21.6667        | 121.5833         | JX946834  |
| WAMR140708    | <i>laevis</i> | Hope Downs, WA              | -22.7328        | 119.4086         | JX946839  |
| WAMR140712    | <i>laevis</i> | Hope Downs, WA              | -22.8369        | 119.3758         | JX946840  |
| WAMR139020    | <i>laevis</i> | Mandora, WA                 | -19.8122        | 121.4736         | JX946842  |
| WAMR139264    | <i>laevis</i> | Meentheena, WA              | -21.2869        | 120.4594         | KM267065  |
| WAMR139283    | <i>laevis</i> | Meentheena, WA              | -21.2900        | 120.4664         | JX946846  |
| WAMR145516    | <i>laevis</i> | Port Hedland, WA            | -21.0600        | 118.7500         | KM267066  |
| WAMR153889    | <i>laevis</i> | WeeliWolli Creeck, WA       | -22.8208        | 119.2869         | JX946851  |
| WAMR157003    | <i>laevis</i> | Fortescue Marsh, WA         | -22.4144        | 119.0067         | JX946852  |
| WAMR157018    | <i>laevis</i> | Fortescue Marsh, WA         | -22.4592        | 119.0364         | JX946853  |
| WAMR157024    | <i>laevis</i> | Fortescue Marsh, WA         | -22.4592        | 119.0364         | JX946854  |
| WAMR157500    | <i>laevis</i> | Fortescue Marsh, WA         | -22.4592        | 119.0364         | JX946855  |

doi:10.1371/journal.pone.0111895.t001

evolution (as preferred by Stamatakis, [37]), and ceasing bootstrapping when MRE-bootstrapping criteria had been reached.

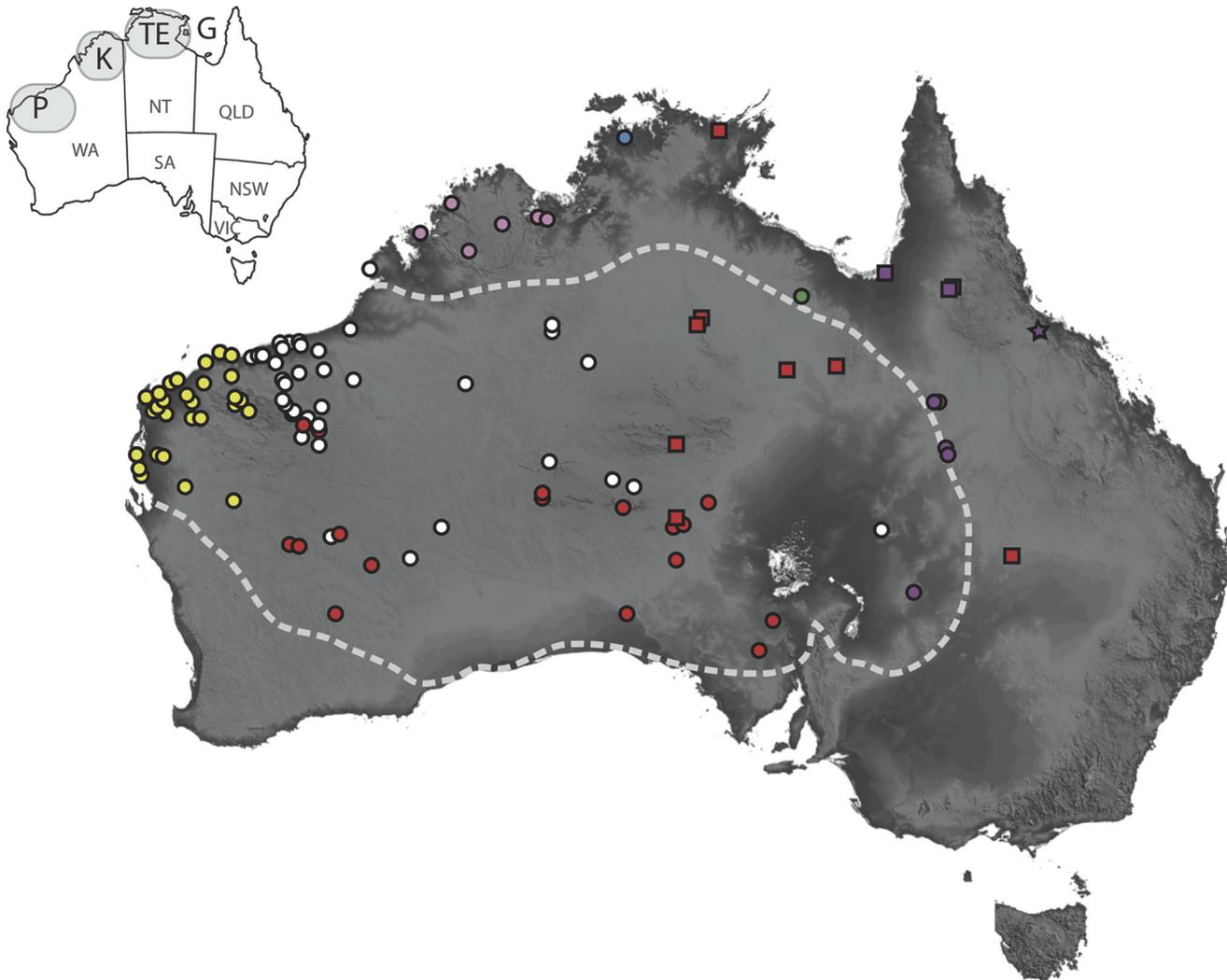
Bayesian analyses in BEAST used models and partitions as suggested by Partitionfinder, the Yule speciation prior (appropriate for analyses including relatively divergent lineages) and a relaxed log-normal clock and with model and partitions applied as above. After initial experimentation with settings and sampling, the final MCMC chains were run for 50 million generations, sampling every 50,000 steps. We estimated a timeframe of divergence using a 3% mean rate of pairwise sequence divergence (with a range between 1–4%) per one million years (see Oliver et al. [16] for justification). Tracer v1.5 [39] was used to confirm stability of parameter estimates and adequate mixing of the MCMC chains, and determine appropriate burn-in and acceptable effective sample sizes (> 200). Maximum clade credibility trees, after exclusion of the first ten million generations (20%), were summarized with TreeAnnotator v1.7.2 [38].

### Biome evolution

Ancestral state analyses were coestimated with topology and divergence dates in BEAST. To assess the number and nature of transitions between biomes, each node was coded as to whether the corresponding specimen was from within (1) or outside (0) the AAZ (defined here by a moisture index [mean annual rainfall divided by evaporation] of less than 0.4 [9]; Fig. 1, dotted line). The biome state of all outgroups was coded as ambiguous because: a) basal relationships within *Diplodactylus* were unresolved, and b) some of these taxa occur in the temperate biome, while this study is focused on transitions between the AMT and AAZ. The pattern of biome evolution was estimated using a simple substitution model for binary data which assumes equal probabilities for transitions between all states [40].

### Population genetics

To infer past demographic fluctuations in response to the climate cycles of the Pleistocene, we calculated nucleotide diversity and tested for population size change using the basic population genetic measurements of Tajima's *D* [41], Fu's *F<sub>s</sub>* [42] and *R<sub>2</sub>* [43] as implemented in DnaSP v. 5.0 [44]. Estimates and significance were calculated with 1000 coalescent simulations against the null hypothesis of a constant population size model, for each population corresponding to



**Fig 1. Distribution of genetically sampled individuals for major genetic lineages in the *D. conspicillatus* complex.** Pink = *D. custos* sp. nov., Blue = *D. hillii*, Green = *D. barraganae* sp. nov., Purple = *D. platyurus* (circle = lineage F, star = lineage G, squares = lineage H), Red = *D. conspicillatus* (squares = northern lineage, circles = southern lineage), White = *D. laevis*, Yellow = *D. bilybara* sp. nov. The dashed line corresponds to the transition between regions with a moisture index (mean annual rainfall divided by evaporation) less than 0.4 (arid) to greater than 0.4 (semiarid to mesic) and is widely used as an approximate boundary of the Australian Arid Zone. Inset map on the top left corner indicates putative regions of endemism mentioned in the text; P = Pilbara, K = Kimberley, TE = "Top End", G = Gulf country.

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the phylogenetically distinct groups based on the mtDNA gene tree. As these historical inferences were based on data from the mitochondrial genome, they should be regarded as a preliminary framework requiring corroboration with appropriate nuclear loci. For major clades intra and inter-specific genetic distances were estimated using Arlequin v. 3.11 [45].

### Morphometrics

All measurements (except SVL) and bilateral counts were recorded from the left side. The following measurements were taken using Mitutoyo electronic callipers: snout to vent length (SVL), tip of snout to anterior margin of cloaca with body straightened; tail length (T), from posterior margin of cloaca to tip of tail; tail width (TW), widest point across original tail; head

length (HL), mid anterior margin of ear to tip of snout; head width (HW), widest point of head, usually corresponding with, or slightly posterior to, position of ear opening; head depth (HD), lower jaw to top of head at mid orbit; snout length (S), tip of snout to anterior margin of orbit; eye to ear (EE), posterior margin of orbit to mid anterior margin of ear; length of forelimb (L1) and hindlimb (L2), from insertion to tip of longest digit (claw included), with limb stretched straight perpendicular to body; and (AG) axilla to inguinal region with body straightened.

The following scale counts and characters were recorded: subdigital scales from tip of digit (4<sup>th</sup> finger, 4<sup>th</sup> toe) to basal junction of 3<sup>rd</sup> and 4<sup>th</sup> digits (series includes enlarged distal pair); supralabial and infralabial scale rows (beginning immediately posterior to rostral and mental scales, and terminating where there is a noticeable reduction in size, or the labial scales begin to pull away from the lip line [approximately level with mid orbit]); number of small scales contacting the posterior edges of the rostral and mental scales; the number of scales in a longitudinal series along the length of the original tail (along vertebral line); the number of scales across the original tail (transverse count taken across the large scale row closest to widest point of tail); the size of the back, nape and head scales (relative to flank and lateral neck scalation); the presence or absence of a small medially projecting process on the posterior edge of the mental; and finally, the size of the 1<sup>st</sup> supralabial in relation to the rest of the supralabial row. Specimens included in the morphometric assessment are listed within the species accounts. Additional material examined is listed in [S1 Appendix](#).

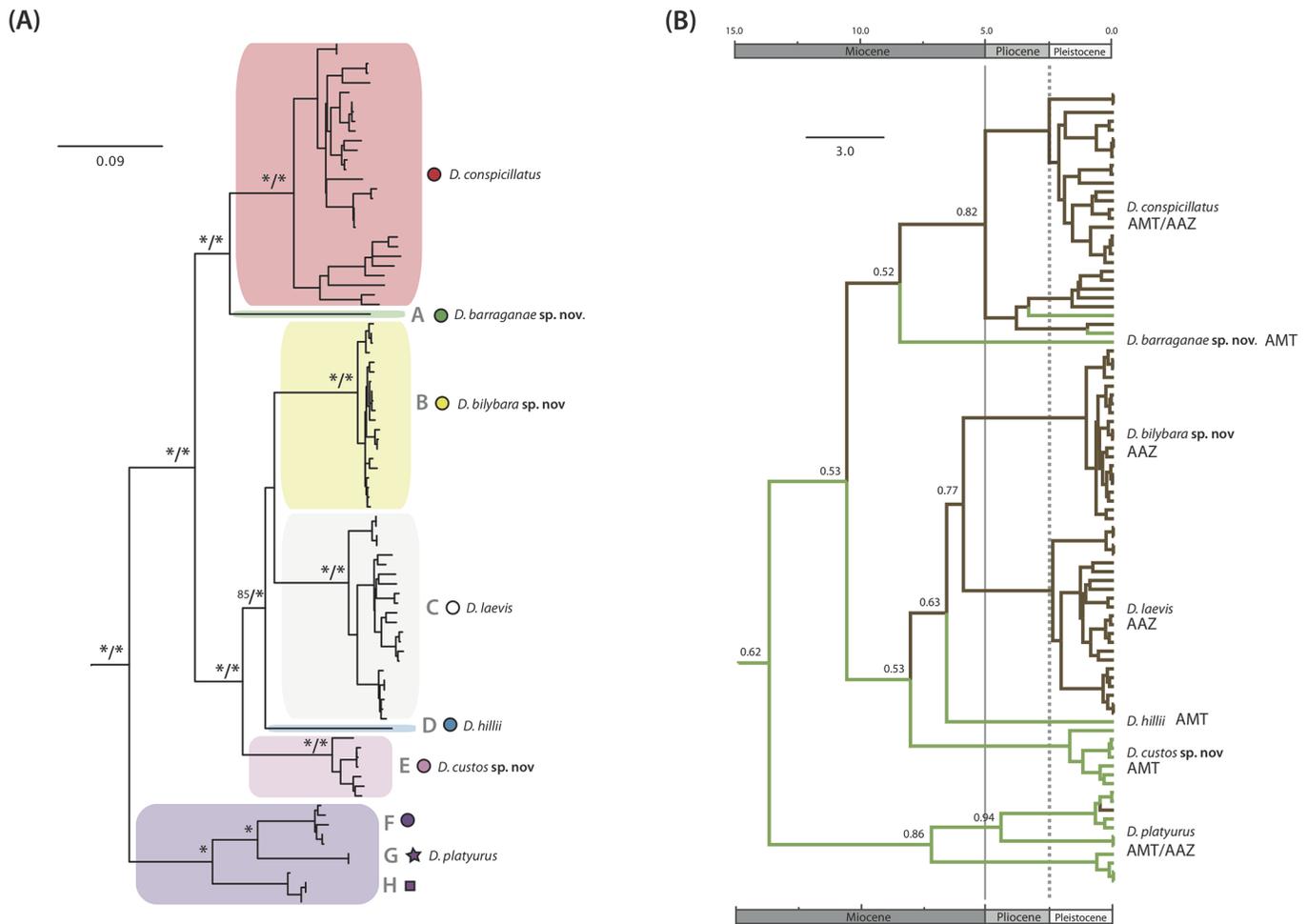
## Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "<http://zoobank.org/>". The LSID for this publication is: urn:lsid:zoobank.org:pub:C410144B-EC99-4AA4-8780-A2858356CF32. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

## Results

### Phylogenetic relationships

Monophyly of *D. conspicillatus sensu lato* was strongly supported in all analyses ([Fig. 2A–B](#)). Within this clade we identified the nine major lineages corresponding to the candidate species identified by Oliver et al. [30], specifically; *D. conspicillatus sensu stricto*—widespread in the arid zone and extending into the AMT; lineage A—Gulf region, north Queensland; lineage B—western Pilbara and Carnarvon region, Western Australia; lineage C—widespread arid zone; lineage D—western Top End, Northern Territory; lineage E—Kimberley, Western Australia; lineage F—Channel Country, western and central Queensland and far north-west New South Wales; lineage G—around Townsville, Queensland; and lineage H—gulf country, north Queensland ([Fig. 1](#)). Monophyly of all major clades is strongly supported, and mean uncorrected genetic divergence between lineages is relatively high (11.3–22.5%) ([S1A Table](#)). Lineages B, C, D and E form a clade that is well supported as sister to another clade comprising *D. conspicillatus sensu stricto* and lineage A. Collectively these clades (*D. conspicillatus sensu stricto* and



**Fig 2. Phylogenetic summaries.** (A) Maximum likelihood phylogeny based on the mtDNA gene *nd2* estimated using RaxML for all major lineages within the *D. conspicillatus* complex. Lineage names A-H follow Oliver et al. 2009. Clades are colour-coded to match distributions in Figs. 1 and 3. Nodes with ML support above 95 and Bayesian support (BEAST) above 99 (respectively) are indicated with an asterisk (\*). (B) Chronogram and ancestral biome states for the seven species in the revised *D. conspicillatus* group estimated using BEAST and calibrated with a 3% pairwise mean rate of molecular evolution. Green lineages are from outside the central Australian arid zone (defined by a moisture index of less than 0.4), brown lineages are from inside the Australian arid zone, and the probability (i.e. percentage of reconstructions that feature the observed state) of the inferred ancestral habitat is indicated for major nodes.

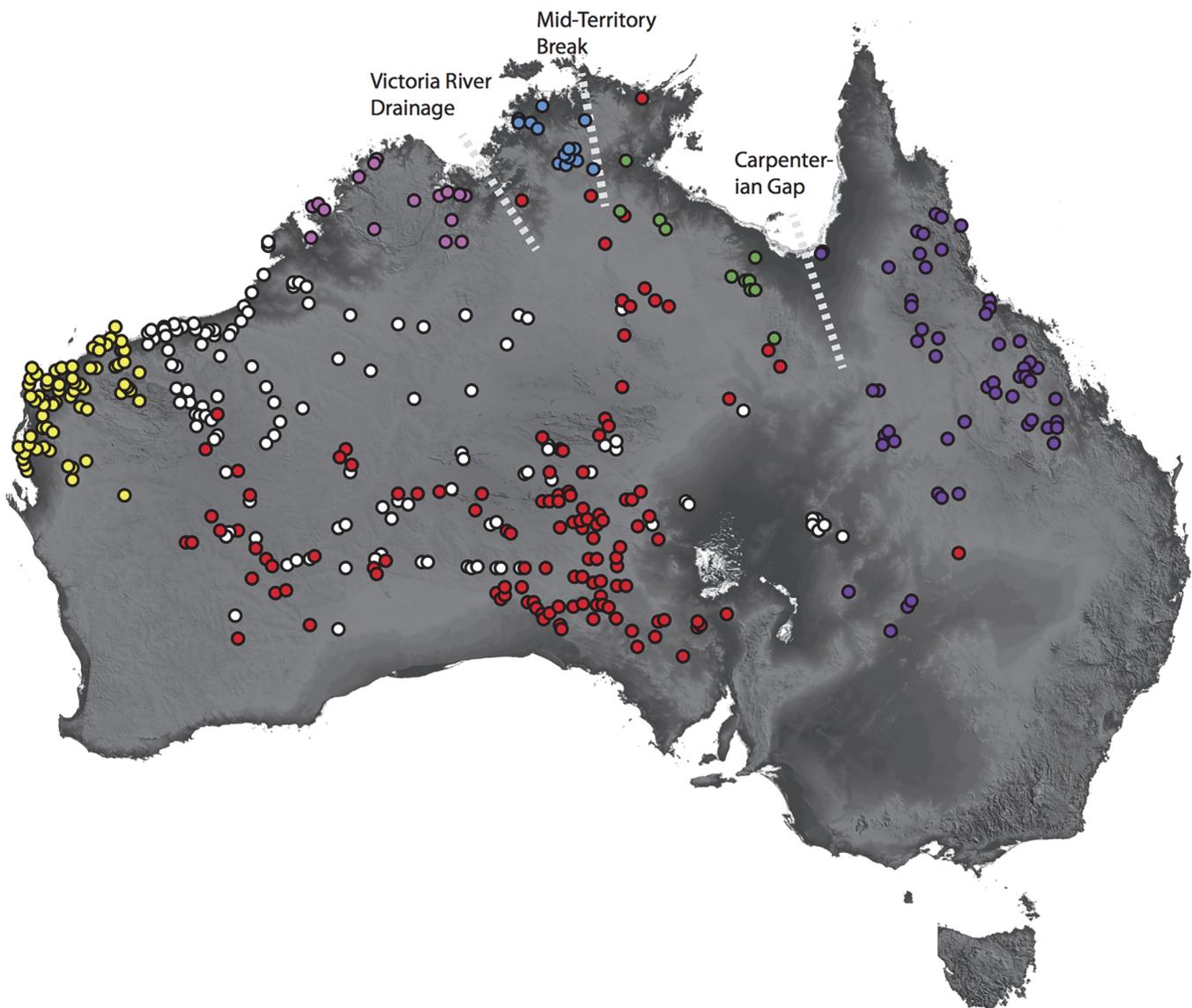
doi:10.1371/journal.pone.0111895.g002

A–E) are well supported as sister to the most divergent clade of the complex which contains lineages F–H from eastern Australia.

### Divergence dates and biome evolution

Topology and support values for the phylogeny of the *D. conspicillatus* complex co-estimated by BEAST were congruent to those from RaxML (Fig. 2A–B). Age estimates derived from application of a mean pairwise sequence divergence rate of 3% per million years suggests the deepest divergences within the complex (including the majority of the lineages and major clades discussed above) occurred in the late Miocene (~5–10mya). Where dense sampling was available the accumulation of diversity within most candidate species is estimated to have occurred during the Pleistocene, with the exception of the clade comprising lineages F–H which includes a number of deep and relatively poorly sampled lineages distributed across Queensland.

Distributional data based on morphotyped samples indicates that of the nine major lineages in the *D. conspicillatus* complex, five (A, D, E, G and H) are absent from the central arid zone (and are mostly restricted to the AMT), two (*D. conspicillatus sensu stricto* and F) occur in the both AMT and AAZ, and two (lineages B and C) are restricted to the AAZ (although the range of the former is centred on the comparatively mesic Pilbara [see [discussion](#) below]) (Fig. 3). Support for most ancestral state reconstructions was relatively weak, but our results suggest that monsoonal environments are ancestral and also provide strong evidence that there have been multiple transitions between the arid and monsoonal areas (Fig. 2B).



**Fig 3. Distribution of species in the *Diplodactylus conspicillatus* complex based on morphological analyses of holdings in Australian museums.** Pink = *D. custos* sp. nov., Blue = *D. hillii*, Green = *D. barraganae* sp. nov., Purple = *D. platyurus*, Red = *D. conspicillatus*, White = *D. laevis*, Yellow = *D. bilybara* sp. nov. Dashed lines indicate approximate locations of biogeographic breaks mentioned in the text.

doi:10.1371/journal.pone.0111895.g003

## Population genetics

Genetic sampling for a number of lineages was sparse, and only *D. conspicillatus sensu stricto* ( $n = 28$ ), lineage B ( $n = 60$ ) and lineage C ( $n = 62$ ) were well sampled with good geographic spread across their distributions (S1B Table). *Diplodactylus conspicillatus sensu stricto* included two divergent sublineages ( $>10\%$  divergence) with distributions in arid and monsoonal areas of Queensland and the Northern Territory, and in arid South Australia and Western Australia, respectively. These two sublineages also showed evidence of further structure (especially the north sublineage which showed mean genetic divergence of 6.7%). Lineage B showed low structure across its distribution in the western/southern Pilbara and Carnarvon Basin (mean 1.3%), while lineage C was characterised by moderate mitochondrial haplotypic diversity (mean 3.9%), especially in the western edge of its range in the northeastern Pilbara and surrounding regions.

Our analyses of population size change using summary statistics indicate that lineages B and C from the AAZ both had significant and large negative values for  $F_u$ 's  $F_s$  ( $-33.0$  and  $-14.3$ , respectively)—consistent with a signature of contiguous range expansion [42]. Tajima's  $D$  measurements were significantly negative only for lineage B. The other widespread arid zone lineage *D. conspicillatus sensu stricto* had small negative values ( $-2.55$ ), however these measurements were again not significant. There was no evidence of deviation from neutral expectations in the largely AMT lineages E or F–H (considered together), which can be interpreted demographically as stable populations in mutation-drift equilibrium [42] (S1C Table). As sampling for all of these northern lineages was very sparse these results should be interpreted with caution.

## Morphology

Morphological analyses of genotyped specimens revealed a suite of characters that diagnosed most of the major lineages identified (see Table 2): the presence or absence of a) a well developed canthal stripe (Fig. 4A–B), b) an enlarged 1<sup>st</sup> supralabial (Fig. 4C–D), c) enlarged plate-like scales on the mid-dorsum and nape (Fig. 5 A–D), d) clearly defined transverse rows of enlarged scales across the original tail, and e) original tail with a pointed, attenuated tip (Fig. 6A–F). Using these characters we were readily able to assign specimens to most of the lineages identified by the molecular analyses, and determine the identity of museum specimens for which molecular data were unavailable. The exception to this general pattern was the three eastern lineages (F, G, H), which could be readily diagnosed from all other lineages in lacking a distinctively enlarged first supralabial scale and in having no (or a poorly developed) canthal stripe, but aside from evidence of size differentiation did not show such consistent diagnostic morphological features from each other.

## Discussion

### Species diversity

Delimiting species boundaries involves integration of independent data sources to identify distinct evolutionary lineages [46], ideally including information from multiple nDNA loci, morphology, geography, ecology and reproduction [47]. The limitations of using mtDNA alone to infer species boundaries and historical phylogeography are widely recognised [48]. However, six of the nine major mitochondrial lineages we identified (*D. conspicillatus sensu stricto* and lineages A–E) are deeply divergent from each other and in addition can be readily diagnosed by a suite of morphological characters (distinctive features of scalation on the dorsum and original tails). Thus two lines of evidence support the hypothesis that these represent evolutionarily

**Table 2. Summary of key meristic and mensural data for species in the *D.conspicillatus* complex.**

| Character                                       | <i>D. conspicillatus</i>          | <i>D. hillii</i>                  | <i>D. laevis</i>                  | <i>D. platyurus</i>                | <i>D. barraganae sp. nov.</i>     | <i>D. bilybara sp. nov.</i>       | <i>D. custos sp. nov.</i>         |
|---|-----------------------------------|-----------------------------------|-----------------------------------|------------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|
| <b>SVL</b>                                      | 54.4 ± 4.0<br>(47.1–62.7, n = 32) | 46.3 ± 5.5<br>(25.1–52.3, n = 19) | 54.9 ± 4.7<br>(42.4–64.9, n = 30) | 48.7 ± 5.2<br>(40.6–60.2, n = 36)  | 41.8 ± 6.8<br>(25.1–49.5, n = 17) | 48.8 ± 5.2<br>(39.2–60.8, n = 28) | 50.6 ± 5.8<br>(42.2–58.2, n = 13) |
| <b>AG (% SVL)</b>                               | 50.4 ± 0.0<br>(45.7–57.4, n = 32) | 48.5 ± 0.0<br>(43.9–56.2, n = 19) | 51.8 ± 0.0<br>(46.0–57.3, n = 30) | 48.8 ± 0.0<br>(42.4–56.4, n = 32)  | 49.9 ± 0.0<br>(45.1–55.8, n = 17) | 49.6 ± 0.0<br>(44.6–54.2, n = 27) | 49.3 ± 0.0<br>(45.7–52.8, n = 10) |
| <b>Forelimb (% SVL)</b>                         | 30.7 ± 0.0<br>(27.7–34.0, n = 32) | 31.7 ± 0.0<br>(29.2–36.0, n = 19) | 29.5 ± 0.0<br>(25.1–33.9, n = 30) | 32.43 ± 0.0<br>(28.1–37.3, n = 34) | 32.8 ± 0.0<br>(29.8–35.0, n = 17) | 31.1 ± 0.0<br>(24.9–35.9, n = 28) | 31.1 ± 0.0<br>(26.8–35.6, n = 13) |
| <b>Hindlimb (% SVL)</b>                         | 33.5 ± 0.0<br>(28.7–37.3, n = 32) | 34.0 ± 0.0<br>(30.4–37.9, n = 18) | 32.4 ± 0.0<br>(27.8–39.0, n = 30) | 35.8 ± 0.0<br>(30.6–40.8, n = 35)  | 36.0 ± 0.0<br>(33.0–38.8, n = 17) | 33.7 ± 0.0<br>(27.5–38.8, n = 28) | 33.5 ± 0.0<br>(28.1–39.8, n = 13) |
| <b>Tail (% SVL)</b>                             | 39.6 ± 0.0<br>(32.3–44.3, n = 28) | 34.4 ± 0.0<br>(30.6–39.3, n = 19) | 45.7 ± 0.0<br>(36.7–52.3, n = 26) | 35.7 ± 0.0<br>(28.4–42.6, n = 30)  | 36.7 ± 0.0<br>(30.1–43.3, n = 14) | 43.9 ± 0.0<br>(33.9–48.3, n = 22) | 42.1 ± 0.0<br>(34.9–51.3, n = 11) |
| <b>HW (% HL)</b>                                | 80.9 ± 0.1<br>(68.5–91.6, n = 32) | 74.5 ± 0.1<br>(64.2–85.2, n = 18) | 90.9 ± 0.1<br>(79.4–98.7, n = 29) | 81.5 ± 0.0<br>(73.3–89.4, n = 33)  | 81.1 ± 0.1<br>(73.1–92.9, n = 17) | 87.1 ± 0.0<br>(79.9–92.1, n = 28) | 81.5 ± 0.1<br>(73.7–89.1, n = 12) |
| <b>HD (% HL)</b>                                | 50.2 ± 0.0<br>(43.6–55.5, n = 32) | 47.9 ± 0.0<br>(43.8–54.4, n = 19) | 54.0 ± 0.0<br>(47.8–64.0, n = 30) | 47.1 ± 0.1<br>(36.0–54.4, n = 33)  | 47.7 ± 0.0<br>(40.1–53.4, n = 17) | 49.8 ± 0.0<br>(43.7–55.7, n = 28) | 47.3 ± 0.0<br>(42.5–52.5, n = 12) |
| <b>Snout (% HL)</b>                             | 46.6 ± 0.0<br>(42.8–52.0, n = 32) | 47.0 ± 0.0<br>(44.6–50.5, n = 19) | 46.0 ± 0.0<br>(42.7–49.7, n = 30) | 45.0 ± 0.0<br>(42.0–47.6, n = 37)  | 46.5 ± 0.0<br>(42.7–53.4, n = 17) | 45.3 ± 0.0<br>(43.3–47.9, n = 28) | 44.5 ± 0.0<br>(38.8–48.3, n = 12) |
| <b>EE (% HL)</b>                                | 28.6 ± 0.0<br>(25.4–31.5, n = 32) | 25.9 ± 0.0<br>(21.8–30.4, n = 19) | 29.6 ± 0.0<br>(24.2–34.6, n = 30) | 26.8 ± 0.0<br>(23.4–32.8, n = 33)  | 27.0 ± 0.0<br>(24.8–30.4, n = 17) | 28.2 ± 0.0<br>(24.5–33.5, n = 28) | 27.6 ± 0.0<br>(24.3–30.4, n = 12) |
| <b>Rostral contact</b>                          | 5.2 ± 0.5<br>(5–7, n = 32)        | 5.0 ± 0.0<br>(5, n = 19)          | 5.1 ± 0.3<br>(5–6, n = 30)        | 8.7 ± 1.7<br>(5–13, n = 35)        | 5.1 ± 0.4<br>(5–6, n = 17)        | 5.3 ± 0.5<br>(5–6, n = 28)        | 5.6 ± 0.9<br>(5–8, n = 14)        |
| <b>Mental contact</b>                           | 11.2 ± 1.0<br>(9–13, n = 32)      | 10.1 ± 1.1<br>(8–12, n = 19)      | 12.1 ± 1.5<br>(10–15, n = 30)     | 10.6 ± 1.5<br>(8–15, n = 36)       | 11.1 ± 1.1<br>(10–14, n = 17)     | 11.3 ± 1.2<br>(9–14, n = 28)      | 12.3 ± 1.5<br>(10–15, n = 16)     |
| <b>Supralabials</b>                             | 15.6 ± 2.2<br>(12–20, n = 32)     | 18.4 ± 2.2<br>(14–24, n = 18)     | 15.6 ± 2.2<br>(12–20, n = 32)     | 15.5 ± 1.6<br>(11–19, n = 37)      | 17.4 ± 1.4<br>(15–19, n = 17)     | 16.8 ± 1.9<br>(13–20, n = 27)     | 15.9 ± 1.1<br>(14–18, n = 15)     |
| <b>Infralabials</b>                             | 14.9 ± 2.3<br>(10–19, n = 32)     | 17.4 ± 2.5<br>(13–21, n = 16)     | 15.7 ± 2.2<br>(11–20, n = 30)     | 15.8 ± 1.7<br>(12–20, n = 37)      | 16.2 ± 1.0<br>(13–18, n = 17)     | 17.0 ± 2.7<br>(12–21, n = 27)     | 16.9 ± 2.7<br>(13–21, n = 14)     |
| <b>lamellae finger 4</b>                        | 11.1 ± 0.9<br>(10–13, n = 32)     | 11.8 ± 1.0<br>(10–14, n = 19)     | 11.5 ± 1.0<br>(10–13, n = 29)     | 10.9 ± 1.1<br>(9–13, n = 35)       | 10.9 ± 1.4<br>(8–14, n = 17)      | 11.5 ± 1.7<br>(8–15, n = 28)      | 11.0 ± 1.6<br>(9–16, n = 15)      |
| <b>Lamellae toe 4</b>                           | 12.7 ± 1.2<br>(11–16, n = 32)     | 13.1 ± 0.9<br>(12–15, n = 19)     | 13.6 ± 1.1<br>(11–16, n = 29)     | 11.9 ± 1.2<br>(9–15, n = 36)       | 12.2 ± 1.4<br>(10–15, n = 17)     | 13.2 ± 1.5<br>(10–17, n = 28)     | 11.9 ± 1.2<br>(10–15, n = 15)     |
| <b>TW/TL</b>                                    | 46.7 ± 0.0<br>(39.7–56.4, n = 28) | 54.6 ± 0.1<br>(40.4–72.5, n = 18) | 44.9 ± 0.1<br>(34.4–58.5, n = 26) | 60.8 ± 0.1<br>(44.3–78.8, n = 30)  | 54.6 ± 0.1<br>(46.8–63.8, n = 14) | 46.7 ± 0.0<br>(41.2–58.1, n = 22) | 46.0 ± 0.1<br>(35.0–54.7, n = 10) |
| <b>Scale rows on tail</b>                       | 32.7 ± 2.5<br>(28–39, n = 28)     | 25.6 ± 2.3<br>(23–30, n = 19)     | 43.0 ± 2.5<br>(37–50, n = 28)     | 25.1 ± 3.2<br>(20–34, n = 33)      | 34.9 ± 2.4<br>(31–39, n = 14)     | 40.1 ± 4.7<br>(31–49, n = 23)     | 33.4 ± 3.9<br>(28–41, n = 12)     |
| <b>Scales across tail</b>                       | 12.7 ± 0.9<br>(12–15, n = 28)     | 11.8 ± 1.5<br>(10–15, n = 18)     | 14.2 ± 1.3<br>(12–19, n = 28)     | 13.2 ± 1.5<br>(10–18, n = 33)      | 13.9 ± 1.4<br>(12–16, n = 14)     | 13.2 ± 1.3<br>(10–15, n = 24)     | 12.9 ± 0.9<br>(12–14, n = 12)     |
| <b>Canthal stripe bold, clearly defined</b>     | Yes                               | Yes                               | Yes                               | No                                 | Yes                               | Yes                               | Yes                               |
| <b>1st supralabial large (contacting nasal)</b> | Yes                               | Yes                               | Yes                               | No                                 | Yes                               | Yes                               | Yes                               |
| <b>Tail shape</b>                               | Spade-like                        | Spade-like                        | Attenuated tip                    | spade-like                         | spade-like                        | Attenuated tip                    | Attenuated tip                    |
| <b>Tail scales in rows</b>                      | Yes                               | No                                | Yes                               | Yes                                | Yes                               | Yes                               | Yes                               |
| <b>Mid dorsal scales enlarged</b>               | Yes                               | No                                | Yes                               | Yes                                | No                                | Yes                               | Yes                               |
| <b>Scales on nape enlarged</b>                  | No                                | No                                | Yes                               | No                                 | No                                | No                                | No                                |

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distinct and diagnosable lineages (species). Three further mitochondrial lineages identified previously (F–H) [30] form a strongly supported clade that can be readily diagnosed from all other members of this complex by their distinctive labial scalation, but are more difficult to diagnose from each other, and are represented by few samples in our analyses. *Diplodactylus conspicillatus sensu stricto* also includes two moderately divergent sublineages (Fig. 2) that were flagged but not named by Oliver et al. [30]. Genetic divergences between these sublineages are

lower than between the recognised candidate taxa, sampling for one is again sparse, and we did not find diagnostic morphological characters. More detailed sampling and additional nDNA data sources are required to resolve the taxonomic status of these remaining mitochondrial lineages; and for the time being we note their potential significance, but do not recognise any as distinct species.

Formal diagnoses and descriptions of the seven species we recognise within the *D. conspicillatus* complex are provided in the systematics section at the end of this paper, however for the remainder of this discussion we consider each of these seven species as separate entities and use our revised binomial arrangement (see Figs. 1–3 for a summary of phylogenetic and distributional information).

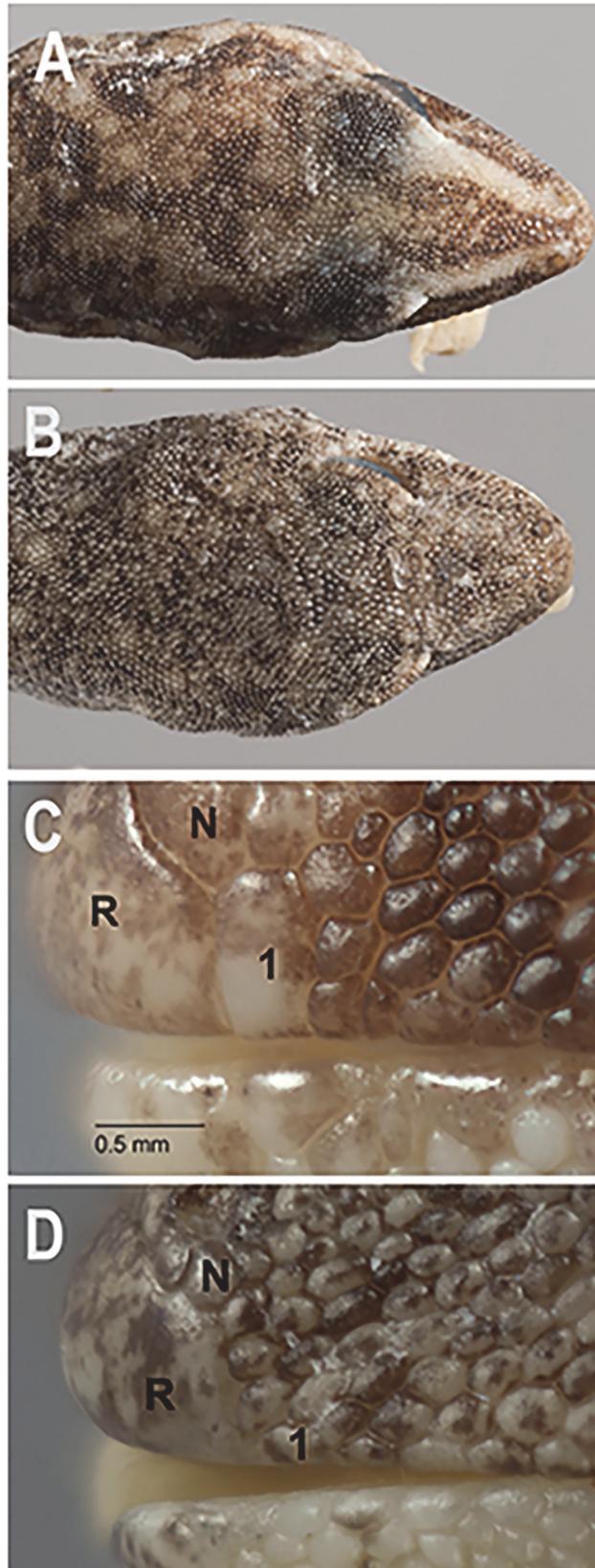
## Geographic structuring and bioregions

This study has confirmed that species diversity within the *D. conspicillatus* complex in both the AAZ and AMT is much higher than previously recognised. While significant sampling gaps remain (especially in northern Australia), based on combined genetic datasets and morphological assessments, we were able to infer the broad geographic distributions of most taxa. Of the seven species, three are endemic to the AMT, two are endemic to AAZ and two occur in both biomes. Our systematic analysis of this previously undetected diversity therefore provides opportunities to contrast patterns of diversity within biomes, and examine the potential timing and nature of transitions between them.

The distributions of the species endemic to the AMT broadly correspond to separate regions of endemism; specifically the Kimberley, Top End and Gulf [16,17, 49], and are separated by putative biogeographic barriers [49,50] (Fig. 3). *Diplodactylus custos* sp. nov. is endemic to the Kimberley region. The moderate genetic diversity of this species contrasts with very high genetic diversity of some saxicoline gecko lineages endemic to the same region [6,16,23] but is similar to Kimberley endemic toadlet lineages more strongly associated with savanna woodlands [49]. Based on current sampling, the eastern extent of the range of *D. custos* sp. nov. appears to broadly correspond with the putative Victoria River drainage barrier [50,51]. Genetic sampling for the remaining two AMT endemics was threadbare. However, based on diagnostic morphological data, *D. hillii* is only known from the western Top End (east of the Arnhemland Escarpment). A disjunction in this region (the Mid-Territory Break) has been detected in *Uperolia* toadlets [49] and may be related to variations in geology and topography around the Arnhem Escarpment. The distribution of *D. barraganae* sp. nov. along the Gulf of Carpentaria also mirrors that of a number of other lizard and frog clades [16,49]. Another putative biogeographic barrier, the Carpentaria Gap [17,49,52], separates *D. barraganae* sp. nov. from the easternmost species *D. platyurus*. In this region the clay plains in the hinterland of the Gulf of Carpentaria may form an important divide between the open woodlands of the Top End and Cape York Peninsula [17].

*Diplodactylus platyurus* has a distribution centred on Queensland, ranging from subhumid areas in the east and north and extending into the periphery of the AAZ in the west. This species contains two deeply divergent lineages from the AMT (Fig. 2, lineages G and H), while samples from a wide region along the eastern periphery of AAZ (lineage F) cluster together in a third lineage. The distribution of lineage F corresponds with the periodically flooded Channel country in western Queensland, a region that provides a set of microhabitats that are not typical of the AAZ, and is home to a suite of taxa that are absent from less watered areas to the west [16,53,54].

*Diplodactylus conspicillatus* also occurs in the AMT and AAZ, although the vast majority of its range is in the latter biome. This species includes divergent sublineages distributed to the



**Fig 4. Variation in snout colouration and scalation.** (A) Canthal stripe present (*D. conspicillatus* SAMA R32133); (B) Canthal stripe absent or very weakly developed (*D. platyurus* AMS R158426). Condition A applies to all members of the *D. conspicillatus* group except *D. platyurus*. (C) 1<sup>st</sup> supralabial (1) greatly enlarged and contacting nasal scale (N) (*D. conspicillatus* SAMA R42589); (D) 1<sup>st</sup> supralabial (1) not enlarged and widely separated from ventral edge of nasal scale (N) (*D. platyurus* AMS R 158426). Condition C is found in all members of the *D. conspicillatus* group except *D. platyurus*. Note in images C & D that R = rostral scale (Images: A & B Jeff Wright, QM; C & D Geoff Thompson, QM).

doi:10.1371/journal.pone.0111895.g004

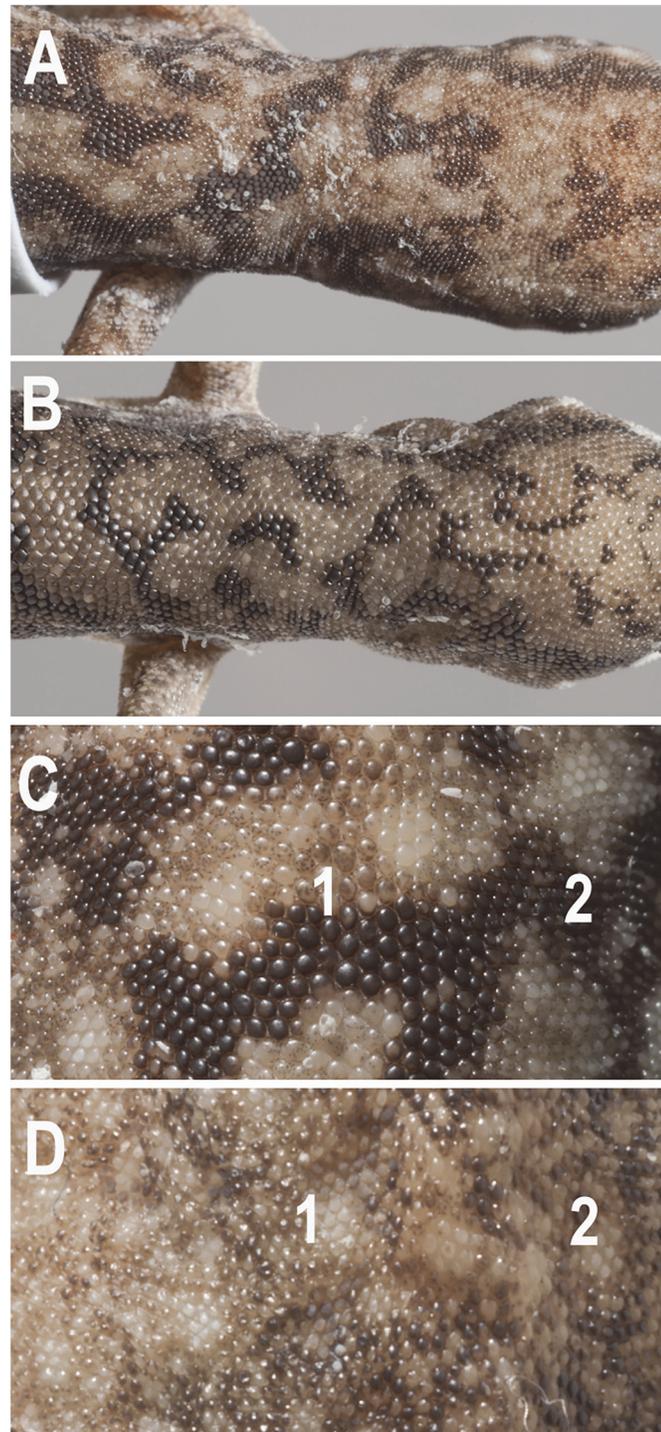
north and west of the Lake Eyre Basin, respectively, and does not show a strong signal of range expansion (although sampling for the north lineage was sparse). These data suggest that this clade has persisted and diversified within or close to the edge of the AAZ since the late Miocene. The potential roles of the vast lower Lake Eyre Basin and highly mobile sand dunes of the Simpson Desert in shaping phylogeographic patterns within this region warrant further investigation [55,56]. The distribution of these two major sublineages also broadly corresponds with the transition from the slightly higher and more reliable summer rainfall deserts in the north, to the drier and more winter rainfall deserts to the south [57,58]; these gradients of seasonality and precipitation may provide climatic axes over which taxa could diversify within the AAZ.

Only two species (*Diplodactylus bilybara* sp. nov. and *D. laevis*) have distributions entirely confined to the AAZ, and both show a strong signal of population expansion and relatively shallow intraspecific genetic diversity over most of their ranges. Low genetic diversity has been detected in a number of widespread arid zone taxa, and is thought to reflect relatively recent and major demographic shifts through severe glacial cycles of the Plio-Pleistocene [7,9,14,18,59]. The distribution of the two AAZ endemic taxa in this gecko complex is also outwardly contrasting; *Diplodactylus bilybara* sp. nov. is restricted to the southern and coastal west Pilbara and Carnarvon regions, while *Diplodactylus laevis* has a vast distribution across central Australia. However, mitochondrial diversity within the latter species is concentrated along the westernmost portion of its range, close to the range of the former [24]. This distribution of phylogenetic diversity supports previous work suggesting that the Pilbara and nearby areas have been an important zone of persistence and diversification at the western periphery of the arid zone [6,7,15].

### Contrasting diversification in the AMT and AAZ

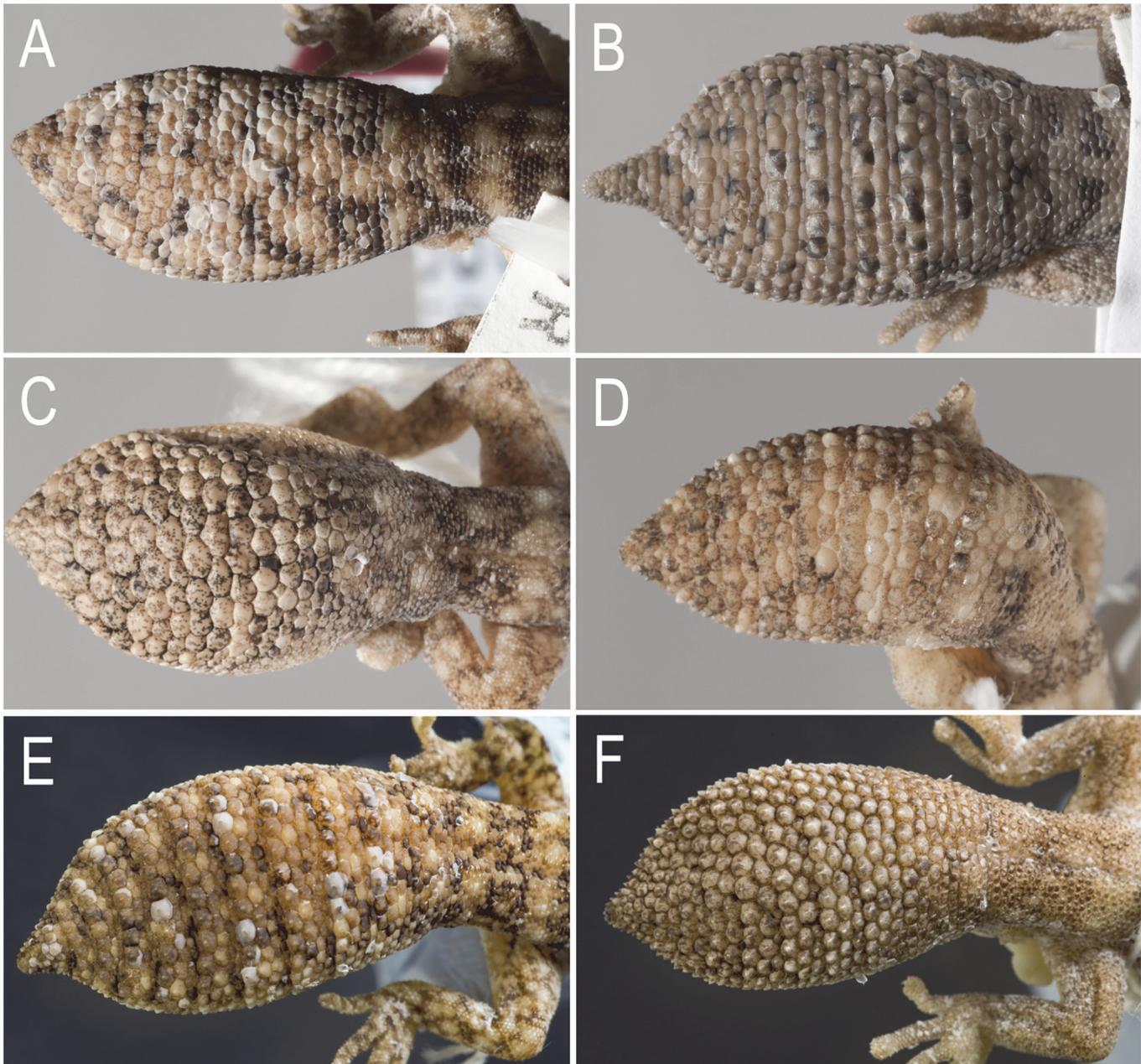
The overall timeframe and pattern of divergences in the *D. conspicillatus* complex implies that intensifying aridity since the late Miocene has played a central but at times contrasting role in shaping diversification in the AMT and AAZ [9]. Lineages in older and shrinking mesic zones (such as the AMT) are restricted to relatively small and largely allopatric patches of habitat, a distribution indicative of long-term persistence, but with increasing attenuation and potentially non-adaptive diversification [6,8,9]. In contrast, the vast sandy plains of the central AAZ appear to have a more dynamic recent history of ecological adaptation, colonisations and large scale range shifts, but less in the way of intra-regional diversification and speciation [9,14].

Bayesian reconstruction of biome shifts within the *D. conspicillatus* complex suggests that mesic biomes are ancestral. While support for many ancestral state reconstructions in the tree is low, this overall pattern is consistent with the widely held idea that the Australian arid biota is largely derived from peripheral and more mesic biomes [9,14,60]. Furthermore, as intimated above, our simple binary classification of arid vs not arid is also probably overly simplistic; while peripheral regions such as the Pilbara (*D. bilybara* sp. nov.) and much of the Channel country (*D. platyurus* lineage F) are technically within the AAZ, compelling arguments can be made as to why they could be viewed as mesic refugia [24,53,61]. Under this interpretation only two widespread species (*D. conspicillatus* and *D. laevis*) would be considered successful



**Fig 5. Variation in dorsal scalation.** Arrangement of scales on neck and back of head—(A) scales small, only slightly larger those on side of neck (*D. conspicillatus* SAMA R42569); (B) *D. laevis* (SAMA R56481) scales on nape and back of head large and plate-like and continuous with enlarged dorsal scales on trunk. Condition A applies to all members of the *D. conspicillatus* group except *D. laevis*. (C) Plate-like vertebral scales (1), appreciably larger than those of dorsolateral area (2) (*D. conspicillatus* SAMA R42569); (D) Dorsal scales granular, those of vertebral area (1) not appreciably larger than those of the dorsolateral area (2) (*D. hillii* NTM R27363). Condition D only occurs in *D. hillii* and *D. barraganae* **sp. nov.** (Images: A–C, Jeff Wright QM; D, Peter Waddington QM).

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**Fig 6. Scalation and shape of original tails.** (A) *D. conspicillatus* (SAMA R32133) tail spade-like and lacking attenuated tip; dorsal scale arrangement transverse, includes rows of both large and small scales. (B) *D. laevis* (SAMA R56481) tail ends in distinct attenuated tip; dorsal scale arrangement transverse, includes rows of both large and small scales (photographs—Jeff Wright, QM). (C) *D. hillii* (NTM R24364) tip spade-like; dorsal scales relatively large and not arranged in clear transverse rows. (D) *D. barraganae* (NTM R21395) tip spade-like; dorsal scales arranged in transverse rows which may include rows of both large and small scales. (E) *Diplodactylus bilybara* (SAMR22819) short to moderate, acute attenuated extension at tip; alternating transverse rows of large and smaller dorsal scales (F) *D. custos* (WAMR164780) tip moderately attenuated; dorsal scales arranged in transverse rows of relatively uniform size (Images: Jeff Wright, QM).

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colonists of the AAZ, and the diversity in this zone would be rendered more clearly depauperate, recent and derived than that of the AMT.

Our phylogeny also strongly indicates there have been repeated, independent transitions between the AMT and the AAZ; detectable at both interspecific (*D. barraganae* **sp. nov.** and *D.*

*conspicillatus*) and intraspecific levels (*D. conspicillatus* and *D. platyurus*). In an analysis of the plant biota of the Southern Hemisphere (including Australia), Crisp et al. [60] found that transitions between biomes were relatively rare in general, and transitions into arid biomes from monsoonal (savanna) environments were particularly rare. However, at least in Australia, the AMT remains the least studied of the major biomes [17,62] and this pattern may to some extent have reflected a lack of data. Even in this study, our sampling from the AMT is also sparse, and additional material will likely refine understanding. However, this and other broadscale analyses increasingly suggest that the history and evolution of many lineages in the the AMT and AAZ has been intimately linked since at least the late Miocene [14,16].

A final notable pattern is that the two most widespread arid zone taxa (*D. conspicillatus* and *D. laevis*) have broadly overlapping distributions in the southern and eastern arid zone (Figs. 1 & 3); the only instance of widespread sympatry within the *D. conspicillatus* complex. Relatively closely related congeners with overlapping distributions in the AAZ have been found in other widely distributed Australian lizard radiations [12,21,63]—sympatric diversity in these closely related lizard taxa may be further evidence of a relatively dynamic recent history of range expansion and ecological diversification in the vast but young arid biome [9].

### Hyper-diverse species complexes and evolutionary biology

Nearly 100 new and widely accepted Australian squamate species have been described since 2000; indeed 2007 was the most 'productive' year on record for Australian reptile taxonomy (30 well-characterised species) [64]. While some of this new biodiversity represents singletons or other novelties uncovered by fieldwork, many 'new' species have been detected within morphologically cohesive nominal 'species' that actually comprise a larger number of unrecognised taxa (five or more). In the Australian context such complexes are particularly well documented in geckos [7,8,14,16,25,61,65,66], but have also been detected in blindsnakes [67], skinks [68–70], *Donnellan pers com*], and dragons [27]. While in some cases these complexes appear to comprise genuinely morphologically cryptic taxa, in others (such as the *D. conspicillatus* group) careful work often reveals a suite of diagnostic morphological characters.

There is little sign that the rate of discovery is slowing down, and if anything, it may increase in the short-term as sampling across northern Australia becomes more comprehensive, and researchers assemble increasingly large genomic datasets and develop new analytical methods [23,71]. Even our assessment of the *D. conspicillatus* group is likely to be an underestimate; there is further deep genetic diversity in *D. conspicillatus* and *D. platyurus*, many areas remain poorly sampled, and there are two morphologically distinct specimens from Cape York in north-Queensland for which no genetic data is available (see below). Thus, as with so many Australian lizard groups, further analyses will likely show that species diversity still remains underestimated.

Many arguments for the importance of continued efforts to properly understand this biodiversity for conservation and management purposes have been outlined in a compelling fashion elsewhere [22,72]. However we would like to conclude by further re-emphasising that systematic work on these complexes also has a tendency to reveal interesting macro-evolutionary patterns. For example, using the complexes of Australian lizards listed earlier in this section as examples; systematic work has revealed parthenogenesis [56], ancient vicariance and long-term persistence [8,61], rapid radiation [70], morphological conservatism or parallelism [27,67,68] and provided insight into the comparative history of biomes or regions of endemism ([14,24], this study). Further work to resolve other species complexes will continue to provide a framework for broader insights into macroevolutionary processes.

## Systematics

### Nomenclatural Synopsis

*Diplodactylus conspicillatus* was described from specimens collected by Mr P. M. Byrne at Charlotte Waters in the southern Northern Territory (NT). In subsequent taxonomic work three additional, closely allied taxa have been named: *Diplodactylus hillii* Longman [73] from Port Darwin, N.T.; *Gymnodactylus laevis* Sternfeld [74] from Hermannsburg Mission, N.T. and *Diplodactylus platyurus* Parker [75] from Torrens Creek, Queensland (QLD).

*Diplodactylus hillii* (as *D. hillii*) was placed in the synonymy of *D. conspicillatus* by Kluge [76]. In this work Kluge only examined type material held in Australian museums and no consideration was given to the taxonomic status of *G. laevis* or *D. platyurus*. However, when Kluge revisited *D. conspicillatus* for his revision of the genus [77], both *G. laevis* and *D. platyurus* were also listed with *D. hillii* in the synonymy of *D. conspicillatus* (although the *G. laevis* type material is not listed amongst the specimens examined). Two of these synonyms (*D. hillii* and *D. platyurus*) were resurrected from the synonymy of *D. conspicillatus* by Wells and Wellington [78] but, as no justification was given, this action was widely ignored. Kluge's *D. conspicillatus* synonymy was followed by Cogger [29] who examined the type specimens of all the listed synonyms.

Based on a combination of morphology and genetics the available names can readily be assigned to the various taxa under consideration here. Key diagnostic characters are discussed in detail in the species accounts.

### Species group diagnosis

Our concept of the *D. conspicillatus* group includes only species that are part of a strongly supported clade of related forms that have previously been synonymised or confounded with the nominate species. This is contra Kluge [77] and Storr et al. [79], who included the nominate species and some or all of *D. kenneallyi*, *D. pulcher* and *D. savagei*; the phylogenetic relationships of which, based on available data, remain unclear. However, they do not show any evidence of a strong or close affinity to the *D. conspicillatus* group [25].

All species in the *Diplodactylus conspicillatus* group can be distinguished from their congeners by the following combination of characters: all or most supralabials small and granular, at most only one enlarged anterior (1<sup>st</sup>) supralabial; terminal lamellae on fingers at most only slightly wider than digit; other prominent enlarged subdigital lamellae absent; tail short, as wide or wider than body, depressed with heterogenous scalation, usually bearing large plate-like scales and/or conical tubercles arranged in transverse rows; and dorsal colouration extremely variable, but never consisting of large clearly defined bands or blotches. Comparisons in the following species accounts are restricted to taxa in the *D. conspicillatus* species group only.

The order of authorships for the three new species herein do not follow that of the paper as a whole.

#### *Diplodactylus conspicillatus* Lucas & Frost 1897

Variable Fat-tailed gecko

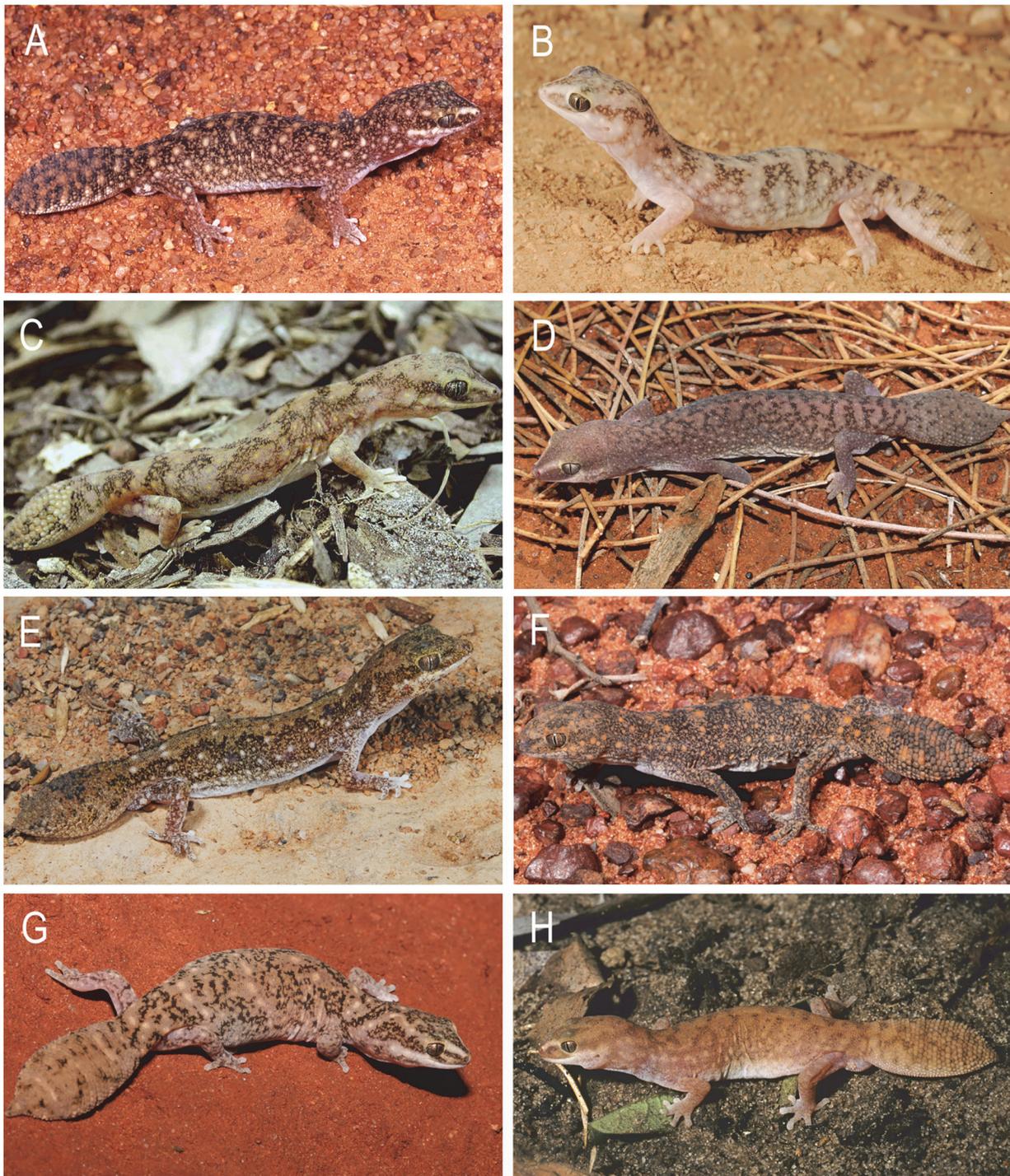
Figs. [4A](#), [4C](#), [5A](#), [5C](#), [6A](#), [7A & B](#), [8](#)

**Material Examined.** NMV D7535, Charlotte Waters (25° 55' S, 134° 55' E) NT, **lectotype**; NTM R24076–77, Arafura Swamp, Arnhem Land (12° 32' 42" S, 134° 54' 24" E) NT; SAMA R38819, 1km E of Three Ways (19° 26' S, 134° 13' E) NT; NTM R9525, Frenena (19° 26' S, 135° 24' E) NT; QM J92288, S of Mt Isa (21° 08' 43" S, 139° 15' 41" E) QLD; NTM R22130, Toko

Ra., Tobermorey Stn (22° 44' S, 137° 56' E) NT; WAM R110767, Jimblebar East (23° 23' 46" S, 120° 18' 36" E) WA; WAM R110770, Jimblebar East (23° 26' 26" S, 120° 20' E) WA; WAM R166300, 16.8km ENE Blackstone (25° 56' 07" S, 128° 26' 16" E) WA; SAMA R50114, 2.3km WSW of Sentinel Hill (26° 05' 17" S, 132° 25' 41" E) SA; SAMA R52781, 11.7km SSW of Mount Sarah homestead (27° 01' 32" S, 135° 13' 16" E) SA; SAMA R44870, 6km WSW of Womikata Bore homeland (26° 06' 33" S, 132° 05' 57" E) SA; SAMA R46981, 5.6km SSE Mosquito Camp Dam, New Crown Stn (26° 09' 28" S, 134° 30' 49" E) SA; SAMA R51587, 36.9km ESE of Amata (26° 16' 58" S, 131° 29' 12" E) SA; SAMA R44864, 8km NE of Mt Woodroffe (26° 17' 10" S, 131° 48' 20" E) SA; SAMA R38849, 6km W Namatjira/Larapinta Drive junction, Namatjira drive (26° 46' S, 133° 27' E) NT; SAMA R51514, 3.3km SW of Indulkana (26° 59' 18" S, 133° 16' 58" E) SA; SAMA R41859, 5km S of Blue Hills Bore (27° 10' 39" S, 132° 52' 06" E) SA; AMS R125042, Cunnamulla (28° 04' S, 145° 41' E) QLD; SAMA R42569, SAMA R42574, 169km NE of Emu, GI 51 (28° 14' S, 133° 20' E) SA; SAMA R42589, 20km W (road) of base camp 2 (28° 15' S, 133° 08' E) SA; WAM R85850, 39km E Laverton (28° 28' S, 122° 50' E) WA; AMS R58090, 35.9km WSW of Ely Hill (28° 28' 51" S, 134° 03' 41" E) SA; SAMA 26581, 25km SSW Mabel Ck homestead (29° 10' S, 134° 15' 30" E) SA; SAMA 26227, 30km SW Mabel Ck homestead (29° 10' 30" S, 134° 08' E) SA; SAMA R59454, 62.6km NW Maralinga (29° 46' 14" S, 131° 06' 29" E) SA; SAMA R61024, 218.2km WNW Tarcoola (29° 50' 42" S, 132° 31' 59" E) SA; SAMR59401, 12.6km WNW Maralinga (30° 05' 52" S, 131° 28' 06" E) SA; SAMA R32133, 10km SSW Maralinga (30° 15' 01" S, 131° 32' 45" E) SA; SAMA R20884, Olympic Dam area Roxby Downs (30° 23' S, 136° 53' E) SA; SAMA R45246, Salt Ck crossing, E of Lake Gairdner (31° 33' 20" S, 136° 21' 45" E) SA.

**Diagnosis.** A large member of the *D. conspicillatus* group (max SVL 62 mm) with a bold canthal stripe and a greatly enlarged first supralabial (contacting ventral edge of nasal scale). Mid-dorsal scales on trunk plate-like and markedly larger than smaller dorsolateral scales. Scales on nape granular and only slightly larger than granules on side of neck. Original tail spade-like and lacking an acute attenuated extension at tip. Scales on dorsal surface of tail arranged in transverse rows (which usually include rows of both large and small scales). Pattern generally spotted and often with numerous dark blotches that contrast strongly with base colour (Fig. 7A–B).

**Description.** SVL mm 47.05–62.71 (n = 32, mean = 54.40, SD = 4.04). Proportions as % SVL: AG 45.72–57.43 (n = 32, mean = 50.36, SD = 0.03); T 32.30–44.27 (n = 28, mean = 39.63, SD = 0.03); HL 16.38–19.90 (n = 31, mean = 18.53, SD = 0.01). **Head:** moderate and not strongly differentiated from neck; snout longer than diameter of eye. HW 68.5–91.6% HL (n = 32, mean = 80.93, SD = 0.05); HD 43.6–55.5% HL (n = 32, mean = 50.2, SD = 0.04); S 42.8–52.0% HL (n = 32, mean = 46.63, SD = 0.02); EE 25.4–31.5% HL (n = 32, mean = 28.6, SD = 0.02). Covered in small granular scales; rostral shield large and lacking a medial groove, hexagonal with 5–7 scales in contact with its posterior margin (n = 32, mean = 5.19, mode = 5, SD = 0.48); mental shield hemispherical but sometimes with a slight process extending medially from its posterior margin, 9–13 scales contacting posterior edge (n = 32, mean = 11.16, mode = 12, SD = 1.04); supralabials 12–20 (n = 32, mean = 15.63, mode = 15, SD = 2.16) with the first enlarged and contacting ventral edge of nasal scale (Fig. 4C), the remaining series are small and not differentiated from the adjacent loreal scales; infralabials 10–19 (n = 32, mean = 14.91, mode = 15, SD = 2.32), all small and undifferentiated from adjacent chin scales; eye large, pupil vertical with crenulated margin; ear small and usually horizontally elliptic. **Neck:** broad with small granular scales on dorsal surface that are only slightly larger than the adjacent scales on the lateral surfaces (Fig. 5A). **Trunk:** moderate and somewhat stout; scales generally granular but a broad zone of larger, plate-like scales is present along the back and these contrast in size with the smaller granules on the flanks (Fig. 5C); granules small on ventral surface but increase



**Fig 7. Species of the *D. conspicillatus* complex in life.** (A) *Diplodactylus conspicillatus* from 10km north of Barkley Hwy on Ranken to Alexander Station Road, north-eastern Northern Territory (Image: Ross Sadlier); (B) *Diplodactylus conspicillatus* Alice Springs, Northern Territory (Image: Eric Vanderduys); (C) *D. hillii*, Dorat Road, Northern Territory (Image: Paul Horner); (D) *Diplodactylus laevis* in life from Morgan Range, Western Australia (Image: Mark Hutchinson); (E) *Diplodactylus platyurus*, Brooklyn Station, north Queensland (Image: Eric Vanderduys); (F) *Diplodactylus platyurus* Myendetta Stn, Charleville, Queensland (Image: Steve Wilson); (G) *Diplodactylus bilybara* **sp. nov.** Onslow, Western Australia (Image: Ryan Ellis); (H) *Diplodactylus custos* **sp. nov.** Gibb River Road turnoff via Wyndham, Western Australia (Image: Steve Wilson). There are currently no images available of *D. barraganae* **sp. nov.** in life.

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**Fig 8. Lectotype of *D. conspicillatus* (NMV D7535).** Charlotte Waters, Northern Territory. (Image—Katie Smith, NMV).

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in size on pectoral region; preanal pores absent; a small cluster of postanal tubercles present in both sexes but larger and more prominent in males **Limbs:** moderate; forelimb 27.67–34% SVL ( $n = 32$ , mean = 30.74, SD = 0.02), hindlimb 28.67–37.28% SVL ( $n = 32$ , mean = 33.50, SD = 0.02); digits short and squat, lacking any distal expansion; subdigital lamellae granular (not a clearly defined series except for small distal pair), 10–13 beneath fourth finger ( $n = 32$ , mean = 11.13, mode = 11, SD = 0.93), 11–16 beneath fourth toe ( $n = 32$ , mean = 12.72, mode = 12, SD = 1.22). **Original tail:** short, wide 39.7–56.4% tail length ( $n = 28$ , mean = 46.7, SD = 0.04), spade-like and bluntly pointed (lacking acute attenuated tip: Fig. 6A); scales large and plate-like, arranged in clear transverse pattern that usually incorporates rows of both large and small scales (Fig. 6A); larger scales with a short bluntly to sharply-tipped medial tubercle; 28–39 ( $n = 28$ , mean = 32.71, mode = 35, SD = 2.49) medial scale rows on tail from fracture plane (1<sup>st</sup> autotomy septum) to tip; 12–15 ( $n = 28$ , mean = 12.68, mode = 12, SD = 0.92) rows of scales across original tail (large row closest to maximum width); ventral scales considerably smaller than dorsal scales. **Regrown tail:** with rounded distal end and more uniform scalation that is not arranged in clear transverse rows.

**Pattern (in spirit).** Variable. Most specimens tan to mid-brown and heavily chequered with small dark blotches that may coalesce to produce a reticulated appearance (lighter individuals more uniform; mid-brown, finely peppered with darker markings and bearing pale spots on dorsal and lateral surfaces). Pale spots generally present, most prominent on flanks. In some

specimens there is reduced pigmentation on the vertebral zone producing as a ragged-edged vertebral stripe (one specimen, WAM R110770, has a well-defined dark vertebral stripe bordered on either side by a pale paravertebral stripe). Head generally with darker crown but paler towards periphery. A prominent, pale canthal stripe present, extending from anterior edge of orbit to tip of snout and producing a distinctive 'v' shaped marking which contrasts with the darker dorsal and lateral head markings. A broad dark zone on side of face extends posteriorly beyond eye to temporal region. A pale zone below eye extends to ear. Limbs mottled or spotted and inner digits of forelimb with reduced pigmentation. Ventral surfaces off-white, immaculate.

**Comparisons.** *Diplodactylus conspicillatus* is readily distinguished from *D. platyurus* in possessing an enlarged first supralabial that contacts the ventral edge of the nasal scale (*vs* 1<sup>st</sup> supralabial small and not differentiated from the rest of the supralabial row). It is distinguished from *D. barraganae* **sp. nov.** and *D. hillii* in having enlarged, plate-like mid-dorsal scales that are conspicuously larger than the dorsolateral scales (*vs* mid-dorsals small and granular, only slightly larger than dorsolateral scales). It is separated from the remaining three species in this complex (*D. laevis*, *D. bilybara* **sp. nov.** and *D. custos* **sp. nov.** by the shape of its original tail which is spade-like and lacks an acute attenuated tip (*vs* original tail bearing a short attenuated tip).

**Distribution and Ecology.** Very widely distributed throughout much of the arid zone; extending west to the eastern edge of the Pilbara and Western Australian Goldfields, east to Cunnamulla in south central Queensland, and south to the northern edge of the Nullarbor Plain in South Australia (Fig. 3). There are also scattered records from the Australian Monsoonal tropics in the Northern Territory, including two specimens from a high rainfall zone in north-eastern Arnhemland. Throughout this broad region this species inhabits a very wide range of habitats ranging from sparsely vegetated Gibber plains to open woodlands, but is generally associated with harder stony, clay and compacted sandy substrates.

**Comments.** Examination of the lectotype (NMV D7535; Fig. 8) shows it to be a poorly preserved specimen that looks to be slightly dessicated, is lacking a tail but has a rusted pin protruding from the tail base. Despite its poor condition, it clearly exhibits large plate-like scales on the vertebral region of its back accompanied by small, granular scales on the nape. The only other morphotype that occurs in the vicinity of the Northern Territory/South Australian border (*Diplodactylus laevis*) has large plate-like scales on both the vertebral region and the nape and is clearly not conspecific with NMV D7535.

The wide range of this species and observed deep phylogenetic structure suggests additional taxonomic investigations are necessary.

#### ***Diplodactylus hillii* Longman 1915**

*D. conspicillatus* (in part; Kluge 1963)

*D. conspicillatus* (in part; Cogger, H.G. in Cogger *et. al.*, 1983)

'conspicillatus' D (Oliver *et al.* 2009)

Northern Fat-tailed gecko

Figs. 5D, 6C, 7C, 9

**Material Examined.** QM J1994, Port Darwin (13° 21' S, 130° 42' E) NT, **holotype**; NTM R17871, Arnhem Hwy, 5km E Corroboree Taven (12° 45' S, 131° 29' E) NT; NTM R9933, Reynolds River, Litchfield NP (13° 16' S, 130° 41' E) NT; NTM R17894, Kakadu NP, headwaters of Katherine River (13° 16' 12" S, 133° 00' 36" E) NT; NTM R20552, Stuart Hwy, Near Robin Falls (13° 21' S, 131° 08' E) NT; NTM R27363, Dorat Rd, Daly River Region (13° 30' S, 131°



**Fig 9. Holotype of *D. hillii* (QMJ 1994).** Port Darwin, Northern Territory (Image—Jeff Wright, QM).

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17' E) NT; NTM R25027, Douglas Stn, Daly River Region (13° 31' 13" S, 131° 16' 09" E) NT; NTM R11690, Katherine Gorge NP (14° 18' 48" S, 132° 32' 54" E) NT; NTM R0802, Katherine, 10 Miles N (14° 22' S, 132° 19' E) NT; NTM R0152–53, Katherine, 2 miles N (14° 27' S, 132° 16' E) NT; NTM R3772–73, Manbuloo Stn (14° 31' S, 132° 12' E) NT; NTM R6300, Katherine, 40Km South (14° 39' S, 132° 26' E) NT; NTM R4514, S of Katherine, Stuart Hwy (14° 40' S, 132° 40' E) NT; NTM R0364–65, 5 miles N Katherine (14° 44' S, 132° 04' E) NT; NTM R24364, King River, Katherine (14° 46' 29" S, 132° 15' 10" E) NT; NTM R23310, Elsey NP (14° 54' 54" S, 133° 13' 45" E) NT.

**Diagnosis.** A moderate-sized member of the *D. conspicillatus* group (max SVL 52 mm) with a bold canthal stripe and greatly enlarged first supralabial (contacting ventral edge of nasal

scale). Mid-dorsal scales on trunk small and only slightly larger than dorsolateral scales. Original tail spade-like and lacking an acute attenuated extension at tip. Scales on dorsal surface of original tail all large and not arranged in clearly defined transverse rows (pine cone-like appearance).

**Description.** SVL mm 25.09–52.34 ( $n = 19$ , mean = 46.31, SD = 5.52). Proportions as % SVL: AG 43.87–56.20 ( $n = 19$ , mean = 48.50, SD = 0.03); T 30.59–39.32 ( $n = 19$ , mean = 34.42, SD = 0.03); HL 17.44–24.19 ( $n = 19$ , mean = 19.93, SD = 0.01). **Head:** moderate and not strongly differentiated from neck; snout longer than diameter of eye. HW 64.19–85.17% HL ( $n = 18$ , mean = 74.47, SD = 0.05); HD 43.8–54.4% HL ( $n = 19$ , mean = 47.9, SD = 0.03); S 44.62–50.47% HL ( $n = 19$ , mean = 47.0, SD = 0.01); EE 21.79–30.39% HL ( $n = 19$ , mean = 25.93, SD = 0.02); covered in small granular scales; rostral shield large and lacking a medial groove, hexagonal with 5 scales in contact with its posterior margin ( $n = 19$ ); mental shield hemispherical, usually with a moderate process extending medially from its posterior margin, 8–12 scales contacting posterior edge ( $n = 19$ , mean = 10.11, mode = 11, SD = 1.10); supralabial scales 14–24 ( $n = 18$ , mean = 18.39, mode = 20, SD = 2.20) with the first enlarged and contacting ventral edge of nasal scale, the remaining series are small and not differentiated from the adjacent loreal scales; infralabial scales 13–21 ( $n = 16$ , mean = 17.38, mode = 19, SD = 2.50), all small and undifferentiated from adjacent chin scales; eye large, pupil vertical with crenulated margin; ear small, round to horizontally elliptic. **Neck:** broad with small granular scales on dorsal surface that are only slightly larger than the adjacent scales on the lateral surfaces. **Trunk:** moderate and somewhat stout; mid-dorsal scales only slightly larger than dorsolateral scales (Fig. 5D); granules small on ventral surface but increase in size on pectoral region; preanal pores absent; a small cluster of postanal tubercles present in both sexes but larger and more prominent in males. **Limbs:** moderate; forelimb 29.19–36.03% SVL ( $n = 19$ , mean = 31.67, SD = 0.02); hindlimb 30.36–37.94% SVL ( $n = 18$ , mean = 34, SD = 0.02); digits moderate with no or only slight distal expansion; subdigital lamellae granular (not a clearly defined series except for small distal pair); 10–14 lamellae beneath fourth finger ( $n = 19$ , mean = 11.79, mode = 11, SD = 0.98); 12–15 lamellae beneath fourth toe ( $n = 19$ , mean = 13.11, mode = 13, SD = 0.94) **Original tail:** short, wide 40.35–72.49% tail length ( $n = 18$ , mean = 54.62, SD = 0.07); spade-like and bluntly pointed (lacking an acute attenuated tip; Fig. 6C); scales large and plate-like, not arranged in clearly defined transverse bands (scales more or less of uniform size; Fig. 6C) with short blunt to sharp medial tubercle; 23–30 ( $n = 19$ , mean = 25.58, mode = 25, SD = 2.27) medial scale rows on tail from fracture plane (1<sup>st</sup> autotomy septum) to tip; 10–15 ( $n = 18$ , mean = 11.83, mode = 12, SD = 1.50) rows of scales across original tail (large row at maximum width); ventral scales considerably smaller than dorsal scales. **Regrown tail:** not assessed but likely to be as for other species.

**Measurements and scale counts of holotype.** QM J 1994 (male, Fig. 9). SVL = 47.42mm, AG = 22.88mm, L1 = 13.84mm, L2 = 15.46mm, HL = 9.28mm, HD = 4.63mm, HW = 6.97mm, S = 4.42mm, EE = 2.43mm, TL = 14.52mm, TW = 9.35mm, scales contacting posterior edge of rostral = 5, scales contacting posterior edge of mental = 9, lamellae beneath 4<sup>th</sup> finger = 12, lamellae beneath 4<sup>th</sup> toe = 14, medial scale rows on tail from fracture plane (1<sup>st</sup> autotomy septum) to tip = 29, rows of scales across original tail 14, supralabials = 18, infralabials = 19.

**Pattern (in spirit).** Variable. Most specimens tan to mid-brown and heavily marked with dark, irregular bands that form a broad reticulum on upper lateral / paravertebral zone and may extend to lower flanks. Vertebral zone with a ragged dark edge; generally free of pattern but sometimes the dark flank pattern may bridge this zone or the vertebral line may carry a row of small dark blotches (some individuals with a finer, lighter reticulum over entire dorsal surface which is marked with numerous small pale spots). Head with a pale crown that is continuous with the vertebral zone. A pale canthal stripe present, extending from anterior edge of

orbit to tip of snout and producing a distinctive 'v' shaped marking which has dark edging. A poorly defined pale zone below eye extends to the ear. Limbs finely spotted. Inner digits with reduced pigmentation. Original tail with little pattern or with darker bars similar to those on flanks. Ventral surfaces off-white, immaculate.

**Comparisons.** *Diplodactylus hillii* is readily distinguished from *D. platyurus* in possessing an enlarged first supralabial that contacts the ventral edge of the nasal scale (vs 1<sup>st</sup> supralabial small and not differentiated from the rest of the supralabial row). It is distinguished from *D. conspicillatus*, *D. laevis*, *D. bilybara* **sp. nov.** and *D. custos* **sp. nov.** in having small mid-dorsal scales that are only slightly larger than the dorsolateral scales (vs mid-dorsal scales conspicuously larger than the smaller dorsolateral scales). It is further separated from *D. laevis*, *D. bilybara* **sp. nov.** and *D. custos* **sp. nov.** in lacking an acute attenuated tip to the original tail (vs attenuated tip present). *Diplodactylus hillii* most resembles *D. barraganae* **sp. nov.** with which it shares small mid-dorsal scales and a blunt, spade-like original tail. These two species differ most in the configuration of the scales on the original tail (enlarged scales not in clearly defined transverse rows and mostly subequal for *D. hillii* vs clearly defined rows of both large and small scales for *D. barraganae* **sp. nov.**).

**Distribution and Ecology.** Found in eastern and central "Top End", from close to Darwin south as far as Elsey National Park (Fig. 3). Its habitat preferences within this area have not been determined.

**Comments.** The holotype of *D. hillii*, (QMJ 1994; Fig. 9), was examined and exhibits a unique scale configuration found only in *D. conspicillatus sensu lato* populations from the N.T. occurring above 15° S (i.e. scales on dorsal surface of original tail all large and not arranged in clearly defined transverse rows).

***Diplodactylus laevis* (Sternfield, 1924)**

*Gymnodactylus laevis* Sternfield, 1924

*D. conspicillatus* (in part; Kluge 1967)

*D. conspicillatus* (in part; Cogger, H.G. in Cogger *et. al.*, 1983)

'conspicillatus' C (Oliver *et al.* 2009)

Desert Fat-tailed gecko

Figs. 5B, 6B, 7D, 10

**Material Examined.** SMF8242, Hermannsburg Mission NT, **lectotype**; WAM R168509, Coulomb Point (17° 27' 44" S, 122° 09' 09" E) WA; NTM R32478–79, Tanami (19° 54' S, 130° 41' E) NT; NTM R32472, Lake Surprise (20° 06' S, 131° 00' 28" E) NT; WAM R161640, 12.5km NNE Goldsworthy (20° 14' 31" S, 119° 34' 28" E) WA; NTM R15137, NTM R15157, NTM R15191–92, Sangster's Bore, 12km SW (20° 52' S, 130° 16' E) NT; NTM R18018, Lake Mackay (22° 29' S, 129° 04' E) NT; WAM R166303, 3.2km N Pungkulpirri Waterhole (24° 37' 43" S, 128° 45' 20" E) WA; SAMA R36126, SAMA R36129, SAMA R36149, SAMA R36151, Yulara town site (25° 14' S, 131° 01' E) NT; SAMA R29928, 22km along Mulga Pk Rd SSE Curtin Springs homestead (25° 30' S, 131° 49' E) NT; SAMA R29936, 24km along Mulga Pk Rd SSE Curtin Springs homestead (25° 31' S, 131° 49' E) NT; SAMA R49965, 46.6km E of Purni Bore (26° 19' 18" S, 136° 33' 40" E) SA; SAMA R63874, 100.9km N Innamincka (26° 50' 16" S, 140° 40' 57" E) SA; SAMA R63894, 76.5km N Innamincka (27° 03' 03" S, 140° 40' 21" E) SA; SAMA R56481, 7.4km ESE (106 degrees) Mount Hoare (27° 04' 37" S, 129° 46' 22" E) SA; SAMA R56495 (27° 05' 03" S, 129° 44' 20" E) SA; SAMA R49077, SAMA R 49081, 1.7km NE of Candradecka Dam (27° 12' 04" S, 140° 52' 42" E) SA; WAM R172202, Great Victoria Desert



**Fig 10. Lectotype of *Gymnodactylus laevis* (SMF8242).** Hermannsburg Mission, Northern Territory. (Image: Dr Hal Cogger). This specimen was removed from the gut of a *Varanus gouldii* and is partially digested and in poor condition.

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(28° 20' 01" S, 127° 23' 50" E) WA; SAMA R62236, 184km SSW Wartaru (28° 30' 28" S, 129° 00' 17" E) SA; SAMA R62383, 164.7km SSE Wartaru (28° 31' 55" S, 129° 57' 27" E) SA; SAMA R62397, 164.7km SSE Wartaru (28° 32' 01" S, 129° 54' 43" E) SA; SAMA R62346, 166.7km SSE Wartaru (28° 32' 33" S, 130° 04' 18" E) SA; SAMA R57170, 11.2km E Vokes Hill Corner (28° 33' 42" S, 130° 47' 40" E) SA.

**Diagnosis.** A large member of the *D. conspicillatus* group (max SVL 65 mm) with a bold canthal stripe and a greatly enlarged first supralabial (contacting ventral edge of nasal scale). Mid-dorsal scales on trunk plate-like and markedly larger than smaller dorsolateral scales. Scales on nape and top of head also plate-like and whilst sometimes smaller than those on back, still considerably larger than the small granules on side of neck. Original tail sharply-pointed and terminating with an acute attenuated extension at tip. Scales on dorsal surface of tail arranged in transverse rows (which include rows of both large and small scales). Pattern generally reticulated.

**Description.** SVL mm 42.39–64.85 (n = 30, mean = 54.89, SD = 4.72). Proportions as % SVL: AG 46–57.31 (n = 30, mean = 51.82, SD = 0.03); T 36.73–52.26 (n = 26, mean = 45.72, SD = 0.04); HL 15.31–19.45 (n = 30, mean = 17.30, SD = 0.01). **Head:** moderate and not strongly differentiated from neck; snout longer than diameter of eye. HW 79.40–98.7% HL (n = 29, mean = 90.90, SD = 0.05); HD 47.8–64% HL (n = 30, mean = 54.0, SD = 0.04); S 42.68–49.7% HL (n = 30, mean = 46, SD = 0.02); EE 24.2–34.6% HL (n = 30, mean = 29.64, SD = 0.03). Dorsal surface covered with enlarged scales that are continuous with the enlarged, plate-like dorsal scales on the trunk; rostral shield large and lacking a medial groove, hexagonal with 5–6 scales in contact with its posterior margin (n = 30, mean = 5.07, mode = 5, SD = 0.25); mental shield hemispherical but sometimes with a slight process extending medially from its posterior margin, 10–15 (n = 30, mean = 12.13, mode = 11, SD = 1.50) scales contacting posterior edge; supralabial scales 14–20 (n = 30, mean = 16.37, mode = 15, SD = 1.45) with the first enlarged and contacting ventral edge of nasal scale, the remaining series are small and not differentiated from the adjacent loreal scales; Infralabial scales 11–20 (n = 30, mean = 15.7, mode = 17, SD =

2.18), all small and undifferentiated from adjacent chin scales; eye large, pupil vertical with crenulated margin; ear small, round to horizontally elliptic. **Neck:** broad with enlarged scales on dorsal surface which are substantially larger than adjacent scales on the lateral surfaces (Fig. 5B). **Trunk:** moderate and somewhat stout; scales generally granular but a broad zone of larger, plate-like scales is present along mid-dorsum and these contrast in size with the smaller dorsolateral scales; granules small on ventral surface but increase in size on pectoral region; preanal pores absent; a small cluster of postanal tubercles present in both sexes but larger and more prominent in males **Limbs:** moderate; forelimb 25.08–33.9% SVL ( $n = 30$ , mean = 29.52, SD = 0.02); hindlimb 27.82–39% SVL ( $n = 30$ , mean = 32.17, SD = 0.03); digits short and squat, lacking any distal expansion; subdigital lamellae granular (not a clearly defined series except for small distal pair); 10–13 beneath fourth finger ( $n = 29$ , mean = 11.52, mode = 11, SD = 0.95); 11–16 beneath fourth toe ( $n = 29$ , mean = 13.59, mode = 13, SD = 1.12); **Original tail:** short, wide 34.4–58.5% tail length ( $n = 26$ , mean = 44.9, SD = 0.06), with an acute attenuated extension at tip (Fig. 6B); scales large and plate-like, arranged in clear transverse pattern that usually incorporates rows of both large and small scales (Fig. 6B); larger scales with short bluntly to sharply-tipped medial tubercle; 37–50 ( $n = 28$ , mean = 43.04, mode = 42, SD = 2.49) medial scale rows on tail from fracture plane (1<sup>st</sup> autotomy septum) to tip; 12–19 ( $n = 28$ , mean = 14.18, mode = 14, SD = 1.33) rows of scales across original tail (large row at maximum width); ventral scales considerably smaller than dorsal scales. **Regrown tail:** with rounded distal end and more uniform scalation that is not arranged in clear transverse rows.

**Pattern (in spirit).** Variable. Most specimens tan to mid-brown with a darker reticulated pattern of fine to moderate wavy lines that extend over the entire dorsum. Many specimens exhibit fine pale spotting that is most evident on the flanks. Head, as for body with dark reticulations on crown. A pale canthal stripe present, extending from anterior edge of orbit to tip of snout and producing a distinctive 'v' shaped marking which has dark edging. A broad dark zone on side of face extends posteriorly beyond eye to temporal region. A poorly to well-defined pale zone below eye extends to the ear. Limbs weakly mottled or spotted and inner digits with reduced pigmentation. Tail marked with small dark flecks. Ventral surfaces off-white, immaculate.

**Comparisons.** *Diplodactylus laevis* is readily distinguished from *D. platyurus* in possessing an enlarged first supralabial that contacts the ventral edge of the nasal scale (vs 1<sup>st</sup> supralabial small and not differentiated from the rest of the supralabial row). It is distinguished from *D. conspicillatus*, *D. laevis*, *D. bilybara* **sp. nov.** and *D. custos* **sp. nov.** in having enlarged, plate-like scales on the nape and top of head that are appreciably larger than those on the sides of the neck (vs scales on nape granular and not appreciably larger than those on sides of neck). It is most readily distinguished from *Diplodactylus hillii* and *D. barraganae* **sp. nov.** by the shape of its original tail which bears an acute attenuated extension at the tip (vs tail blunt, spade-like without an attenuated tip) and further distinguished from these species by its mid-dorsal scales (mid-dorsals enlarged and plate-like, conspicuously larger than the dorsolateral scales in *D. laevis* vs mid-dorsal scales small, only slightly larger than the dorsolaterals).

**Distribution and Ecology.** Widely distributed over much of the Australian arid zone, occurring from the Dampier Peninsula, Pilbara and Great Victoria Desert in the west, through much of north-western South Australia and the southern half of the Northern Territory, with an apparently isolated eastern population in the Channel Country around north-eastern South Australia (Fig. 3).

**Comments.** A black and white photographic image of the lectotype of *Gymnodactylus laevis* (SMF8242; Fig. 10) was kindly provided by Dr Harold Cogger. The specimen is damaged (partially digested) having been removed from the gut of a *Varanus gouldii* specimen from Hermannsburg Mission, NT. Despite its poor condition, it is possible to determine from the image

that the specimen has an enlarged 1<sup>st</sup> supralabial, enlarged scales on its mid-dorsum, nape and head, an acute attenuated extension at the tip of its original tail and some indication of a reticulated dorsal pattern. Cogger notes from his examination of the specimen that 'colour pattern is light brown or creamish with a series of irregular dark brown spots and patches forming a vague reticulum' (Cogger, unpublished data). This suite of characters fit the specimens examined above, whose distribution encompasses the central Australian region from which SMF8242 was collected. It remains unclear why Mertens [80] chose a partially digested specimen as the lectotype.

***Diplodactylus platyurus* Parker 1926**

*D. conspicillatus* (in part; Kluge 1967)

*D. conspicillatus* (in part; Cogger, H.G. in Cogger *et. al.*, 1983)

'conspicillatus' F–H (Oliver *et al.* 2009)

Eastern Fat-tailed gecko

Figs. 4B, 4D, 7E–F, 11

**Material Examined.** BMNH 1946.8.11.38, Torrens Ck (21°25'S, 145°14'E) QLD, **holotype**; QM J71803, 15km N Mt Carbine towards Laura (16° 30' S, 145° 03' E) QLD; QM J91172, near Mt Carbine township (16° 31' 51" S, 145° 06' 18" E) QLD; QM J69713, Fossilbrook, Burlington Stn (17° 48' 30" S, 144° 23' 30" E) QLD; QM J58912, Normanton, 8.2km W of, on Cloncurry Rd (17° 44' S, 141° 02' E) QLD; QM J58919, Normanton, 16.0km West of, on the Cloncurry Rd



**Fig 11. Holotype of *D. platyurus* (BMNH 1946.8.11.38).** Torrens Ck, Queensland. (Image: Dr Hal Cogger).

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(17° 48' S, 141° 01' E) QLD; QM J77374, Florey St, Wulguru, Townsville (19° 20' S, 146° 49' E) QLD; QM J92286, Mingela Road near Townsville ~ (19°53'S, 146°38'E) QLD; SAMA R63337, Mingela (19° 52' 12" S, 146° 37' 48" E) QLD; QM J82303, Blackbraes NP (19° 23' 31" S, 144° 09' 01" E) QLD; QM J80633, Blackbraes NP (19° 23' 57" S, 144° 09' 03" E) QLD; QM J63337, Porcupine Gorge NP (20° 23' S, 144° 26' E) QLD; QM J47527, Torrens Ck, 12km NNE (20° 39' S, 145° 05' E) QLD; QM J54321, Hughenden, 9.6km NE (20° 47' 48" S, 144° 20' E) QLD; QM J44369, Dalrymple town reserve 107, Freehold Portion (20° 57' S, 147° 05' E) QLD; QM J81437, Morrinya NP (21° 23' S, 144° 58' E) QLD; QM J81752, Lenton Downs (21° 33' 23" S, 148° 08' 24" E) QLD; QM J68966, BHP S Walker Ck Coal Mine, 40km W Nebo (21° 44' 36" S, 148° 24' 50" E) QLD; QM J81306, 27.5km N Moranbah (21° 46' S, 148° 00' E) QLD; QM J69765, Moranbah, 5km S (22° 02' S, 148° 03' E) QLD; SAMA R63336, Winton, (22° 27' S, 142° 57' E) QLD; QM J92287, Winton (22° 28' 42" S, 142° 53' 31" E) QLD; QM J63083, Blair Athol Coal Mine (22° 42' S, 147° 33' S) QLD; QM J78200, Junee SF9 (22° 48' 24" S, 149° 59' 56" E) QLD; QM J45804, Bluff, 1.8km E (23° 35' S, 149° 06' E) QLD; QM J83120, Blackwater, 21.3km SW (23° 43' 50" S, 148° 44' 37" E) QLD; QM J47655, Blackdown Tableland NP, The Gap (23° 48' S, 149° 08' E) QLD; QM J90778, Noonbah homestead, 3.4km NNE (24° 04' 51" S, 143° 11' 54" E) QLD; AMS R60250, 37km N of Blackall on Landsborough QLD (24° 08' S, 145° 21' E) QLD; QM J56888, Waterloo site 1 (24° 16' S, 143° 13' E) QLD; QM J89191, Tyrone, approx 70km NW of Charleville—3km S of old north Tyrone homestead (25° 58' 55" S, 145° 44' 17" E) QLD; QM J35697, Ambathala NRS, 1km S Ra Tank (26° 01' 30" S, 145° 04' 30" E) QLD; QM J74874, Mariala Nature Ref. Site, No. 3 hut (26° 04' 48" S, 145° 06' E) QLD; QM J79909, Mariala (26° 05' 30" S, 145° 04' 15" E) QLD; AMS R158426, Sturt NP, Silver City Hwy., Wittabrinna Ck Crossing (29° 22' 38" S, 142° 02' 08" E) NSW; AMS R132996, Wanaaring, 4km W of Wanaaring at Turnoff To Wilcannia (29° 42' S, 144° 07' E) NSW; AMS R165698, Nocolche Nature Reserve, 11km West of Wanaaring—Wilcannia Rd (29° 52' 08" S, 144° 00' 34" E) NSW; AMS R162733, Lake Peery NP (30° 43' 28" S, 143° 29' 15" E) NSW.

**Diagnosis.** A large member of the *D. conspicillatus* group (max SVL 60 mm) lacking a well-defined canthal stripe and without a greatly enlarged first supralabial (first supralabial not in contact with ventral edge of nasal scale). Dorsal scales on trunk plate-like and markedly larger than smaller dorsolateral scales. Scales on nape granular and only slightly larger than granules on side of neck. Scales on dorsal surface of tail arranged in transverse rows (often of uniform size but can include rows of both large and small scales). Pattern generally with dark, heavily spotted flanks and a series of pale vertebral blotches or a continuous pale vertebral zone.

**Description.** SVL mm 40.55–60.21 (n = 36, mean = 48.71, SD = 5.20). Proportions as % SVL: AG 42.39–56.37 (n = 32, mean = 48.83, SD = 0.03); T 28.38–42.56 (n = 30, mean = 35.67, SD = 0.03); HL 17.38–22.41 (n = 36, mean = 19.74, SD = 0.01). **Head:** moderate and not strongly differentiated from neck; snout longer than diameter of eye. HW 73.3–89.41% HL (n = 33, mean = 81.53, SD = 0.04); HD 36–54.44% HL (n = 33, mean = 47.1, SD = 0.05); S 42.02–47.61% HL (n = 37, mean = 45.01, SD = 0.01); EE 23.42–32.78% HL (n = 33, mean = 26.84, SD = 0.02); covered in small granular scales; rostral shield large and lacking a medial groove, hexagonal with 5–13 scales in contact with its posterior margin (n = 35, mean = 8.69, mode = 9, SD = 1.68); mental shield hemispherical, usually with a moderate process extending medially from its posterior margin, 8–15 scales contacting posterior edge (n = 36, mean = 10.58, mode = 11, SD = 1.54); supralabial scales 11–19 (n = 37, mean = 15.51, mode = 15, SD = 1.61), the first not enlarged and subequal with the rest of the supralabial row which are not differentiated from the adjacent loreal scales (Fig. 4D); infralabial scales 12–20 (n = 37, mean = 15.76, mode = 16, SD = 1.69), all small and undifferentiated from adjacent chin scales; eye large, pupil vertical with crenulated margin; ear small, round to horizontally elliptic. **Neck:** broad with small granular scales on dorsal surface that are only slightly larger than the adjacent scales on

the lateral surfaces. **Trunk:** moderate and somewhat stout; scales of dorsum plate-like and markedly larger than smaller granules on flanks; granules small on ventral surface but increase in size on pectoral region; preanal pores absent; a small cluster of postanal tubercles present in both sexes but larger and more prominent in males. **Limbs:** moderate; forelimb 28.11–37.26% SVL ( $n = 34$ , mean = 32.43, SD = 0.02); hindlimb 30.61–40.76% SVL ( $n = 35$ , mean = 35.80, SD = 0.03); digits moderate with no or only slight distal expansion; subdigital lamellae granular (not a clearly defined series except for small distal pair); 9–13 lamellae beneath fourth finger ( $n = 35$ , mean = 10.94, mode = 10, SD = 1.11); 9–15 lamellae beneath fourth toe ( $n = 36$ , mean = 11.86, mode = 12, SD = 1.20). **Original tail:** short, wide 44.34–78.82% tail length ( $n = 30$ , mean = 60.81, SD = 0.08); spade-like and bluntly pointed (lacking an acute attenuated tip); scales arranged in clear transverse bands which incorporate rows of both large and small scales (or consist of scales that are more or less uniform in size), each with a short blunt to sharp medial tubercle; 20–34 ( $n = 33$ , mean = 25.06, mode = 26, SD = 3.16) medial scale rows on tail from fracture plane (1<sup>st</sup> autotomy septum) to tip; 10–18 ( $n = 33$ , mean = 13.24, mode = 13, SD = 1.50) rows of scales across original tail (large row at maximum width); ventral scales considerably smaller than dorsal scales. **Regrown tail:** with rounded distal end and more uniform scalation that is not arranged in clear transverse rows.

**Pattern (in spirit).** Variable. Most specimens tan to mid-brown with varying degrees of spotting; most prominent on flanks. Dorsum with an overlay of fine, dark reticulations or a more solid dark pattern. Vertebral zone with reduced pigment but often broken by transverse bars, isolating a series irregular pale blotches along back. In some specimens the vertebral zone is largely unpatterned and has a wavy edge where it borders the darker paravertebral zone. Head, as for dorsal ground colour with scattered dark flecks or blotches. Canthal stripe absent or very weak without sharply defined edges and not contrasting strongly with other facial markings. Limbs with fine reticulations, inner digits of forelimb with reduced pigmentation. Ventral surfaces off-white, immaculate.

**Comparisons.** *D. platyurus* is readily distinguished from *D. conspicillatus*, *D. laevis*, *D. hillii*, *D. bilybara* sp. nov., *D. custos* sp. nov. and *D. barraganae* sp. nov. by the condition of the 1<sup>st</sup> supralabial (small and not differentiated from the rest of the supralabial row in *D. platyurus* vs greatly enlarged and contacting ventral edge of nasal scale) and by the absence of a well-defined canthal stripe (vs canthal stripe well-developed).

**Distribution and Ecology.** Occurs over much of eastern and central Queensland, from the Normanton and around Cairns in the north, south to around Rockhampton in the east, and throughout much of the channel country to west of the Great Dividing Range, extending south as far as north-west New South Wales and north-east South Australia (Fig. 3). Occurs in sub-humid to arid woodland habitats on a range of sand and clay based substrates (A. Emmott pers. com).

**Comments.** A black and white photographic image of the holotype of *Diplodactylus platyurus* (BMNH 1946.8.11.38; Fig. 11) was kindly provided by Dr Harold Cogger. The specimen, from Torrens Ck, Qld (21°25'S, 145°14'E) has an undifferentiated supralabial row (i.e. no enlarged supralabials) a character that is only found in the most easterly populations of the *D. conspicillatus* group occurring in Queensland and NSW. A specimen from Torrens Ck, QM J47527 (the type locality), displaying this character is included in the material examined.

The taxonomic assignment of two specimens from the Edward River region on western Cape York Peninsula (QM J58251 Melon Yard, Strathgordon H, 14°43'12"S, 142°18'E and QM J81110 Edward River, 14°24'36"S, 142°09'36"E) remains unresolved. Whilst this population is geographically most proximate to *D. platyurus*, these specimens have an enlarged 1<sup>st</sup> supralabial and may represent an additional taxon not included in our limited genetic sampling.

***Diplodactylus barraganae* Couper, Oliver & Pepper sp. nov.**



**Fig 12. Holotype of *D. barraganae* sp. nov. (NTM R21395).** Musselbrook Reserve, Border Waterhole, Northern Territory/Queensland border. (Image: Jeff Wright).

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'conspicillatus' A (Oliver et al. 2009)

Gulf Fat-tailed gecko

Figs. [6D](#), [12](#)

**Holotype.** NTM R21395, Musselbrook Reserve, Border Waterhole (18° 36' 30" S, 137° 59' 18" E) NT/QLD border.

**Paratypes.** NTM R21886, NTM R21892, Sherwin Ck / Roper River Junction (14° 40' S, 134° 22' E) NT; NTM R21088, Carpentaria Hwy, 100km E Stuart Hwy (16° 25' 35" S, 134° 10' 48" E) NT; NTM R20606, Cape Crawford Area (16° 42' 07" S, 135° 31' 04" E) NT; NTM R20605, Cape Crawford Area (16° 53' 42" S, 135° 40' 31" E) NT; QM J11035–37, Doomadgee Mission Stn (17° 55' 48" S, 138° 49' 12" E) QLD; QM J51987, Lawn Hill NP (18° 42' 30" S, 138° 28' 30" E) QLD; QM J75143, Lawn Hill (18° 42' 30" S, 138° 28' 48" E) QLD; QM J52723, Lawn Hill Stn, Century Project Site (18° 45' S, 138° 35" E) QLD; AMS R162275, Riversleigh World Heritage Area (19° 00' 11" S, 138° 40' 03" E) QLD; QM J85474, Riversleigh (19° 00' 47" S, 138° 40' 06" E) QLD; QM J49251, Gregory R, nr 'Rackham's Roost', Riversleigh Stn (19° 02' S, 138° 45" E) QLD; AMS R17974 –, 75, Mount Isa (20° 44' S, 139° 29' E) QLD.

**Etymology.** Named for María Elena Barragán (Fundacion Herpetologica Gustavo Orces. Quito, Ecuador) in recognition of her contributions to reptile conservation and public education.

**Diagnosis.** A small member of the *D. conspicillatus* group (max SVL 49 mm) with a bold canthal stripe and greatly enlarged first supralabial (contacting ventral edge of nasal scale). Mid-dorsal scales on trunk small and only slightly larger than the dorsolaterals. Original tail spade-like and lacking an acute attenuated extension at tip. Scales on dorsal surface of tail arranged in transverse rows (which include rows of both large and small scales). Pattern not strongly contrasting, usually some indication of a pale, jagged-edged vertebral zone.

**Description.** SVL mm 25.05–49.47 (n = 17, mean = 41.75, SD = 6.80). Proportions as % SVL: AG 45.12–55.81 (n = 17, mean = 49.85, SD = 0.03); T 30.12–43.32 (n = 14, mean = 36.70, SD = 0.03); HL 17.83–22.12 (n = 17, mean = 20.11, SD = 0.01). **Head:** moderate and not strongly differentiated from neck; snout longer than diameter of eye. HW 73.1–92.91% HL (n = 17, mean = 81.1, SD = 0.06); HD 40.1–53.4% HL (n = 17, mean = 47.7, SD = 0.04); S 42.66–53.43% HL (n = 17, mean = 46.54, SD = 0.02); EE 24.8–30.43% HL (n = 17, mean = 27, SD = 0.02). Covered in small granular scales; rostral shield large and lacking a medial groove, hexagonal with 5–6 scales in contact with its posterior margin (n = 17, mean = 5.12, mode = 5, SD = 0.40); mental shield hemispherical, usually with a moderate process extending medially from its posterior margin, 10–14 scales contacting posterior edge (n = 17, mean = 11.41, mode = 11, SD = 1.10); supralabial scales 15–19 (n = 17, mean = 17.35, mode = 19, SD = 1.42) with the first enlarged and contacting ventral edge of nasal scale, the remaining series are small and not differentiated from the adjacent loreal scales; infralabial scales 13–18 (n = 17, mean = 16.24, mode = 16, SD = 1.01), all small and undifferentiated from adjacent chin scales; eye large, pupil vertical with crenulated margin; ear small, round to horizontally or vertically elliptical. **Neck:** broad with small granular scales on dorsal surface that are only slightly larger than the adjacent scales on the lateral surfaces. **Trunk:** moderate and somewhat stout; scales of dorsum small, only slightly larger than dorsolateral scales; granules small on ventral surface but increase in size on pectoral region; preanal pores absent; a small cluster of postanal tubercles present in both sexes but larger and more prominent in males. **Limbs:** moderate; forelimb 29.83–35% SVL (n = 17, mean = 32.80, SD = 0.02); hindlimb 33.04–38.76% SVL (n = 17, mean = 36.03, SD = 0.02); digits moderate with slight distal expansion; subdigital lamellae granular (not a clearly defined series except for small distal pair); 8–14 beneath fourth finger (n = 17, mean = 10.94, mode = 11, SD = 1.37); 10–15 beneath fourth toe (n = 17, mean = 12.18, mode = 13, SD = 1.35); **Original tail:** short, wide 46.81–63.84% tail length (n = 9, mean = 54.58, SD = 0.07), spade-like and bluntly pointed (lacking an acute attenuated extension at tip; Fig. 6D); scales large and plate-like, arranged in clear transverse pattern that usually incorporates rows of both large and small scales (Fig. 6D); larger scales with short bluntly to sharply-tipped medial tubercle; 31–39 (n = 14, mean = 34.92, mode = 36, SD = 2.43) medial scale rows on tail from fracture plane (1<sup>st</sup> autotomy septum) to tip; 12–16 (n = 14, mean = 13.93, mode = 15, SD = 1.44) rows of scales across original tail (large row at maximum width); ventral scales considerably smaller than dorsal scales. **Regrown tail:** with rounded distal end and more uniform scalation that is not arranged in clear transverse rows.

**Measurements and scale counts of holotype.** NTM R21395 (male, Fig. 12) SVL = 40.58mm, AG = 18.31mm, L1 = 13.09mm, L2 = 13.94mm, HL = 8.25mm, HD = 3.33mm, HW = 6.38mm, S = 3.71mm, EE = 2.14mm, TL = 14.77mm, TW = 7.2mm, scales contacting posterior edge of rostral = 6, scales contacting posterior edge of mental = 11, lamellae beneath 4<sup>th</sup> finger = 10, lamellae beneath 4<sup>th</sup> toe = 11, medial scale rows on tail from fracture plane (1<sup>st</sup> autotomy septum) to tip = 36, rows of scales across original tail 16, supralabials = 16, infralabials = 16.

**Pattern (in spirit).** Tan to mid-brown, suffused with darker pigment on back and flanks. Pattern incorporates diffuse spotting and obscure reticulations and a pale, continuous or broken, vertebral zone. Head with numerous dark scales that often form a fine netted pattern. A

moderately well-developed pale canthal stripe present, extending from anterior edge of orbit to tip of snout and producing a distinctive 'v' shaped marking. A diffuse dark zone on side of face extends posteriorly beyond eye to temporal region. Limbs obscurely marked with vague spotting or netted pattern and inner digits of fore and hindlimb with reduced pigmentation. Ventral surfaces off-white, immaculate.

**Comparisons.** *Diplodactylus barraganae* **sp. nov.** is readily distinguished from *D. platyurus* in possessing an enlarged first supralabial that contacts the ventral edge of the nasal scale (vs 1<sup>st</sup> supralabial small and not differentiated from the rest of the supralabial row). It is distinguished from *D. conspicillatus*, *D. laevis*, *D. bilybara* **sp. nov.** and *D. custos* **sp. nov.** in having small mid-dorsal scales that are only slightly larger than the dorsolaterals (vs mid-dorsals enlarged and plate-like, conspicuously larger than the dorsolaterals) and further distinguished from *D. laevis*, *D. bilybara* **sp. nov.** and *D. custos* **sp. nov.** by the shape of the original tail (tail blunt, spade-like without an acute attenuated extension at tip in *D. barraganae* **sp. nov.** vs tail with an acute attenuated extension at tip).

**Distribution and Ecology.** Occurs over a broad band along the southern edge of the Gulf of Carpentaria, from the Roper River region in the northwest, east and south as far as Mt Isa (Fig. 3). The holotype was collected in 'open woodland on red sandy soil' (P. Horner pers. com.).

*Diplodactylus bilybara* Couper, Pepper & Oliver **sp. nov.**

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'conspicillatus' B (Oliver et al. 2009)

Western Fat-tailed Gecko

Figs. 6E, 7G, 13

**Holotype.** WAM R174500 (formerly SAMA R22820), 21km S Barradale (22° 55' S, 114° 46'E) WA.

**Paratypes.** WAM R132531-32, Burrup Peninsula (20° 40' 36" S, 116° 45' 08" E) WA; WAM R132529, Burrup Peninsula (20° 40' 49" S, 116° 44' 37" E) WA; WAM R110058, 3.5km S Karratha (20° 46' 04" S, 116° 50' 31" E) WA; WAM R110027, 6km S Karratha (20° 47' 40" S, 116° 51' 24" E) WA; WAM R165155, 8.5km WSW Yanyare River mouth (20° 50' 40" S 116° 22' 02" E) WA; WAM R159892, WAM R159894, WAM R159940, WAM R159947, 10km S Mallina homestead (20° 58' 10" S, 118° 02' 54" E) WA; WAM R165177, 9.5km ESE Marda Pool (21° 03' 47" S, 116° 14' 00" E) WA; WAM R110182, WAM R110218, WAM R110220, 12.5km SW Millstream (21° 40' 37" S, 116° 58' 30" E) WA; WAM R134523, 8km N Exmouth (21° 52' 12" S, 114° 07' 01" E) WA; WAM R110148, 8km S Coolawanyah (21° 52' 55" S, 117° 47' 40" E) WA; WAM R163018, 7km SSE Mount Minnie (22° 10' 10" S, 115° 33' 39" E) WA; WAM R162059, 19.5km SSW Mount Amy (22° 25' 09" S, 115° 50' 16" E) WA; WAM R162052-53 21km SSE Mount Amy (22° 26' 05" S, 115° 55' 49" E) WA; WAM R158331, WAM R159932, Giralia homestead (22° 41' 38" S, 114° 23' 28" E) WA; SAMA R22905, 6km S Barradale (22° 52' S, 114° 52' E) WA; SAMA R22818, 11km S Barradale (22° 52' 30" S, 114° 50' E) WA; SAMA R22819, 9km S Barradale (22° 53' S, 114° 52' E) WA; SAMA R22821 21km S Barradale (22° 55' S, 114° 46'E) WA; AMS R165713, Jack Hills (26° 03' 24" S, 117° 12' 58" E) WA.

**Etymology.** Refers to the Pilbara region where this species occurs. The name Pilbara is said to be derived from the Aboriginal word *bilybara*, meaning 'dry' in the languages of the Nyamal and Banyjima people.

**Diagnosis.** A large member of the *D. conspicillatus* group (max SVL 63 mm) with a well-defined canthal stripe and a greatly enlarged first supralabial (first supralabial contacts ventral



**Fig 13. Holotype of *Diplodactylus bilybara* sp. nov. (WAM R174500).** 21km south of Barradale, Western Australia. (Image: Peter Waddington, QM).

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edge of nasal scale). Dorsal scales on trunk plate-like and markedly larger than smaller dorso-laterals. Scales on nape granular and only slightly larger than granules on side of neck. Original tail with a short to moderate, acute attenuated extension at tip; scales on dorsal surface of tail arranged in transverse rows (often in a pattern of one large row followed by two small rows; scales in the small rows  $\sim \frac{1}{4}$  the size of the scales in the adjacent large rows. Pattern variable; reticulated or with obscure transverse bands and generally incorporating numerous small pale spots. Dark pigment on crown and snout contrast markedly with pale canthal stripe and lower jaw colour which extends posteriorly as a pale bar towards the ear opening.

**Description.** SVL mm 39.2–60.8 ( $n = 28$ , mean = 48.83, SD = 5.20). Proportions as % SVL: AG 44.60–54.16 ( $n = 27$ , mean = 49.64, SD = 0.03); T 33.88–48.34 ( $n = 22$ , mean = 43.86, SD = 0.03); HL 15.9–21.04 ( $n = 28$ , mean = 18.57, SD = 0.01). **Head:** moderate and not strongly differentiated from neck; snout longer than diameter of eye. HW 79.89–92.08% HL ( $n = 28$ , mean = 87.05, SD = 0.03); HD 43.7–55.7% HL ( $n = 28$ , mean = 49.8, SD = 0.02); S 43.31–47.87% HL ( $n = 28$ , mean = 45.26, SD = 0.01); EE 24.45–33.54% HL ( $n = 28$ , mean = 28.23, SD = 0.02). Covered in small granular scales; rostral shield large and lacking a medial groove, hexagonal 5–6 scales contacting posterior edge of rostral scale ( $n = 28$ , mean = 5.29, mode = 5, SD = 0.46); mental scale usually without (or with only a slight) process on medial posterior margin, 9–14 scales contacting posterior edge ( $n = 28$ , mean = 11.29, mode = 12, SD = 1.21); supralabial scales 13–20 ( $n = 27$ , mean = 16.78, mode = 17, SD = 1.87), with the first enlarged and contacting ventral edge of nasal scale, the remaining series are small and not differentiated from the adjacent loreal scales; infralabial scales 12–21 ( $n = 27$ , mean = 16.96, mode = 16, SD = 2.70), all

small and undifferentiated from adjacent chin scales; eye large, pupil vertical with crenulated margin; ear small, round to horizontally elliptic. **Neck:** broad with small granular scales on dorsal surface that are only slightly larger than the adjacent scales on the lateral surfaces. **Trunk:** moderate and somewhat stout; scales of mid-dorsum plate-like and markedly larger than dorsolateral scales; granules small on ventral surface but increase in size on pectoral region; preanal pores absent; a small cluster of postanal tubercles present in both sexes but larger and more prominent in males. **Limbs:** moderate; forelimb 24.87–35.85% SVL ( $n = 28$ , mean = 31.13, SD = 0.02); hindlimb 27.46–38.83% SVL ( $n = 28$ , mean = 33.73, SD = 0.02); digits moderate with no or only slight distal expansion; subdigital lamellae granular (not a clearly defined series except for small distal pair which tend to be long and narrow); 8–15 lamellae beneath fourth finger ( $n = 28$ , mean = 11.46, mode = 13, SD = 1.69); 10–17 lamellae beneath fourth toe ( $n = 28$ , mean = 13.18, mode = 13, SD = 1.52). **Original tail:** short, wide 41.16–58.1% tail length ( $n = 22$ , mean = 46.66, SD = 0.04), with a short to moderate, acute attenuated extension at tip (Fig. 6E); scales arranged in clear transverse bands which incorporate rows of both large and small scales (often in a pattern of one large row followed by two small rows, of which the scales in the small rows are much less than  $\frac{1}{2}$  the size of the scales in the large rows (Fig. 6E); each large scale bears a short blunt to sharp medial tubercle); 31–49 ( $n = 23$ , mean = 40.09, mode = 41, SD = 4.73) medial scale rows on tail from fracture plane (1<sup>st</sup> autotomy septum) to tip; 10–15 ( $n = 24$ , mean = 13.21, mode = 14, SD = 1.25) rows of scales across original tail (large row at maximum width); ventral scales considerably smaller than dorsal scales. **Regrown tail:** with rounded distal end and more uniform scalation that is not arranged in clear transverse rows.

**Measurements and scale counts of holotype.** WAM R174500 (male, Fig. 13). SVL = 47.45mm, AG = 23.65mm, L1 = 13.45mm, L2 = 115.97mm, HL = 8.92mm, HD = 4.97mm, HW = 7.91mm, S = 4.27mm, EE = 2.45mm, TL =  $\sim$  16.89mm (tail bent sideways during preservation), TW = 9.8mm, scales contacting posterior edge of rostral = 6, scales contacting posterior edge of mental = 10, lamellae beneath 4<sup>th</sup> finger = 13, lamellae beneath 4<sup>th</sup> toe = 14, medial scale rows on tail from fracture plane (1<sup>st</sup> autotomy septum) to tip = 37, rows of scales across original tail 14, supralabials = 14, infralabials = 20.

**Pattern.** Variable. Generally reddish-brown or grey. Most specimens with a series of irregular, dark wavy bands across back that usually extend across the vertebral zone (only one specimen, WAM R110027 has an unbroken, paler vertebral zone). There is usually some degree of fine spotting on back and flanks and in some specimens the spots extend across the dorsum in transverse rows. The delineation between the base colour and darker dorsal patterns ranges from moderate to sharply contrasting. Head generally with dark crown. A prominent, pale canthal stripe present, extending from anterior edge of orbit to tip of snout and producing a distinctive 'v' shaped marking which contrasts with the darker dorsal and lateral head markings. A broad dark zone on side of face extends posteriorly beyond eye to temporal region. A pale zone below eye extends to ear. Limbs mottled or spotted and inner digits of forelimb with reduced pigmentation. Ventral surfaces off-white, immaculate.

**Comparison.** *Diplodactylus bilybara* **sp. nov.** is readily distinguished from *D. platyurus* in possessing an enlarged first supralabial that contacts the ventral edge of the nasal scale (vs 1<sup>st</sup> supralabial small and not differentiated from the rest of the supralabial row). It is distinguished from *D. conspicillatus*, *D. hillii* and *D. barraganae* **sp. nov.** by the shape of its original tail (tail with short to moderate, acute attenuated extension at tip in *D. bilybara* **sp. nov.** vs tail blunt, spade-like without an attenuated tip). It is distinguished from *D. laevis* by the condition of the scales on the nape and top of head (scales granular and not appreciably larger than those on sides of neck in *D. bilybara* **sp. nov.** vs scales plate-like, appreciably larger than those on the sides of the neck). *D. bilybara* **sp. nov.** is most like *D. custos* **sp. nov.** but differs from this species in the following respects: distal half of original tail with alternating rows of large and small

scales (generally 1 large row followed by 2 small rows)—scales in the small rows  $\sim \frac{1}{4}$  the size of the scales in the adjacent large rows vs tail scalation generally more uniform; if smaller scale rows present, these rarely form a double row and the small scales are  $\sim \frac{1}{2}$  the size of the scales in the adjacent large rows for *D. custos* **sp. nov.**; dark pigment on crown and snout contrast markedly with pale canthal stripe and lower jaw colour which extends posteriorly towards the ear as a pale bar vs dark pigment on crown and snout generally not contrasting sharply with pale canthal stripe and lower jaw colour for *D. custos* **sp. nov.**, trunk heavily pigmented and pattern usually incorporating numerous small pale spots vs body pattern often diffuse and generally without numerous pale spots, usually with wavy, dark transverse bands across back for *D. custos* **sp. nov.**.

**Distribution and Ecology.** Occurs in the Carnarvon, west Pilbara and west Gascoyne regions along the central west coast of Western Australia (Fig. 3). It is most abundant on less rocky habitats such as *Triodia* sandplains and Mulga woodlands on sandy loam substrates (B. Maryan pers. com.).

*Diplodactylus custos* Couper, Oliver & Pepper **sp. nov.**

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‘conspicillatus’ E (Oliver et al. 2009)

Kimberley Fat-tailed gecko

Figs. 6E, 7H, 14

**Holotype.** WAM R164780, The Grotto (15° 43' 04" S, 128° 15' 35" E) WA.

**Paratypes.** WAM R77417, Port Warrender (14° 34' S, 125° 48' 15" E) WA; WAM R78243, Mitchell Plateau (14° 44' S, 125° 44' E) WA; WAM R172916, Doongan Stn (15° 13' 44.5" S, 125° 12' 30.4" E) WA; WAM R132713, 30km SSE Wyndham (15° 42' 43" S, 128° 15' 56" E) WA; SAMA R63942, The Grotto (15° 43' 04" S, 128° 15' 35" E) WA; WAM R162453, 20km W Kununurra (15° 45' 59" S, 128° 40' 18" S) WA; WAM R85120-21, Kununurra (15° 46' S, 128°



**Fig 14. Holotype of *D. custos* sp. nov. (WAM R164780).** The Grotto, Western Australia. (Image: Peter Waddington, QM).

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44' E) WA; WAM R119666, Cockburn Ra. (15° 50' S, 128° 02' E) WA; WAM R172853, Ellenbrae Stn (15° 59' 02" S, 127° 03' 14" E) WA; WAM R145042, Koolan Island (16° 07' 54" S, 123° 45' 29" E) WA; WAM R11255, Wotjulum (16° 11' S, 123° 37' E) WA; WAM R172675, Talbot Bay (16° 20' 07" S, 124° 03' 10" E) WA; WAM R70374, near Lissadell homestead (16° 40' S, 128° 23' 13" E) WA; WAM R103420, WAM R103448, Bungle Bungle NP (17° 24' S, 128° 45' E) WA.

**Etymology.** From the latin for guard, with reference to the Australian Wildlife Conservancy (AWC) and their ambitious and effective conservation and research programs in the Kimberley (where this species is endemic) and elsewhere in Australia. Used as a noun in apposition.

**Diagnosis.** A large member of the *D. conspicillatus* group (max SVL 61 mm) with a well-defined canthal stripe and a greatly enlarged first supralabial (first supralabial contacts ventral edge of nasal scale). Mid-dorsal scales on trunk plate-like and markedly larger than smaller dorsolaterals. Scales on nape granular and only slightly larger than granules on side of neck. Original tail with a short, acute attenuated extension at tip (Fig. 6F); scales on dorsal surface arranged in transverse rows generally of uniform size but if smaller scale rows are present, these rarely form a double row and the small scales are  $\sim \frac{1}{2}$  the size of the scales in the adjacent large rows (Fig. 6F). Dark pigment on crown and snout generally not contrasting sharply with pale canthal stripe and lower jaw colour. Body pattern often diffuse and generally without numerous pale spots; may incorporate wavy, dark transverse bands.

**Description.** SVL mm 42.17–58.23 (n = 13, mean = 50.58, SD = 5.75). Proportions as % SVL: AG 45.7–52.75 (n = 10, mean = 49.32, SD = 0.02); T 34.91–51.34 (n = 11, mean = 42.13, SD = 0.04); HL 16.34–21.15 (n = 13, mean = 18.85, SD = 0.02). **Head:** moderate and not strongly differentiated from neck; snout longer than diameter of eye. HW 73.73–89.14% HL (n = 12, mean = 81.50, SD = 0.05); HD 42.5–52.5% HL (n = 12, mean = 47.3, SD = 0.03); S 38.78–48.32% HL (n = 12, mean = 44.51, SD = 0.03); EE 24.26–30.40% HL (n = 12, mean = 27.62, SD = 0.02). Covered in small granular scales; rostral shield large and lacking a medial groove, hexagonal with 5–8 scales contacting posterior edge of rostral scale (n = 14, mean = 5.57, mode = 5, SD = 0.94); mental scale sometimes with a slight process on medial posterior margin; 10–15 scales contacting posterior edge (n = 16, mean = 12.25, mode = 12, SD = 1.50); supralabial scales 14–18 (n = 15, mean = 15.93, mode = 16, SD = 1.12) with the first enlarged and contacting ventral edge of nasal scale, the remaining series are small and not differentiated from the adjacent loreal scales; infralabial scales 13–21 (n = 14, mean = 16.86, mode = 16, SD = 2.71) all small and undifferentiated from adjacent chin scales; eye large, pupil vertical with crenulated margin; ear small, round to horizontally elliptic. **Neck:** broad with small granular scales on dorsal surface that are only slightly larger than the adjacent scales on the lateral surfaces. **Trunk:** moderate and somewhat stout; scales of mid-dorsum plate-like and markedly larger than smaller dorsolateral scales; granules small on ventral surface but increase in size on pectoral region; preanal pores absent; a small cluster of postanal tubercles present in both sexes but larger and more prominent in males. **Limbs:** moderate; forelimb 26.79–35.62% SVL (n = 13, mean = 31.06, SD = 0.03); hindlimb 28.13–39.82% SVL (n = 13, mean = 33.5, SD = 0.04); digits moderate with slight distal expansion; subdigital lamellae granular and not a clearly defined series (except for small distal pair which tend to be broadly oval and displaced laterally by claw); 9–16 lamellae beneath fourth finger (n = 15, mean = 11, mode = 11, SD = 1.60); 10–15 lamellae beneath fourth toe (n = 15, mean = 11.93, mode = 12, SD = 1.16). **Original tail:** short, wide 35–54.72% tail length (n = 10, mean = 46.0, SD = 0.05) with a short, acute attenuated extension on tip (Fig. 6F); Original tail with scales arranged in clear transverse rows which are largely of uniform size (where rows of smaller scales occur, they are  $\geq \frac{1}{2}$  the size of the scales in the larger scale rows) each scale bearing a bluntly-tipped medial tubercle (Fig. 6F); 28–41 (n = 12, mean = 33.42, mode = 32, SD = 3.90) medial scale rows on tail from fracture plane (1<sup>st</sup> autotomy

septum) to tip; 12–14 ( $n = 12$ , mean = 12.92, mode = 12, SD = 0.90) rows of scales across original tail (large row at maximum width); ventral scales considerably smaller than dorsal scales.

**Regrown tail:** with rounded distal end and more uniform scalation that is not arranged in clear transverse rows.

**Measurements and scale counts of holotype.** WAM R164780 (male, [Fig. 14](#)). SVL = 56.36mm, AG = 27.73mm, L1 = 15.41mm, L2 = 17.61mm, HL = 9.21mm, HD = 4.5mm, HW = 8.21mm, S = 4.45mm, EE = 2.8mm; TL = 22.74mm, TW = 10.45mm, scales contacting posterior edge of rostral = 5, scales contacting posterior edge of mental = 13, lamellae beneath 4<sup>th</sup> finger = 12, lamellae beneath 4<sup>th</sup> toe = 15, medial scale rows on tail from fracture plane (1<sup>st</sup> autotomy septum) to tip = 30, rows of scales across original tail 12, supralabials = 16, infralabials = 20.

**Pattern.** Variable. Tan to grey with darker overlay. Flanks and dorsum not strongly contrasting with ground colour and with or without pale spotting. Vertebral zone broken by dark, obscure to well-formed transverse bars. A pale canthal stripe present, extending from anterior edge of orbit to tip of snout and producing a distinctive 'v' shaped marking that does not contrast sharply with other facial markings. A dark zone on side of face extends posteriorly beyond eye to temporal region. Limbs mottled or spotted and inner digits of forelimb with reduced pigmentation. Ventral surfaces off-white, immaculate.

**Comparison.** *Diplodactylus custos* **sp. nov.** is readily distinguished from *D. platyurus* in possessing an enlarged first supralabial that contacts the ventral edge of the nasal scale (*vs* 1<sup>st</sup> supralabial small and not differentiated from the rest of the supralabial row). It is distinguished from *D. conspicillatus*, *D. hillii* and *D. barraganae* **sp. nov.** by the shape of its original tail (tail with short attenuated tip in *D. custos* **sp. nov.** *vs* tail blunt, spade-like without an attenuated tip). It is distinguished from *D. laevis* by the condition of the scales on the nape and top of head (scales granular and not appreciably larger than those on sides of neck in *D. custos* **sp. nov.** *vs* scales plate-like, appreciably larger than those on the sides of the neck). *D. custos* **sp. nov.** is most like *D. bilybara* **sp. nov.** but differs from this species in the following respects: scalation of original tail reasonably uniform; if smaller scale rows present, these rarely form a double row and the small scales are  $\sim \frac{1}{2}$  the size of the scales in the adjacent large rows *vs* distal half of original tail with alternating rows of large and small scales (generally 1 large row followed by 2 small rows)—scales in the small rows  $\sim \frac{1}{4}$  the size of the scales in the adjacent large rows for *D. bilybara* **sp. nov.**; dark pigment on crown and snout generally not contrasting sharply with pale canthal stripe and lower jaw colour *vs* dark pigment on crown and snout contrast markedly with pale canthal stripe and lower jaw colour which extends posteriorly towards the ear as a pale bar in *D. bilybara* **sp. nov.**; body pattern often diffuse and generally without numerous pale spots, usually with wavy, dark transverse bands across back *vs* trunk heavily pigmented and pattern usually incorporating numerous small pale spots for *D. bilybara* **sp. nov.** Additionally, *D. custos* **sp. nov.** usually has a shorter and less pronounced acute attenuated extension on the original tail tip than *D. bilybara* **sp. nov.**

**Distribution and Ecology.** Known from widespread but scattered localities from across the Kimberley region of north-western Australia, ranging from Kununurra in the north-west, south to Purnululu National Park, to around Derby in the south-west, with additional records from the Yampi Peninsula and high rainfall zone of the north-west Kimberley. Has been recorded from Koolan Island off the west Kimberley, the only insular record of a member of the *D. conspicillatus* complex ([Fig. 3](#)).

A single specimen from Ellenbrae Station in the central Kimberley was collected from open *Eucalyptus* woodland on the top of a stony rise with heavy clay soils, while specimens from around Kununurra were collected from rocky hillsides vegetated with open grassy woodland (P. Oliver pers obs).

### Key to the *Diplodactylus conspicillatus* species group

- 1) 1<sup>st</sup> supralabial enlarged, contacting ventral edge of nasal scale (Fig. 4C) and prominent, pale canthal stripe present (Fig. 4A)—2  
 1<sup>st</sup> supralabial small, subequal to the rest of the supralabial row (Fig. 4D) and no prominent canthal stripe (Fig. 4B)—*platyurus* (eastern Australia, Qld & NSW)
- 2) Mid-dorsal scales small and only a little larger than the dorsolateral scales (Fig. 5D)—3  
 Mid-dorsal scales conspicuously larger than the dorsolateral scales (Fig. 5C)—4
- 3) Original tail bearing alternating transverse rows of different sized scales and rows of larger scales each with a bluntly spinose, central tubercle. More than 30 scales along dorsal midline of tail from fracture plane to tip.(Fig. 6D)—*barraganae* (NW Qld & NE NT)  
 Original tail without clearly defined transverse rows of different sized scales; scales large and slightly spinose (pine cone-like appearance). Fewer than 30 scales on dorsal midline of tail, from fracture plane to tip.(Fig. 6C)—*hillii* (N NT)
- 4) Scales on nape granular, not appreciably larger than those on side of neck (Fig. 5A)—5  
 Scales on nape and top of head plate-like and appreciably larger than those on side of neck (Fig. 5B). Original tail terminating with an acute attenuated extension at tip (Fig. 6B)—*laevis*
- 5) Original tail terminating with a short to moderate, attenuated extension at tip (Figs 6E & F)—6  
 Original tail spade-like, lacking an acute attenuated extension at tip (Fig. 6A)—*conspicillatus*
- 6) Distal half of tail with alternating rows of large and small scales (generally 1 large row followed by 2 small rows); scales in the small rows  $\sim \frac{1}{4}$  the size of the scales in the adjacent large rows (Fig. 6E). Dark pigment on crown and snout contrast markedly with pale canthal stripe and lower jaw colour which extends posteriorly towards the ear as a pale bar (Fig. 7G). Trunk heavily pigmented and pattern usually incorporating numerous small pale spots—*bilybara* (Pilbara, WA)  
 Tail scalation generally more uniform; if smaller scale rows present, these rarely form a double row and the small scales are  $\sim \frac{1}{2}$  the size of the scales in the adjacent large rows (Fig. 6F). Dark pigment on crown and snout generally not contrasting sharply with pale canthal stripe and lower jaw colour (Fig. 7H). Body pattern often diffuse and generally without numerous pale spots; may incorporate wavy, dark transverse bands—*custos* (Kimberley, WA)

## Supporting Information

**S1 Fig. Maximum Likelihood Phylogeny for complete dampling of the *Diplodactylus conspicillatus* complex and outgroups.** Estimated from mitochondrial ND2 data using RAxML with Maximum Likelihood support Bootstrap supports shown for key nodes.  
(PDF)

**S1 Table. A. Measures of inter-specific genetic diversity and divergence.** B. Intra-specific measures of genetic diversity and divergence. C. Diversity and demographic summary statistics.  
(DOCX)

**S1 Appendix. Additional material examined.**  
(DOCX)

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## Author Contributions

Conceived and designed the experiments: PO PC MP. Performed the experiments: PO PC MP. Analyzed the data: PO PC MP. Contributed reagents/materials/analysis tools: PO PC MP. Wrote the paper: PO PC MP.

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