

RECORDS OF THE AUSTRALIAN MUSEUM

Volume 71

Number 5

28 August 2019

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Ctenophorus spinodomus sp. nov., a new species of dragon lizard
(Squamata: Agamidae) from Triodia Mallee habitat of southeast Australia

by

Ross A. Sadler, Don Colgan, Cecilie A. Beatson, and Hal G. Cogger



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Volume 71 Number 5

Published (print and online) 28 August 2019

Price: AUS\$50.00

Printed by Rodenprint, Sydney

ISSN 0067-1975 (print)

ISSN 2201-4349 (online)

The Australian Museum is a statutory authority of, and principally funded by, the NSW State Government.



Clay shingle — Large additions of the new lizard species, the *Eastern Macleay Dragon* — *Lacerta* sp. 3, is listed by Parker **Colman Beason and Gwyger (p. 206)** in response to their finding these lizards from the regional area of south-western New South Wales (see Fig. 1, p. 206). The species occurs in the sandplains of Mallee dunefields of central-west and south-western New South Wales and adjacent areas of inland south-east New South Wales, by central-west and south-west New South Wales in its dependence on the presence of *Myrica humicola* — *Thyridia Mallee* (Table 1).

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<https://doi.org/10.3853/issn.2201-4349>

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Genetic Evidence in Support of the Recognition of the Kaputar Rock Skink, one of New South Wales' Most Range-restricted Vertebrate Species

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ABSTRACT. The existence of the Kaputar Rock Skink, a morphologically distinct *Egernia* population restricted to the Nandewar Ranges in northern New South Wales, has been known for decades. However, no comprehensive description or diagnosis of the taxon has been published in the scientific literature, and its distinctiveness largely assumed. As part of a study investigating the genetic differentiation of faunal populations on the Nandewar Range, comparisons between the Kaputar Rock Skink and east Australian *Egernia striolata*-group species were undertaken. The results indicate that the Kaputar Rock Skink is a distinct genetic lineage, showing species-level divergence from other *Egernia* species. Field studies suggest the Kaputar Rock Skink is restricted to an extremely narrow band of rock habitat above 1000 m or more in elevation, and only occupies retreat and sheltering sites near cliff edges or in areas of extensive outcropping rock. It now appears to be a cool-adapted species constrained to high elevation habitat by niche conservatism. Field studies suggest the availability of suitable habitat on the summit areas of the Nandewar Ranges is highly limited, making it vulnerable to several potentially threatening processes, including anthropogenic climate change. The name *Contundo roomi* was erected for the Kaputar Rock Skink by Wells & Wellington in 1985, and we recommend *Egernia roomi* (Wells & Wellington, 1985) as the name for the Kaputar Rock Skink.

Introduction

The Kaputar Rock Skink, a taxon restricted to the Nandewar Ranges at the eastern edge of the northwest plains of New South Wales (see Fig. 3), has been known for over 25 years, and has appeared as an unnamed species of *Egernia* in the *Field Guide to Reptiles of New South Wales* (Swan *et al.*, 2014; 2017) for over a decade. However, no comprehensive

morphological description or diagnosis for the species has been presented in the scientific literature. Independent information resulting from our recent field and genetic studies support recognition of the Kaputar Rock Skink as a distinct species, one with specific and highly-restricted habitat preferences, and is of particular conservation concern.

The Nandewar Range is the eroded remnant of a massive shield volcano, and rises out of the surrounding landscape

Keywords: Scinidae; *Egernia roomi*; Kaputar; Nandewar Range; Cytochrome b; montane; threatened; climate change

Taxonomic registration: (LSID publication) <http://zoobank.org/297B60F9-4BDF-44A9-911D-40404FF939DC>

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Received: 28 August 2018 **Accepted:** 26 March 2019 **Published:** 28 August 2019 (in print and online simultaneously)

Publisher: The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)

Citation: Sadlier, Ross A., Greta J. Frankham, Cecilie A. Beatson, Mark D. B. Eldridge, and Jodi J. L. Rowley. 2019. Genetic evidence in support of the recognition of the Kaputar Rock Skink, one of New South Wales' most range-restricted vertebrate species. *Records of the Australian Museum* 71(5): 183–197. <https://doi.org/10.3853/j.2201-4349.71.2019.1716>

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Figure 1. The peaks of the Nandewar Range from a distance (*A*) and at its base (*B*) as it rises from the surrounding plains.

to altitudes over 1000 m (Fig. 1). The Australian Museum Research Institute recently undertook field studies to investigate if the Nandewar Range has served as a mesic refuge for reptiles, amphibians and mammals, particularly for taxa shared with the adjacent northern tablelands of the Great Dividing Range. One of the targets for investigation was the Kaputar Rock Skink (Fig. 2), assumed to be allied to the ‘*striolata*-group’ within *Egernia*.

In morphology, the Kaputar Rock Skink is similar in overall appearance to the east Australian members of the *Egernia striolata*-group. This group includes the Tree Skink *Egernia striolata*, the Eastern Crevice Skink *Egernia mcphreei* and the Black Rock Skink *Egernia saxatilis*, the latter comprising two recognized subspecies (*saxatilis saxatilis* and *saxatilis intermedia*). All are of moderate size

(average body length c. 100 mm), have a depressed (ovoid) body form, and all (except the Kaputar Rock Skink) have a textured scale surface that is typically grooved or keeled (Swan *et al.*, 2017). *Egernia striolata*, *E. mcphreei* and *E. saxatilis intermedia* are parapatric in distribution across eastern Australia (Fig. 3). *Egernia striolata* occurs over much of the inland areas of southern and central Queensland, the northern ranges and western division of New South Wales, and into South Australia (Cogger, 2014). By contrast *E. mcphreei* and *E. s. intermedia* have distributions that are much more limited. *Egernia mcphreei* occurs along the north coast of New South Wales, from the Hunter Valley to the Border Ranges region, inland to the eastern edge of the ranges of the northern tablelands (Swan *et al.*, 2017), and *E. saxatilis intermedia* occurs on the central and southern

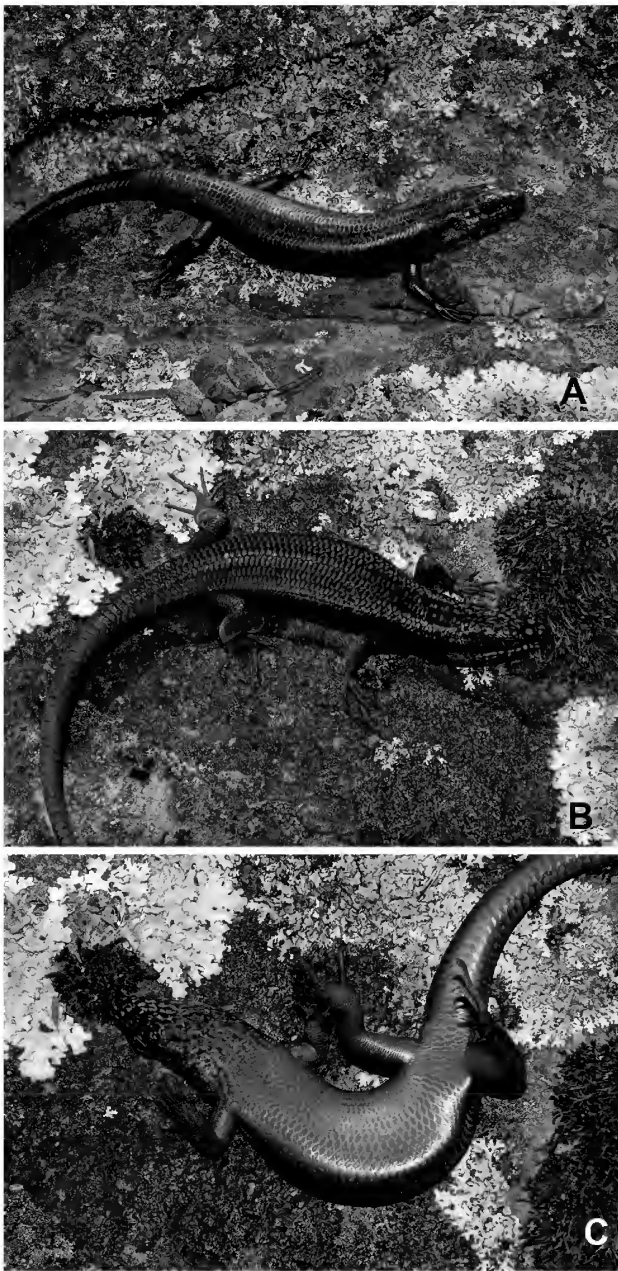


Figure 2. The Kaputar Rock Skink *Egernia roomi* showing the dark dorsal body colouration (A, B) typical of the species, and extensive dull uniform orange colouration to the ventral surface (C) that includes the chest, abdomen and underside of the tail.

tablelands and adjacent areas of the southwest slopes and south coast of New South Wales (Swan *et al.*, 2017), and the ranges of Victoria west to the Grampians (Wilson & Swan, 2017). The nominate subspecies *E. s. saxatilis* is restricted to the Warrumbungle Ranges on the northwest slopes of New South Wales. Here it sits isolated and ‘surrounded’ by *E. striolata*, a scenario not dissimilar to that of the Kaputar Rock Skink. The differences in morphology between the named east Australian *striolata*-group species are subtle (Swan *et al.*, 2017) but their recognition as distinct biological entities has not been questioned, nor has their distinctiveness from the western members of the group that occur primarily in Western Australia (Gardner *et al.*, 2008). As part of our study investigating the extent of genetic differentiation of

fauna populations on the Nandewar Range, we undertook comparisons between the Kaputar Rock Skink and east Australian *striolata*-group species.

To assess the extent of historical connectivity of montane and rocky habitats between the Nandewar and Great Dividing Ranges we also investigated the extent of genetic divergence between populations of two habitat specialists which are distributed on the northern tablelands but extend west to the Nandewar Range, the Tussock Skink *Pseudemoia pagenstecheri* and the Granite Belt Thick-tailed Gecko *Uvidicolus sphyrrurus*. *Pseudemoia pagenstecheri* is a species primarily associated with high elevation woodland habitat with tussock grass groundcover, and has a distribution that extends along the Great Dividing Range in New South Wales and Victoria. Across its range *P. pagenstecheri* occurs as several disjunct regional populations: one in the southern montane environments, one in high elevation forest habitat of the central ranges of New South Wales, and one in high elevation forest habitat of the northern tablelands of New South Wales, with the population on the Nandewar Range an isolated outlier. *Uvidicolus sphyrrurus* is primarily a rock-dwelling species with a distribution that encompasses the northern tablelands of New South Wales and areas of the adjacent north-west slopes. The population on the Nandewar Ranges lies at the western limits of the species’ distribution. It occupies habitat across a broad altitudinal range, indicating a correspondingly broad thermal tolerance, but is highly dependent upon the presence of suitable rock habitat.

Methods and materials

Distribution: The distribution of the Kaputar Rock Skink was assessed from records in the Australian Museum specimen database and from survey work carried out over two days in September 2015 at Kaputar National Park (hereafter KNP). Searches for the Kaputar Rock Skink focused on high elevation rocky habitat, and included sites between 1350 and 1480 m in elevation. The species’ potential Area of Occupancy (the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of occurrence of a taxon—hereafter AOO) and Extent of Occurrence (the area within its ‘extent of occurrence’ which is occupied by a taxon—hereafter EOO) as defined under IUCN Red List criteria (2012) were estimated from areas above 1000 m and 1200 m elevation calculated on a range map created in ArcMap 10.2.2 using the WorldClim Altitude raster (Hijmans *et al.*, 2005). The AOO was measured using the Calculate Geometry tool in ArcMap, and EOO was measured using the IUCN EOO Calculator tool v1.2. In addition, reference was made to the Australian Museum specimen database to determine the geographically nearest records of *E. striolata* for evidence of regional sympatry between the two taxa.

Morphology: Information for morphological comparisons between the Kaputar Rock Skink and east Australian *striolata*-group species *E. striolata*, *E. mcphreei*, *E. saxatilis saxatilis* and *E. saxatilis intermedia* was limited to published information (primarily Swan *et al.*, 2017; Wilson, 2015) for size, body shape, scalation characteristics and colouration, supplemented by personal observations made during the 2015 field survey, as priority over the redescription of the morphology of the species is a work in

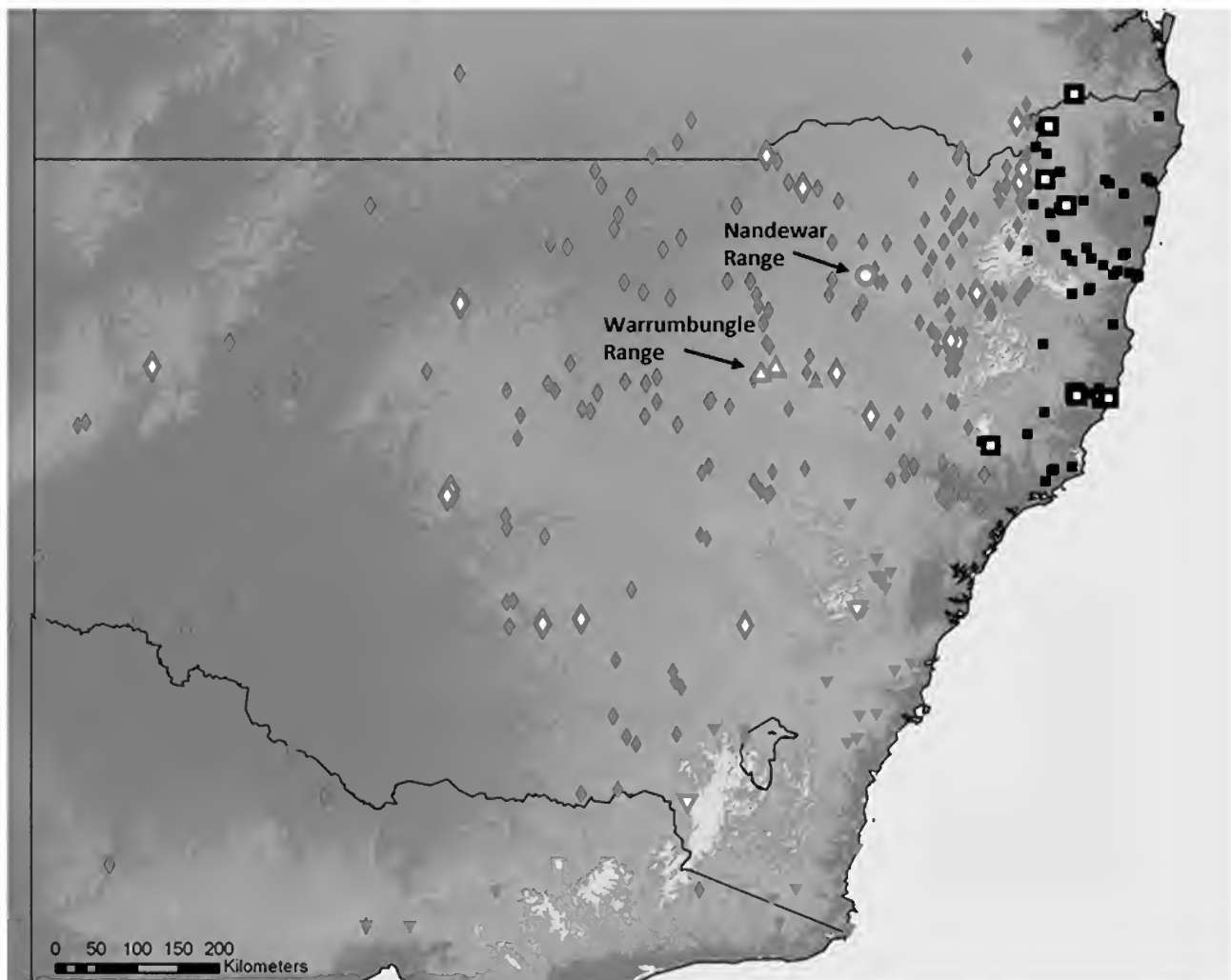


Figure 3. Elevation image of New South Wales showing the distribution of the east Australian *striolata*-group species in the state based on specimen records in the Australian Museum (closed symbols) and those samples analysed in the genetic study (open symbols): *Egernia striolata* (blue diamond), *Egernia saxatilis saxatilis* (red triangle); *Egernia saxatilis intermedia* (red triangle upside-down); *Egernia mcphreei* (black square) and the Kaputar Rock Skink *Egernia roomi* (circle in red).

progress by Dr Glenn Shea, Sydney University.

Genetics: Sampling for genetic comparisons included tissue samples held in the Australian Museum Herpetology Tissue Collection (Appendix 1) of the Kaputar Rock Skink ($n = 5$) and representatives of the described east Australian *striolata*-group species *E. striolata*, *E. mcphreei*, *E. saxatilis saxatilis* and *E. saxatilis intermedia* ($n = 42$). Our sampling for the east Australian *striolata*-group taxa was comprehensive, including representatives from across the geographic range of each species (see Fig. 3). For the widespread species *E. striolata*, 23 samples representing 15 independent locations from across New South Wales were utilized. Four taxa were used as progressive outgroups. Near outgroup taxa included *Egernia formosa*, a representative of the western *striolata*-group species and Cunningham's Skink *Egernia cunninghami* as a representative from the genus *Egernia* not generally considered as a member of the *striolata*-group. More distantly related outgroup taxa included: the Desert Skink *Liopholis inornata* as a representative of a group of species formerly within *Egernia* but now recognized as a distinct genus (Gardner *et al.*, 2007), and the Eastern Blue-tongue Skink *Tiliqua scincoides* as a representative member

of a significantly broader evolutionary group to which the species of *Egernia* also belong (= the *Egernia* group sensu Greer, 1979, later as the *Egernia* subgroup of the *Mabuya* group sensu Honda *et al.*, 2000).

Sampling for *P. pagenstecheri* and *U. sphyrurus*, the two additional species of lizards chosen for the supplemental study, was from tissue samples held in the Australian Museum Herpetology Tissue Collection (Appendix 2). For *P. pagenstecheri* this included samples from the Nandewar Range ($n = 2$), two locations on the northern tablelands ($n = 4$), Coolah Tops, an outlier of the Dividing Range at the head of the Hunter River valley ($n = 1$), and two locations on the southern tablelands ($n = 3$). Sampling for *U. sphyrurus* was modest as only a few samples were available, and included single individuals from Mt Yulladunida on the Nandewar Range, from near Copeton Dam on the western slopes of the northern tablelands, and from Moonbi at the southern end of the northern tablelands.

DNA was extracted from frozen tissues using the ISOLATE II Genomic DNA Kit (Biolone, Australia) under standard conditions and a partial region of the mitochondrial Cytochrome b (*Cyt b*) gene was amplified using the L14841

and H15149 primers (Kocher *et al.*, 1989). *Cyt b* was chosen over more commonly examined mitochondrial DNA (mtDNA) regions in reptiles (e.g., ND2, ND4) as it produced consistent amplification across all examined specimens including outgroups, which could not be achieved using other mtDNA primers. Polymerase Chain Reactions (PCRs) were carried out in 25 µl reactions using 100–500 ng of genomic DNA, 1 × Reaction Buffer (Bioline MyTaq Red Reagent Buffer; Bioline, Australia), 2 pmol of each primer and 0.5U Bioline MyTaq Red DNA polymerase. Negative controls were included in each PCR. PCRs were carried out under the following cycling conditions; Initial 94°C (3 min) denature, followed by 38 cycles of 94°C (20 sec) denature; 55°C (40 sec) annealing; 72°C (40 sec) extension, followed by a final 72°C extension step. Amplified PCR products were cleaned using ExoSap-IT© (USB Corporation, Cleveland, Ohio, USA) and sequencing was resolved on an AB 3730xl Sequencer at the Australian Genome Research Facility, Australian Museum, Sydney. Sequences were checked and edited with reference to chromatograms using Sequencher v 5.3.2 (Gene Codes Corporation, Ann Arbor, MI, USA) and lodged with GenBank. Sequences were aligned using the Clustal X algorithm implemented in MEGA 7 (Tamura *et al.*, 2013).

Phylogenetic relationships among haplotypes were estimated using maximum likelihood (ML) and Bayesian inference (BI). An appropriate model of evolution (HKY + Γ) was determined using MEGA v 6 (Nei & Kumar, 2000; Tamura *et al.*, 2013), based on the Bayesian Information Criterion (BIC scores) and Akaike information criterion, corrected (AICc scores) and all phylogenetic analyses were carried out using this model.

Maximum Likelihood (ML) was estimated using MEGA v 6 (Tamura *et al.*, 2013) with 500 bootstrap replicates. Bayesian Inference (BI) analysis was conducted in MrBayes 3.2 (Ronquist *et al.*, 2012). Metropolis-Coupled Markov Chain Monte Carlo sampling was used to calculate posterior probability. The analyses were run using default settings for priors. Two independent analyses ran simultaneously with four chains per run (1 cold, 3 hot). The chains were run for 1 million generations and sampled every 100 generations to obtain 10,000 sampled trees. Tracer 1.6 (Rambaut *et al.*, 2014) was used to check for chain convergence and adequate Effective Sample Size (> 200). Bootstrap values (percentages) and posterior probabilities (decimals) were used to assess the level of branch support. Values over 80% and 0.90 were considered well supported branches (Fig. 5).

Results

Distribution: Based on specimen records in the Australian Museum, the Kaputar Rock Skink has only been rarely recorded prior to our study. The earliest records are a single specimen from ‘Mt Kaputar’ collected by W. McReddie in December 1965, and two others from ‘Mt Kaputar top’ collected by P. Room in December 1975—no further data accompanies these specimens. A collection of eight specimens was made by the senior author in October 1980, one from Mt Kaputar (c. 1480 m), the remainder from the northwest side of Mt Dowe (c. 1420–1440 m). A further two specimens were collected on the Mt Kaputar summit by G. Swan and D. O’Mealy in 1998 from rockpiles. Field work

undertaken in September 2015 detected the Kaputar Rock Skink at two sites, Mt Dowe (the same site investigated in 1980) and The Governor (c. 1370 m). As such, the species has been detected from three separate locations with certainty c. 2 km (Mt Dowe to Mt Kaputar) to 3 km straight line distance apart (Mt Dowe and Mt Kaputar to The Governor), and covering a range of altitudes between 1370 and 1480 m.

Evidence of regional parapatry between *Egernia striolata* and the Kaputar Rock Skink was identified based on records in the Australian Museum specimen collection. *Egernia striolata* was found to occur at six areas within a 50 km radius of Mt Kaputar, including Narrabri (c. 35 km SW—AMS R.1050, R.1054–55), Bellata (c. 50 km NW—AMS R.94783), Terry Hie Hie area (c. 40 km N—AMS R.112852), Horton River southwest of Bingara (c. 30 km NE—AMS R.92470, R.92473), Barraba area (c. 50 km E—AMS R.2896–98, R.41828) and Boggabri (c. 50 km S—AMS R.2005, R.4171).

Morphology: Reference to the descriptions of the Kaputar Rock Skink, *E. saxatilis*, *E. mcphreei* and *E. striolata* in Swan *et al.* (2017) and Wilson (2015) identified differences between these taxa relating to average and maximum body size, texture of the dorsal scales, and colouration. Features of dorsal scalation unequivocally differentiate the Kaputar Rock Skink from *E. saxatilis*, the texture of the scales of the Kaputar Rock Skink being smooth or slightly grooved vs the scales having ridges low in profile but peaked and sharp at the posterior end of the scale. Aspects of colouration also serve to distinguish the two species. Both are dark in colouration overall, but the Kaputar Rock Skink has a paler dorsolateral area anteriorly whereas the dorsal colouration of *E. saxatilis* is relatively uniform in pattern—both are similar in ventral colour. Distinguishing the Kaputar Rock Skink from *E. mcphreei* and *E. striolata* is less straightforward from the morphological information published. The Kaputar Rock Skink is smaller in average (105 vs 120 mm) and maximum (121 vs 143 mm) adult body size than *E. mcphreei*, the texture of the scales is smooth or with low and gently rounded ridges

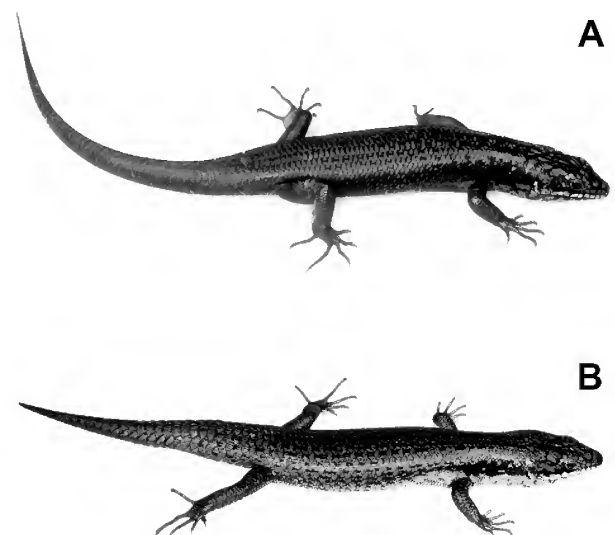


Figure 4. Comparison of dorsal colour pattern between typical individuals of *Egernia roomi* from Mt Dowe (AMS R.97913) and a regionally parapatric *Egernia striolata* from Terry Hie-Hie 40 km north (AMS R.112852).

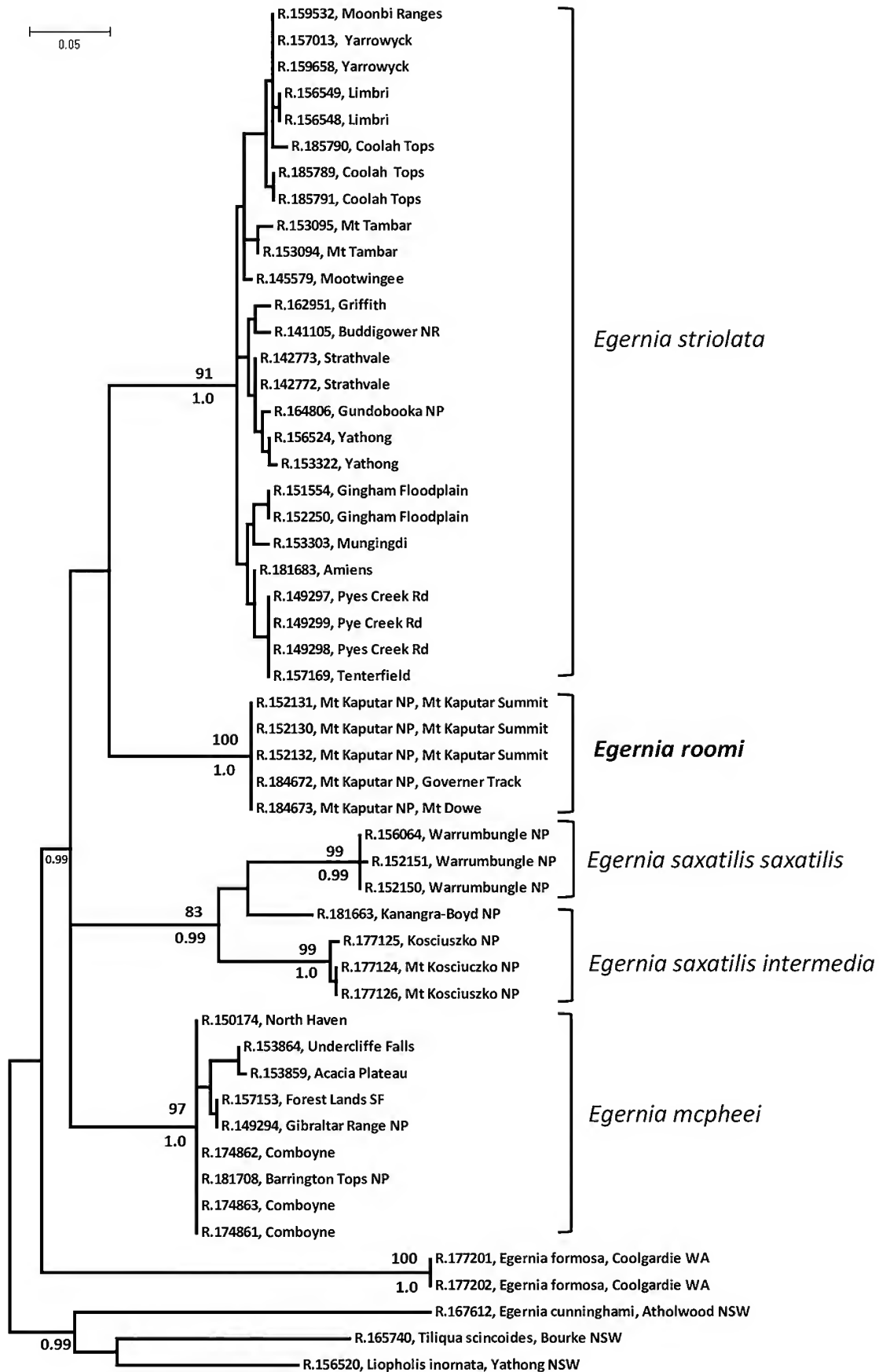


Figure 5. Phylogeny based on Maximum Likelihood estimates of the east Australian *striolata*-group species and selected outgroup taxa inferred from partial *Cytochrome b* sequence. Both Maximum Likelihood and Bayesian Inferred resolved similar topography. Bootstrap values (percentages) are present above the node and posterior probabilities (decimals) are presented below the node, only values over 70% or 0.7 are shown.

Table 1. Matrix of genetic distances in *Cyt b* (range and mean parenthetically) as percentage difference between the east Australian members of the *Egernia striolata*-group and the outgroup taxa used.

	<i>Egernia roomi</i>	<i>E. mcphreei</i>	<i>E. s. saxatilis</i>	<i>E. s. intermedia</i>	<i>E. striolata</i>	<i>E. formosa</i>	<i>E. cunninghami</i>	<i>L. inornata</i>	<i>Tiliqua scincoides</i>
<i>Egernia roomi</i>	0.0								
<i>Egernia mcphreei</i>	12.9–15.9 (13.8)	0.0–2.9 (1.3)							
<i>Egernia s. saxatilis</i>	15.5–16.1 (15.7)	18.5–20.9 (19.5)	0.0–0.4						
<i>Egernia s. intermedia</i>	16.5–18.2 (17.8)	16.1–18.4 (17.6)	9.1–13.7 (12.3)	0.0–1.0 (0.5)					
<i>Egernia striolata</i>	12.4–15.6 (14.0)	12.5–18.3 (14.7)	14.6–18.9 (16.7)	15.0–19.6 (18.0)	0.0–5.3 (3.1)				
<i>Egernia formosa</i>	24.4	19.8–23.4 (22.4)	20.4–21.0 (20.6)	22.7–23.9 (23.2)	20.5–22.6 (21.5)	0.0			
<i>Egernia cunninghami</i>	22.8	18.3–20.0 (19.0)	22.3–22.9 (22.5)	20.5–22.2 (21.1)	18.9–23.8 (21.7)	30.6	—		
<i>Liopholis inornata</i>	18.3	20.0–21.7 (20.0)	19.4–20.0 (19.6)	17.8–18.9 (18.2)	21.6–26.3 (23.5)	25.9	22.5	—	
<i>Tiliqua scincoides</i>	21	20.1–21.2 (20.6)	20.8–21.4 (21.0)	22.6–23.9 (23.2)	18.8–20.8 (19.6)	28.4	27.4	19	—

vs having ridges low in profile with a blunt posterior end, and there are subtle differences in colouration of the dorsal surface (broad paler dorsolateral area anteriorly *vs* overall dark colouration above) and ventral surface (dull but deep orange *vs* orange to orange-yellow). Differences between the Kaputar Rock Skink and *E. striolata* for average (105 *vs* 95 mm) and maximum (121 *vs* 119 mm) adult body size are subtle, as are differences in the texture of the surface of the dorsal scales of the body (smooth to slightly grooved *vs* grooved). However, the two taxa differ markedly in colouration, particularly in the extent of dark markings to the scales of the dorsal surface of the body, in the uniformity and intensity of orange colouration on the ventral surface of the chest, abdomen and underside of the tail, and in the intensity of the blueish-grey throat colour. The dark markings to the dorsal surface of a typical individual of the Kaputar Rock Skink are restricted to the anterior part of the body and tend to coalesce, whereas those of regionally parapatric *E. striolata* are well-defined and continue down the entire length of the body (Fig. 4).

Genetics: DNA sequences were obtained for 278–307 bp of *Cyt b* gene. Both *Maximum Likelihood* and *Bayesian Inference* methods resolved phylogenetic trees with similar topography illustrating that, even with this short *Cyt b* fragment, the east Australian *striolata*-group species *striolata*, *mcphreei*, and *saxatilis* are distinct and well-supported independent genetic lineages (Fig. 5). A deep level of genetic differentiation between these taxa was evident in pairwise comparisons (Table 1). The Western Australian *striolata*-group representative *formosa* was also resolved as a highly-supported and distinct independent genetic lineage. Phylogenetic analyses also resolved all individuals of the Kaputar Rock Skink as a genetic group distinct from all other recognized taxa included in the study. The five individuals sampled came from three locations over two distinct time points (1998 and 2015), and all had the same *Cyt b* haplotype. Although the analysis retrieved *E. striolata* as the sister to the Kaputar Rock Skink, support for this arrangement was low (Fig. 5), highlighting the Kaputar Rock Skink's distinctiveness from *E. striolata*. No evidence of genetic introgression was detected between the individuals representing the Kaputar Rock Skink population and any of the east Australian *striolata*-group species. This is a particularly significant result with respect to *E. striolata*. This species was sampled extensively throughout its range in New South Wales and included populations in moderately close geographical proximity to the Kaputar Rock Skink, as represented by individuals from the Tambar Ranges (c. 120 km south), the Gingham floodplain (c. 150 km north), and Yarrowyck (c. 120 km east on the northern tablelands). Pairwise comparisons between the Kaputar Rock Skink and the east Australian *striolata*-group species (Tables 1 and 2) showed a high level of genetic differentiation for the *Cyt b* gene with *E. striolata* (12.4–15.6%), *E. saxatilis saxatilis* (15.5–16.1%) and *E. saxatilis intermedia* (16.5–18.2%), *E. mcphreei* (12.9–15.9%), and an even higher level when compared to the western *striolata*-group species *E. formosa* (24.4%) and to *E. cunninghami* (22.8%). Comparative levels of genetic differentiation between well-established scincid taxa for the *Cyt b* gene are seen in studies on the Australian scincid genus *Saproscincus* (Sadlier *et al.*, 2005). This study gave average pairwise genetic distances of 11.1–14.3% between the species *S. challengeri* and *S. spectabilis* and

Table 2. Matrix of genetic distances (range, with mean parenthetically) as percentage difference between populations of the east Australian species *Egernia saxatilis*.

		<i>E. s. saxatilis</i> Warrumbungle Ranges n = 3	<i>E. s. intermedia</i> central tablelands n = 1	<i>E. s. intermedia</i> southern tablelands n = 3
<i>Egernia saxatilis saxatilis</i>	Warrumbungle Ranges	0.0–1.0 (0.7)	—	—
<i>Egernia saxatilis intermedia</i>	central tablelands	9.1–9.9 (9.4)	0.0–0.7 (0.4)	—
<i>Egernia saxatilis intermedia</i>	southern tablelands	14.3–14.4 (14.3)	11.6	0.0

16.5–23.7 between *S. challengerii* and *S. rosei*, considered to be ‘relatively deep divergences’. Support for this extent of DNA sequence divergence representing species-level differences comes from an earlier study investigating speciation in *Saproscincus* utilizing allozyme electrophoresis (Sadlier *et al.*, 1993) which independently established the species *S. challengerii* and *S. spectabilis* and *S. rosei* as distinct evolutionary entities.

Relationships amongst the genetic groups representing recognized taxa within the genus *Egernia* were not well resolved, and the values at primary and most secondary nodes within the genus were at best moderate. This was also a feature of an earlier study by Gardner *et al.* (2008) which more broadly sampled taxa across the traditional concept of ‘*Egernia*’ using several genes, and which at that time contained an extensive suite of species.

The comparison of populations of the Tussock Skink *P. pagenstecheri* in the supplemental study showed a low level of differentiation in pairwise comparisons between the Nandewar Range and Coolah Tops samples (3.3%), and with the Riamukka sample from the south of the northern tablelands (4.2%). However, there was markedly higher levels of differentiation with those from Stewarts Brook in the Mt Royal Ranges (12.5–13.0%). Despite being geographically closer to the Nandewar Range, Coolah Tops and Riamukka populations, the population from Stewarts Brook on the Mt Royal Range is genetically more similar to populations from further south. This assessment of variation between populations of *P. pagenstecheri* across its range is limited by the absence of populations from the central tablelands region. However, it is sufficient to indicate the break in connectivity between the Nandewar Range population and proximal populations on the Great Dividing Range (Coolah Tops and Riamukka) is historically recent, and consistent with the breaks for other lizard taxa identified by Colgan *et al.* (2009) attributable to Pleistocene events. The comparison of samples of the Granite Belt Thick-tailed Gecko *U. sphyrurus* was limited in both the geographic coverage and number of samples available (one per location). It revealed a low level of differentiation (1.6%) between individuals from the Nandewar Range and Copeton Dam (110 km NE) and slightly more elevated level of differentiation to Moonbi near Tamworth (3.7%), similar to that between Moonbi and Copeton Dam individuals (4.1%).

Discussion

Recognition of *Egernia roomi* for the Kaputar Rock Skink: The available genetic and morphological data supports recognition of the Kaputar Rock Skink as a distinct species. The taxonomic implications regarding the formal name applicable to the species rest with the legitimacy of the description of the species *Contundo roomi* as proposed by Wells & Wellington (1985) under the requirements of the International Code of Zoological Nomenclature. This name was applied by Wells & Wellington in 1985 to one of two specimens (AMS R.69587) from the summit of Mt Kaputar collected by Peter Room in 1975. While clearly relating to the Kaputar Rock Skink this name has not been applied to this taxon in either the general or scientific literature.

The works by Wells & Wellington (1984, 1985) were the subject of a case presented to the International Commission for Zoological Nomenclature for suppression for nomenclatural purposes by the Australian Society of Herpetologists (1987). In a separate submission Shea (1987) independently assessed the validity of actions contained in these works, and with regard to the description of *Contundo roomi* found that while the diagnosis presented was unworkable, it did not prevent the availability of this name under the code. The ICZN (1991) considered these works by Wells & Wellington to represent a “clear rejection of virtually every tenet of the voluntary code of ethics”, but ruled that the legitimacy of the taxa proposed be determined on a case by case basis against the rules of the ICZN. In a consideration of the type specimens of reptiles described by Wells & Wellington (1984, 1985) residing in the Australian Museum collection *Contundo roomi* was regarded as “innominate” by Shea & Sadlier (1999) in the absence of a workable diagnosis, and was listed as “*Egernia* sp. nov.” pending “completion of studies on the *Egernia striolata* complex by G. Shea”. No comment was given as to why this action was taken in precedence over the earlier statement by Shea (1987) regarding the availability of the name. The only other mention of the name *roomi* is by Cogger (2014) under the account of subspecies of *Egernia saxatilis*, but only in that its status was uncertain.

Our consideration of the availability of the name *Contundo roomi* is that the description of the species by Wells & Wellington (1984) contains a diagnosis in words that purports to distinguish it from specific related taxa, even

if erroneous. As such, we consider it meets the minimum requirements for recognition as a valid description at the time it was published, and as a consequence the name *Contundo roomi* has priority of application to the Kaputar Rock Skink. There is no independent data to support the recognition of the genus *Contundo* as proposed by Wells & Wellington for this species and several other *striolata*-group species, and so the name used for the Kaputar Rock Skink is *Egernia roomi* (Wells & Wellington, 1985). The formal redescription of the Kaputar Rock Skink is part of the ongoing work in progress by Shea on the *striolata*-group mentioned above.

Habitat of the Kaputar Rock Skink: The Nandewar Range is the remnant of the Nandewar Volcano, formed when a series of volcanic eruptions moved across the region 21 and 17 million years ago as the continent drifted slowly northward across a ‘hotspot’ in the Earth’s mantle. The Nandewar Volcano was a shield volcano with gently sloping sides rising to a height of over 2100 m and was 50 km wide. The flows from its vents were extensive, with a north-south extent of about 160 km, and east-west of about 100 km. The next point of crustal weakness to pass above the same hotspot was the Warrumbungle area, where lava extruded from the Warrumbungle Volcano between 17 and 13 million years ago (Brove Mapping Services).

Subsequently millions of years of erosion have created a landscape of lava terraces, volcanic plugs and ring dykes which are major landscape features of the Nandewar Range today. The highest point is Mt Kaputar at 1510 m in elevation, with twelve other peaks of at least 1200 m, by contrast the surrounding plains lie at 230 m (Cartoscope). The Kaputar Plateau and Mt Dowe (both areas from which the Kaputar Rock Skink has been recorded), and Lindsay Rock Tops are ancient trachyte lava terraces, while The Governor (another record site from our survey) is a flat-topped flow remnant carved by erosion.

The Nandewar Range is linked by a narrow corridor of low ranges to the northern tablelands of the Great Dividing Range. The vegetation exhibits both western slopes and tablelands affinities, with the northern tablelands component representing an outlier surrounded by semi-arid plant communities. Areas over 1200 m are above the winter snowline, and at these higher elevations distinct sub-alpine vegetation communities have been identified, including open forests of mountain gum and snow gum with snow grass groundcover on higher elevation slopes and flats, and heathland and open herbfields in exposed areas with thin soils (DEC, 2006).

All records of the Kaputar Rock Skink have been from areas of outcropping rock (Fig. 6) that are part of remnant lava terraces of the Kaputar plateau area between 1360 and 1480 m elevation. All sites have been in close proximity to the periphery or rim of the plateau, not from outcropping rock within woodland of the interior of the plateau. On rock surfaces where it has been observed the species appears to only occupy sheltering sites of rock overlying rock, not rock on soil. This is in keeping with the habits of other members of the *striolata*-group which occupy naturally-existing shelter sites such as rock crevices or, in the case of *E. striolata* and *E. mcphreei*, also the use of tree hollows and gaps in dead and fallen timber. Reference to satellite imagery indicates the majority of escarpment rock habitat lies above 1100 m. Assuming the extent of this high elevation rock habitat to be

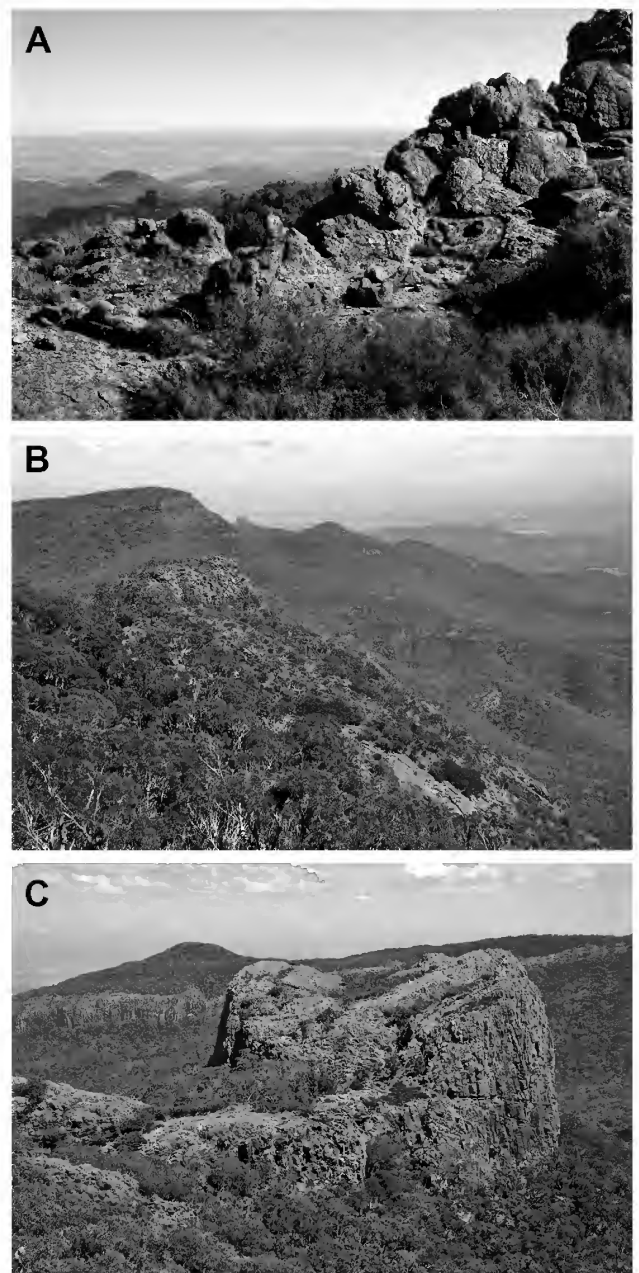


Figure 6. High elevation rock habitat of *Egernia roomi*, the summit region of the Nandewar Range (A, B) and the base of the volcanic plug The Governor (C).

a key factor in the presence of the Kaputar Rock Skink, the potential extent of occurrence of the species (EOO) is small (241 km²), even when based conservatively on an estimate of area above 1000 m in elevation, and the specific area it occupies (AOO) even lower (134 km²).

These observations should be regarded as indicative, given areas of rock habitat lower in elevation have yet to be systematically investigated. However, should future field studies further support the Kaputar Rock Skink as being confined to highly specific high elevation rock microhabitat, the species will have one of the narrowest environmental niches of any reptile species in New South Wales, and one that may become progressively narrower with rising temperature regimes.

Evolutionary History of the Kaputar Rock Skink: The occurrence of species restricted to the higher elevation habitat of isolated peaks and plateaus on mountain chains has been well documented worldwide (see Haines *et al.*, 2017), with the term ‘sky islands’ applied to such scenarios. Niche conservatism in species (Wiens, 2004) has been promoted as the primary driver for historical isolation to mountain tops, whereby taxa that are cool-adapted retreat upward in elevation with the onset of less favourable (warmer) climatic conditions, and theoretically downward under favourable conditions. The size and connectivity of many ‘sky island’ populations are thought to have fluctuated in response to Pliocene-Pleistocene glacial cycles.

In Australia contraction of montane habitat associated with Pliocene-Pleistocene interglacial cycles has been proposed to explain genetic diversification within cool-adapted reptile species in the Australian Alps region of the Great Dividing Range (Haines *et al.*, 2017), with expansion in range associated with periods of cooler conditions during glacial periods. In north-east Australia genetic diversification in moisture-dependent reptile taxa in the humid forests has been attributed to the contraction of forest habitat during periods of aridity associated with Pleistocene glacial cycles, with expansion in range during warmer and moister conditions of interglacial periods, and similar but older events of late-Miocene or early-Pliocene age have been proposed to explain the evolution of deeply divergent taxa restricted to the summit areas of mountain tops c. 1000 m in elevation in the Wet Tropics region of northeast Queensland (Schneider *et al.*, 1998; Schneider & Moritz, 1999; Moritz *et al.*, 2000; Moritz *et al.*, 2012). Either scenario result in the retreat upward in elevation of niche-conservative taxa unable to adapt to the changed conditions at lower elevations, and their isolation in montane refugia.

The study by Colgan *et al.* (2009) of phylogeographic patterns of the montane rock-dependent gecko species *Oedura* aff. *lesueurii* on the northern tableland region utilizing the *Cyt b* gene gave an average nucleotide difference of 8.8% between basal clades, with an estimated time of divergence of c. 3.5 million years ago, towards the early Pleistocene or before. The level of genetic differentiation between the Kaputar Rock Skink and east Australian *striolata*-group species is significantly greater (see Table 1), indicating isolation of the Kaputar Rock Skink to the Nandewar Ranges to be an historically older event than the Pleistocene glacial cycles.

The Kaputar Rock Skink now appears to be restricted to high elevation habitat on the Nandewar Range and to be a ‘cool-adapted’ species. Here we consider the possible evolutionary scenarios that may account for its present day distribution on the montane summits of the Nandewar Range, and other potential contributing factors that may also be involved. Little inference for this being a consequence of a ‘montane’ ancestry are apparent in the scheme of relationships derived from the genetic study, and the species’ apparent reliance on montane habitat of the summit region of the Nandewar Range appear to be independently derived. The question remains as to what factors may have driven both the degree of habitat specificity and geographic isolation.

The summit area of the Nandewar Range has a group of several lizard species (*P. pagenstecheri*, *Acritoscincus platynotum*, *Hemiergus talbingoensis*) and one snake (*Drysdalia coronoides*) whose distributions otherwise are

largely confined to higher elevation habitat of the Great Dividing Range, and could be regarded as ‘cool-adapted’ montane species. The presence of disjunct populations on the Nandewar Range indicates that habitat and climatic conditions suitable for ‘cool-adapted’ species existed at lower elevation in intervening areas historically.

To assess the extent and recency of historical connectivity of habitat suitable for ‘cool-adapted’ species between the Nandewar Range and adjacent northern tablelands we investigated the level of genetic divergence between the Nandewar population of the montane specialist skink *P. pagenstecheri* and other high elevation populations of that species. The level of genetic differentiation between the Coolah Tops, Nandewar Range and Riamukka populations was low, indicating historically recent gene flow between these populations. By implication, habitat with a thermal regime suitable for ‘cool-adapted’ lizard species existed in intervening areas in recent historical times, and its availability would not appear to have been a factor then in maintaining isolation of the Kaputar Rock to the Nandewar Range.

We also considered discontinuity of rocky habitat as a contributing factor to the historical isolation of the Kaputar Rock Skink by investigating the extent of genetic differentiation between several populations of the rock dependant gecko *U. sphyrurus*. Although limited to a few samples, the level of genetic differentiation detected between the Nandewar Range and adjacent western slopes near Copeton and the New England tablelands at Moonbi was low to moderate, but consistent with these being a part of a widespread population with some degree of substructure and no significant barriers to dispersal. From this we infer continuity of structurally suitable rock habitat in the area between the Nandewar Range and Great Dividing Range was likely to be present in historically recent times.

The independent studies undertaken on *P. pagenstecheri* and *U. sphyrurus* indicate neither an absence of thermally suitable montane habitat or lack of structurally suitable rock habitat to be a contributing factor in maintaining isolation of the Kaputar Rock Skink to the Nandewar Range in historically recent times. Rather, it would appear factors responsible for the species current isolation and reliance on high elevation habitat stem from deep in its history, and its biology now compatible only with the environmental niche offered by rock outcrops at high elevation. The term ‘lithoreugia’ was recently proposed by Couper & Hoskin (2008) in describing the historical role of rock habitat as refugia in the evolution of a broad range of reptile species on the coastal ranges of central-east and northern Queensland. Here, the role of rock habitat as refugia for fauna is likely closely linked with its ability to also provide a refuge for the persistence of once more-widespread vegetation types, such as dry rain forest, under periods of historical aridity. This combination of attributes is considered the likely speciation mechanism behind the evolution of a number leaf-tailed geckos in the genus *Phyllurus* in mid-eastern Queensland (Stuart-Fox *et al.*, 2001; Couper & Hoskin, 2008).

The significance of rocky environments—lithoreugia—in the western division of New South Wales as historical refuges for reptiles is now becoming apparent. This is not so much in the context of strongholds for arid zone species from which pulses of expansion and contraction in range emanate, but rather as retreat sites for mesic species once

more widespread in distribution. Several species of lizards with primarily eastern distributions have highly disjunct outlying populations in the west of the state. The most extreme is the population of White's Skink *Liopholis whitii* from the Bynguano Range of Mutawintji National Park, 110 km to the north and east of Broken Hill (Swan & Foster, 2005). *Liopholis whitii* has a core distribution along the Great Dividing Range, but extends also onto the western slopes to the Warrumbungle Ranges, approximately 650 km east of the population at Mutawintji. The extent of differentiation between the Mutawintji population of White's Skink and populations to the east was 3.2–4.3% (16S and ND4 mitochondrial genes combined—Chapple & Keogh, 2004), a level of divergence regarded as consistent with a split of Pliocene–early Pleistocene ancestry. The other example is a disjunct population of the Eastern Ranges Rock Skink *Liopholis modesta* on the Merrimerrriwa Ranges of Yathong National Park in the central-west of the state. This species otherwise has a distribution restricted to the ranges of the northern tablelands and adjacent western slopes, but with populations extending onto the edge of the western plains near Moree and Walgett, 380 km northeast of the Yathong population. The highly disjunct populations of *L. whitii* and *L. modesta* now restricted to rocky ranges in the western division are considered to represent remnant populations from when these primarily 'mesic' species (Chapple & Keogh, 2004) were once more widespread under different and more favourable climatic conditions, but have undergone severe recent historical contractions in range. It is likely the apparently long-term isolation of the Kaputar Rock Skink to the summit region of the Nandewar Range represents a similar scenario, but deeper in time.

A final possible contributing factor in the apparent restriction of the Kaputar Rock Skink to higher elevations on the Nandewar Range could be that of inter-specific competition with populations of *E. striolata* that are likely to occupy the adjacent lowlands. Cogger (1960) reported the east Australian *striolata*-group species *E. striolata* and *E. saxatilis saxatilis* as occurring in local sympatry in the Warrumbungle Ranges, but with mutually exclusive habitat preferences. He found *E. saxatilis saxatilis* to be confined to rock outcrops and screes on the upper parts of bluffs and spires whereas *E. striolata* occupied the surrounding woodland habitat and was strictly arboreal in habits. *Egernia striolata* may have played a similar role in maintaining isolation of the Kaputar Rock Skink by preventing its expansion downward to lower elevations during periods of more favourable climatic conditions historically, and even now. *Egernia striolata* is known from several nearby sites on the adjoining on the adjacent plains, but its occurrence on the lower slopes of the Nandewar Ranges and environs has yet to be established. It is also worth noting here that *E. striolata* has been recorded from c. 1000 m elevation on Coolah Tops, indicating that altitude alone, to this level, is not a barrier to dispersal upward in elevation for the species.

Implications for conservation of the Kaputar Rock Skink: The evidence available so far suggests the current narrow niche preference of the Kaputar Rock Skink is likely a product of its evolutionary history. Its apparent absence from rock or woodland microhabitat at lower elevations likely reflects the thermal unsuitability of microhabitats for the species lower on the ranges, and it requires rock

outcrops at high elevation to provide suitable sheltering and foraging sites within an optimal climatic regime. However, the suitability of high elevation rock outcrops for the Kaputar Rock Skink may also extend to the capability of the rock habitat occupied in buffering against extremes of (low) temperature and dryness. In this respect not all rock habitat may be suitable for the species. Attributes such as the aspect, exposure with respect to the structure of surrounding vegetation and orientation towards the sun, extent of exposed rock, and availability and structure of retreat sites are all likely to determine site suitability. Although rock habitat is in itself robust to the impact of events such as wildfire and or seasonal extremes of heat and dryness (such as experienced in recent *el niño* cycles), these events are likely to affect food availability (both prey items and vegetative matter), and activity regimes (basking and foraging). Taking these factors into account the Kaputar Rock Skink could have an even more restricted area of occurrence, one which could be highly vulnerable to perturbation of its surrounding environment.

Haines *et al.* (2017) provided a comprehensive overview of the impact of climate change on 'sky island' species, focussing on the implications for cool-adapted reptile species. These impacts included a reduction in daily activity periods,

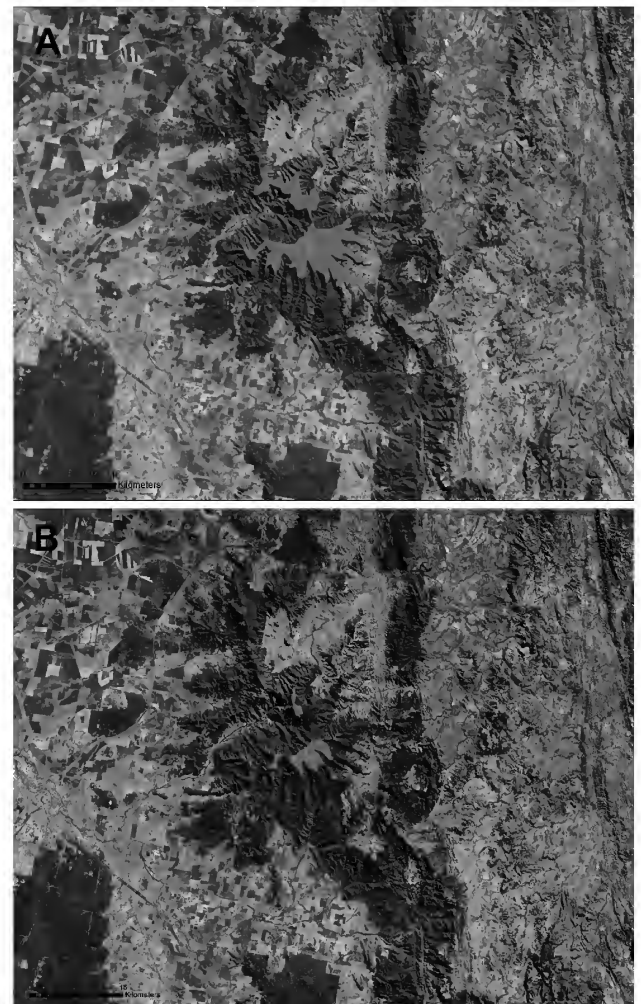


Figure 7. The projected extent of occurrence of the Kaputar Rock Skink *Egernia roomi* on the summit region of the Nandewar Range (area in blue) above 1000 m in elevation (A) and above 1200 m, with the 3 sites (red circles) from which the species has been recorded.

physiological stress, increased competition from other species in the face of a shrinking ecosystem, and greater disconnectivity between isolate populations. Based on the information currently available, a similar suite of impacts are likely to affect the Kaputar Rock Skink with climatic warming.

Current New South Wales and federal threatened species legislation (*Environment Protection and Biodiversity Conservation Act 1999*; *Biodiversity Conservation Act 2016*) uses the tenets of IUCN Red List criteria in assessing levels of threat to species. The Kaputar Rock Skink has a predicted area of occupancy (AOO) considerably less than 500 km² and only occurs at one location (the Nandewar Range), and on this basis meets the geographic range criteria for consideration as highly threatened. However, the status of the species with regard to observed, estimated, inferred or projected threats that could affect the quality of its very specific preferred habitat requires further investigation (Fig. 7).

Among the potential threats that could complicate the long-term integrity of the preferred habitat of the Kaputar Rock Skink are the impact of invasive species, fire, human visitation and climate change. Goats can alter the ecology of rocky habitat and the areas immediately adjacent, and their control has been identified as a management priority for KNP (Hunter, 2015) and is part of the park management plan (DEC, 2006). The impact of an intense fire event on resident populations could lie more with the after-effects associated with loss of surrounding vegetation, including reduced invertebrate prey for food and altered microclimate. Human-mediated disturbance of habitat is an issue at sites close to the edge of cliff lines that are readily accessible by walking tracks. Trampling of low vegetation was evident at many sites, and disturbed rocks were observed at Mt Dowe, The Governor and elsewhere in KNP during our 2015 field studies, the latter presumably by persons wanting to locate reptiles. Habitat disturbance of this kind was observed over an extensive area of granite outcrops in the vicinity of Kanangra Walls on the central tablelands (RAS, pers. obs.), resulting in a reduction of sheltering sites for populations of *E. saxatilis intermedia*, the Black Rock Skink. Altering the placement of rocks likely alters the microenvironment beneath the rock, rendering it unsuitable for reptiles that utilize rock crevices as sheltering sites.

However, the most significant threat to the extent of suitable habitat available to the Kaputar Rock Skink comes from an inferred narrowing of the available altitudinal niche occupied by the species from climate change induced warming. Distinct sub-alpine vegetation communities occur on the Nandewar Range at areas above the snowline at 1200 m in elevation. The Kaputar Rock Skink has so far only been recorded from between 1360 and 1480 m in elevation. It is possible its lower elevational range is also limited by similar environmental parameters that restrict the elevational limits of sub-alpine vegetation communities on the Nandewar Range. If this is the case, an estimate of area of Area of Occupancy (AOO) of 134 km² and Extent of Occurrence (EOO) of 241 km² being based on most high elevation rock habitat being above 1000 m in elevation, could represent a substantial overestimate of potential area occupied by the species. A reduction in range of elevation of only 200 m to areas above the snowline at >1200 m (still 150 m below the lowest known record) would result in a significant reduction of predicted area AOO to 30 km² and EOO to 122 km².

ACKNOWLEDGMENTS. We thank Mrs Mary Holt and the late Dr John Holt for funding and James Faris (OEH, Narrabri) for advice and support. Timothy Cutajar produced the map of *striolata*-group species presented in Fig. 3 and predicted areas of occurrence in Fig. 7, and Corin Sadlier for assistance with Fig. 4.

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Appendix 1

Specimens of east Australian members of the *Egernia striolata*-group and the outgroup taxa used in the genetics study. Written locations are generalized for brevity, full location data resides in the Australian Museum Herpetology collection registers. Australian Museum, Sydney (AMS) register numbers are prefixed R.

AMS	GenBank No.	species	location
R.152130	MN270184	<i>E. roomi</i>	Mt Kaputar NP, Mt Kaputar summit (30°16'23"S 150°09'51"E)
R.152131	MN270185	<i>E. roomi</i>	Mt Kaputar NP, Mt Kaputar summit (30°16'23"S 150°09'51"E)
R.152132	MN270186	<i>E. roomi</i>	Mt Kaputar NP, Mt Kaputar summit (30°16'23"S 150°09'51"E)
R.184673	MN270187	<i>E. roomi</i>	Mt Kaputar NP, Mt Dowe (30°17'01"S 150°10'01"E)
R.184672	MN270188	<i>E. roomi</i>	Mt Kaputar NP, Governor Track (30°15'58"S 150°08'44"E)
R.149294	MN270189	<i>E. mcphreei</i>	Gibraltar Range NP (29°31'03"S 152°21'33"E)
R.150174	MN270190	<i>E. mcphreei</i>	North Haven (31°38'S 152°49'E)
R.153859	MN270191	<i>E. mcphreei</i>	Acacia Plateau (28°17'41"S 152°26'35"E)
R.153864	MN270192	<i>E. mcphreei</i>	Undercliffe Falls (28°38'49"S 152°09'59"E)
R.157153	MN270193	<i>E. mcphreei</i>	Forestlands State Forest, Bald Rock (29°13'41"S 152°07'25"E)
R.174861	MN270194	<i>E. mcphreei</i>	Comboyne (31°34'12"S 152°27'25"E)
R.174862	MN270195	<i>E. mcphreei</i>	Comboyne (31°34'12"S 152°27'25"E)
R.174863	MN270196	<i>E. mcphreei</i>	Comboyne NR, Mt Bulli (31°36'S 152°28'E)
R.181708	MN270197	<i>E. mcphreei</i>	Barrington Tops NP (near Guest House) (32°09'07"S 151°31'21"E)
R.152150	MN270198	<i>E. s. saxatilis</i>	Warrumbungle NP, Timor Rock (31°15'59"S 149°09'31"E)
R.152151	MN270199	<i>E. s. saxatilis</i>	Warrumbungle NP, Timor Rock (31°15'59"S 149°09'31"E)
R.156064	MN270200	<i>E. s. saxatilis</i>	Warrumbungle NP, Timor Rock (31°15'59"S 149°09'31"E)
R.177124	MN270201	<i>E. s. intermedia</i>	Kosciuszko NP, near Clover Flat camping area (36°05'11"S 148°11'03"E)
R.177125	MN270202	<i>E. s. intermedia</i>	Kosciuszko NP, near Clover Flat camping area (36°05'11"S 148°11'03"E)
R.177126	MN270203	<i>E. s. intermedia</i>	Kosciuszko NP, near Clover Flat camping area (36°05'11"S 148°11'03"E)
R.181663	MN270204	<i>E. s. intermedia</i>	Kanangra-Boyd NP (33°58'S 150°03'E)
R.181683	MN270205	<i>E. striolata</i>	Amiens (28°35'41"S 151°48'44"E)
R.157169	MN270206	<i>E. striolata</i>	Tenterfield (29°06'56"S 151°53'13"E)
R.149297	MN270207	<i>E. striolata</i>	Pyes Creek Road (29°15'40"S 151°50'35"E)
R.149298	MN270208	<i>E. striolata</i>	Pyes Creek Road (29°15'40"S 151°50'35"E)
R.149299	MN270209	<i>E. striolata</i>	Pyes Creek Road (29°15'40"S 151°50'35"E)
R.159658	MN270210	<i>E. striolata</i>	Yarrowyck (30°28'21"S 151°22'17"E)
R.157013	MN270211	<i>E. striolata</i>	Yarrowyck (30°28'21"S 151°22'17"E)
R.159532	MN270212	<i>E. striolata</i>	Moonbi Ranges (30°59'33"S 151°05'00"E)
R.156548	MN270213	<i>E. striolata</i>	Limbri (31°00'53"S 151°10'04"E)
R.156549	MN270214	<i>E. striolata</i>	Limbri (31°00'53"S 151°10'04"E)
R.153094	MN270215	<i>E. striolata</i>	Mt Tambar, Tambar Springs (31°21'10"S 149°49'41"E)
R.153095	MN270216	<i>E. striolata</i>	Mt Tambar, Tambar Springs (31°21'10"S 149°49'41"E)
R.185789	MN270217	<i>E. striolata</i>	Coolah Tops (31°49'14"S 150°12'18"E)
R.185790	MN270218	<i>E. striolata</i>	Coolah Tops (31°49'14"S 150°12'18"E)
R.185791	MN270219	<i>E. striolata</i>	Coolah Tops (31°49'17"S 150°12'19"E)
R.151554	MN270220	<i>E. striolata</i>	Gingham floodplain (29°19'20"S 149°27'24"E)
R.152250	MN270221	<i>E. striolata</i>	Gingham floodplain (29°15'49"S 149°18'00"E)
R.153303	MN270222	<i>E. striolata</i>	Mungindi (28°58'06"S 149°03'20"E)
R.164806	MN270223	<i>E. striolata</i>	Gundabooka NP, Mt Gundabooka (30°35'27"S 145°41'09"E)
R.162951	MN270224	<i>E. striolata</i>	Griffith (34°06'18"S 146°35'48"E)
R.142772	MN270225	<i>E. striolata</i>	Strathvale, 5 km N Strathvale (34°07'S 148°49'E)
R.142773	MN270226	<i>E. striolata</i>	Strathvale, 5 km N Strathvale (34°07'S 148°49'E)
R.141105	MN270227	<i>E. striolata</i>	Buddigower NR (34°03'S 147°01'E)
R.156524	MN270228	<i>E. striolata</i>	Yathong (32°41'48"S 145°32'33"E)
R.153322	MN270229	<i>E. striolata</i>	Yathong (32°37'56"S 145°35'10"E)
R.145579	MN270230	<i>E. striolata</i>	Mootwingee (31°17'S 142°18'E)
R.177201	MN270231	<i>E. formosa</i>	Coolgardie (31°00'46"S 121°16'56"E)
R.177202	MN270232	<i>E. formosa</i>	Coolgardie (31°00'46"S 121°16'56"E)
R.167612	MN270233	<i>E. cunninghami</i>	Atholwood (28°59'32"S 151°08'42"E)
R.165740	MN270234	<i>Tiliqua scincoides</i>	Bourke-Wanaaring Rd, 108 km W Bourke (29°58'S 144°58'E)
R.156520	MN270235	<i>Liopholis inornata</i>	Yathong NR (32°34'20"S 145°22'56"E)

Appendix 2

Specimens of *Pseudemoia pagenstecheri* and *Uvidicolus sphyrurus* used in supplementary genetics study, all in Australian Museum, Sydney (AMS); register numbers are prefixed R.

AMS	GenBank no.	species	location
R.153074	MN270236	<i>P. pagenstecheri</i>	Mt Kaputar NP, Dawsons Spring (30°16'51"S 150°09'50"E)
R.152142	MN270237	<i>P. pagenstecheri</i>	Mt Kaputar NP, Mt Kaputar summit (30°16'23"S 150°09'51"E)
R.152167	MN270238	<i>P. pagenstecheri</i>	Coolah Tops NP, Norfolk Falls (31°44'43"S 150°00'38"E)
R.148168	MN270239	<i>P. pagenstecheri</i>	Riamukka State Forest, Grundy Fire Tower Area (31°19'39"S 151°39'21"E)
R.148170	MN270240	<i>P. pagenstecheri</i>	Riamukka State Forest (North Side), Grundy Fire Tower Area
R.147100	MN270241	<i>P. pagenstecheri</i>	Stewarts Brook State Forest, Polblue Swamp (31°57'16"S 151°25'42"E)
R.147101	MN270242	<i>P. pagenstecheri</i>	Stewarts Brook State Forest, Polblue Swamp (31°57'16"S 151°25'42"E)
R.177158	MN270243	<i>P. pagenstecheri</i>	Kosciuszko NP, Snowy Mountains Hwy (35°43'01"S 148°31'48"E)
R.177160	MN270244	<i>P. pagenstecheri</i>	Kosciuszko NP, Snowy Mountains Hwy (35°43'01"S 148°31'48"E)
R.148523	MN270245	<i>P. pagenstecheri</i>	Kosciuszko NP, Charlottes Pass
R.140837	MN270246	<i>U. sphyrurus</i>	Moonbi Lookout (30°59'S 151°05'E)
R.140838	MN270247	<i>U. sphyrurus</i>	Gum Flat, between old Howell Mine and Copeton Dam (29°56'S 151°01'E)
R.152351	MN270248	<i>U. sphyrurus</i>	Kaputar National Park, Mt. Yulladunida (30°17'18"S 150°04'55"E)

Ctenophorus spinodomus sp. nov., a New Species of Dragon Lizard (Squamata: Agamidae) from Triodia Mallee Habitat of Southeast Australia

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ABSTRACT. Research into geographic variation in the agamid lizard *Ctenophorus fordi* supports a pattern of regional lineage diversity identified in earlier genetic studies, and provides new information on differences in morphology diagnostic of these lineages. One of the most genetically divergent and morphologically distinctive of these lineages is that consisting of populations from Triodia Mallee habitat of the red sandplains of inland southeast Australia. Populations from this region are the sister lineage to all other “*C. fordi*”, a suite of four genetically regionally discrete lineages distributed across the arid inland of southern Australia. They can be distinguished by a unique black “T” shaped chest pattern in adult males which, in combination with certain features of body proportions and scalation, diagnose the lineage from all other “*C. fordi*”. On the strength of these differences we describe populations belonging to this lineage as a new species, *Ctenophorus spinodomus* sp. nov. This new species is highly restricted in the habitat it occupies, and its ecology tied to a reliance on the presence of *Triodia* hummock grass groundcover (spinifex) for shelter, foraging and social interactions. It appears to be most abundant in areas of extensive and healthy *Triodia* that develop 20–50 years post-burn, and as a consequence too many or too few fires can both have negative impacts on the suitability of hummock grass groundcover for this species. Mallee habitat in southeast Australia is fragmented, and large fires in the smaller isolated areas of habitat could result in loss of suitable habitat for the species, resulting in localized extinction with no opportunity for recruitment. These factors in combination with ongoing loss of habitat place the remaining populations of *C. spinodomus* sp. nov. at a high level of vulnerability.

Introduction

The agamid lizard *Amphibolurus fordi* was described by Storr in 1965 from populations in inland southwest Western Australia as part of a review of the *Amphibolurus maculatus* species group (Storr, 1965). It was named for Julian Ford, accomplished Western Australian naturalist and collector of the holotype, and was initially called Ford’s Dragon. The name *fordi* along with the common

name Mallee Dragon was subsequently applied in a broader geographical sense by Cogger (1975) to include the east Australian populations of what was previously regarded as *Amphibolurus maculatus* (Cogger, 1967). This concept of the species having a broad distribution across the arid interior of southern Australia, from near Kalgoorlie in Western Australia to central-western New South Wales (Cogger, 1975 and subsequent editions) has remained for the past 40 years.

Keywords: Agamidae; dragon lizard; *Ctenophorus*; Triodia Mallee; taxonomy; new species; Eastern Mallee Dragon

Taxonomic registration: (LSID publication) <http://zoobank.org/07502465-79E0-44F2-8A51-EC4F78DE208B>

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Received: 20 December 2018 **Accepted:** 29 July 2019 **Published:** 28 August 2019 (in print and online simultaneously)

Publisher: The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)

Citation: Sadlier, Ross A., Don Colgan, Cecilie A. Beatson, and Hal G. Cogger. 2019. *Ctenophorus spinodomus* sp. nov., a new species of dragon lizard (Squamata: Agamidae) from Triodia Mallee habitat of southeast Australia. *Records of the Australian Museum* 71(5): 199–215.

<https://doi.org/10.3853/j.2201-4349.71.2019.1700>

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Cogger undertook detailed studies of the ecology of the eastern-most populations in central-west New South Wales as the subject of a doctoral thesis (Cogger, 1969), later publishing on the thermal preferences (1974) and reproductive cycles and social behaviour (1978) of the species. His studies identified the presence of *Triodia* hummock grass as a crucial component of the species' environment in the population studied, a trait found to be broadly applicable to populations inhabiting the red sand plains of inland southeast Australia. Houston (1978) in his illustrated treatise of the agamid and varanid lizards of South Australia identified three races of *Amphibolurus fordi* in the state, based primarily on variation in colouration, particularly the pattern of dark markings on the throat and chest of adult males. In this work Houston identified a race in the arid northern interior of the state (presumably contiguous with the Western Australian populations), one restricted to the Eyre Peninsula, and one from the southeast of the state (presumably contiguous with the inland New South Wales population). In reference to comment made by Cogger on the habitat specificity of the species in New South Wales, Houston stated that colonies of the northern race also occupied bluebush and tussock grass habitat.

Populations in the far northwest of New South Wales (Swan, 1990; Swan *et al.*, 2004, 2017) and the adjacent areas of far southwest Queensland (Covacevich & Couper, 1991) have also been referred to as *C. fordi* for a number of years, but the identity of these populations with respect to their morphology and biology lay largely unknown, as did their relationship to the populations in central New South Wales or those in adjacent areas of inland northern South Australia. Field studies undertaken at Sturt National Park by the Australian Museum in collaboration with the Australian Herpetological Society in the period 1997–1998 provided the samples required to undertake detailed morphological and genetic studies into the taxonomic status of the population far northwest New South Wales. Further, these field studies identified the population in this region as able to occupy red-sand plain dune systems independent of the presence of *Triodia* hummock grass, as also stated earlier by Houston (1978) for the northern South Australian populations, and in sharp contrast to the dependence on *Triodia* reported by Cogger for populations in central-west New South Wales. The differences in habitat preference provided by these field studies called into question the conspecificity of these eastern populations, and a genetic study of *Ctenophorus fordi* populations across the species range was undertaken to assess the extent of differentiation between populations in New South Wales, and how this related to the morphological races earlier identified by Houston and to the type population in southwest Western Australia.

The results of our morphological and genetic investigations into the easternmost populations of *C. fordi* dependent on *Triodia* Mallee habitat of inland southeast Australia revealed it to be highly differentiated in morphology and forming a discrete genetic group that is the sister to all other "*C. fordi*". Further, it found *C. fordi* to be a composite of distinct lineages, each falling discretely within a single major geographical biome.

In the interim period since our studies commenced an independent genetic study of *Ctenophorus maculatus* and related species, including *fordi*, has been undertaken by Edwards *et al.* (2015) to determine the evolutionary history

of signalling and associated morphological traits in this group of agamid lizards. The lineages retrieved by this study were broadly complementary with ours, lending further support for these as geographically discrete evolutionary entities.

The primary purpose of the results presented here is the formal taxonomic recognition of the lineage from *Triodia* Mallee habitat of inland southeast Australia identified by our genetic study. The formal treatment of the other lineages found within *C. fordi* will soon be presented by Edwards & Hutchinson (pers. comm.) as part of an overall revision of *Ctenophorus maculatus* and related species.

Materials and methods

Genetic study. We used the CTAB method (Saghai-Maroo *et al.*, 1984) to extract DNA from small samples of tail tips for 25 specimens from 11 individual locations across the range of *C. fordi* (Appendix 1), and from an individual of *Ctenophorus maculatus* s.s. for outgroup comparison. The final DNA pellet was dissolved in 100 μ L TE buffer.

PCR was conducted with Red Hot™ thermostable DNA polymerase (Advanced Biotechnologies, Leatherhead, Surrey) according to the manufacturer's protocol in a reaction volume of 50 μ L 0.05 mM dNTPs, 2.5 mM MgCl₂, 12.5 pmol of each primer and 1 μ L of a dilution (usually 1 in 25) of the DNA sample. The cycling protocol was an initial denaturation step of 94°C for 2 min, followed by 10 cycles of 94°C for 30 sec annealing for 30 sec, 72°C for 1 min, and 23 cycles of (94°C for 30 sec, annealing for 30 sec, 72°C for 1 min with a final extension step of 72°C for 10 min.

Three segments of the mitochondrial genome were amplified using the following sets of primers. 12S ribosomal RNA-1478 (5'-TGACTGCAGAGGGTGA CGGGCGGTGTGT-3') (Kocher *et al.*, 1989) and 12S rDNA1 (5'-AAAAAGCTTCAAACCTGGGATTAGATACCCC-3') (Nedbal *et al.*, 1994); 16S ribosomal RNA—16Sar (5'-CGCCTGTTTAAACAAAACAT) and 16Sbr (5'-CCG GTCTGAACCTCAGATCACGT-3') both from Simon *et al.* (1994); and part of NADH dehydrogenase subunit 4—ND4 (5'-TGACTACCAAAGCTCATGTAGAAGC-3'), the tRNA-Histidine gene, the tRNA-Serine gene part of the tRNA Leucine 2 gene (5'-TTTACTTGGAT TGCACCA-3') both from O'Connor and Moritz (2003) as modified from Arevalo *et al.* (1994). An internal primer was used to complete the sequence of this segment which was ND4INTF (5'-CCHCCDWCHATYAAAYHTHATAGGAGA). The annealing temperatures were 52°C for the 12S rRNA and 16S rRNA segments and 52–54°C for the NAD/Tleu segment.

Reaction products were resolved on 2% agarose gels containing ethidium bromide. All single band products were purified using the QIAquick™ PCR Purification Kit (Qiagen). Products were sequenced in both directions using each of the original primers individually with the DyeDeoxy™ Terminator sequencing method (Big Dye™ version 3.0) according to the manufacturer's protocols except that the reactions were scaled down to 10 μ L, containing 2 μ L of Big Dye. After purification (by ethanol precipitation), the sequencing reactions were run on an Applied Biosystems (ABI)® 310 DNA Sequencing System. The consensus sequence for each individual was obtained using Sequence Navigator.

Alignments of the DNA sequences were made using the default parameters in ClustalX (Thompson *et al.*, 1997).

BioEdit (Hall, 1999) was used for sequence inspection, file formatting and dataset concatenation. Maximum likelihood (ML) analyses were conducted at the CIPRES Science Gateway (Miller *et al.*, 2010) using RAxML (Stamatakis *et al.*, 2008), assuming no invariable sites, estimating base frequencies, and assessing node support by rapid bootstrap with the number of replicates determined by the software, according to the MRE-based bootstopping criterion (Pattengale *et al.*, 2010). The data from the three segments of the mitochondrial genome were treated as independent partitions in the analysis.

MEGA 7 Molecular Evolutionary Genetics Analysis version 7.0 (Kumar *et al.*, 2016) was used for the calculation of genetic distances.

Morphological study. We examined 149 specimens from over 30 locations across the range of the genetic lineages included under *C. fordi* (Appendix 2) for the mensural and scalation characters listed below.

Scalation. Upper labial scale rows (ULS)—number of scale rows along the upper jaw from 1st scale behind the rostral to the last obviously enlarged scale posteriorly; subdigital lamellae of the 4th toe (SDL) counted from the apex of the 3rd and 4th toes of the hindfoot to the last scale at the claw; femoral pore scales (FPS) the number of pore bearing scales along the femur of the hindlimb counted as left and right values from the midline between the hindlimbs to the furthest extent along the hindlimb approaching the tibia. Bilateral scalation characters were scored on both sides and the mean value used in the analysis and description of each species.

Measurements. Snout to vent length (SVL)—measured from tip of the snout to the posterior edge of the anal scales; axilla to groin length (AGL)—measured from posterior edge at base of forelimb to anterior edge at base of hindlimb; tail length (TLL)—measured from the posterior edge of the anal scales to the tip of the tail on complete original tails only; hindlimb length (HLL)—measured from the middle of the base of the hindlimb to tip of fourth toe (not including the nail); head length (HDL)—measured down the midline from the back of the skull to the tip of the snout at mid rostrum; head width (HDW)—measured across the head from the posterior edge of the last upper labial scale either side. Body measurements presented in the diagnosis are for adult individuals only, as determined by reproductive maturity. Head length, axilla to groin length, tail length and hindlimb length are expressed as a percentage of snout to vent length, and head width is expressed as a percentage of head length.

Variation between regionally discrete “Groups” that each comprised clusters of populations belonging to a distinct genetic clade, or fell within the regional boundaries of a clade, was assessed using independent two sample t-tests for all morphometric and scalation characters. Only characters with a high P-value approaching $P \leq 0.001$ (denoted in text with a single asterisk * after character state) are considered as likely to reflect unambiguous species level differences (less than one in a thousand chance of being wrong), while those with a $P > 0.001$ but less than < 0.01 (denoted in text with a double asterisk **) are suggestive of a significant trend in character difference. Samples from locations in geographically disjunct regions contained within the geographic range of a lineage identified by the genetic study were also tested for internal geographic variation, i.e.

populations from central-west NSW vs populations from southwest NSW. In the absence of internal geographic variation samples from locations within the geographic range of the lineages identified by the genetic study were then pooled for the purpose of cross-comparison between lineages. All pooled populations were tested for sexual dimorphism in scalation and mensural characters using independent two-sample t-tests. Sexual dimorphism was found to be present at varying levels of significance, and as such inter and intra population level differences are presented separately for each sex.

We follow the lead of Pepper *et al.* (2011) in adopting the approach of De Queiroz (2007) that the common primary definition of a species is a group of metapopulations that are evolving independently. Further, we concur that the diagnosis of “cryptic” taxa, separately-evolving entities that have not differentiated morphologically from close relatives, is problematic. The lineages identified by the molecular data residing under *C. fordi* show both divergent evolution and lack of mixing of gene pools, demonstrating they each individually comprise a metapopulation that no longer engages in reticulate evolution with neighbouring allopatric or parapatric populations belonging to other genetic lineages, despite their close (relative) proximity in some cases. This is a scenario similar to that presented by Pepper *et al.* (2011) for four of the six species of diplodactylid geckos in the genus *Rhynchoedura*, once considered a single widespread species throughout the arid interior of much of the continent.

Results

Genetic study. The optimal overall ML tree had a *ln* likelihood of -4047.75. The number of rapid bootstrap replicates was 204, as determined by the MRE bootstopping criterion. Analyses of the data set of the mitochondrial ND4, 12S and 16S genes, individually and combined, identified five well-supported branches exclusive of the outgroup (Fig. 1) as follows:

- [Group 1] populations from central-west and southwest New South Wales (NSW).
- [Group 2] populations from inland southwest Western Australia (WA).
- [Group 3] populations from the Strzelecki and Tarari dune systems of northeast South Australia (SA) and adjacent northwest NSW, and east Gawler dune system of inland central SA.
- [Group 4] populations from the Great Victoria Desert of central-west SA.
- [Group 5] populations from Eyre Peninsula in SA.

All groups comprise regionally discrete clusters of populations (Fig. 2), usually from two or more locations, though one, Group 4 from the Great Victoria Desert, is represented by a single population. Group 1 populations from central-west and southwest NSW comprise a highly divergent strongly supported monophyletic lineage. The basal dichotomy in the phylogeny is for the Group 1 populations as the sister to all other groups currently under *C. fordi*, but with low support for this relationship ($< 50\%$). Group 2 populations from inland southwest WA (hereafter

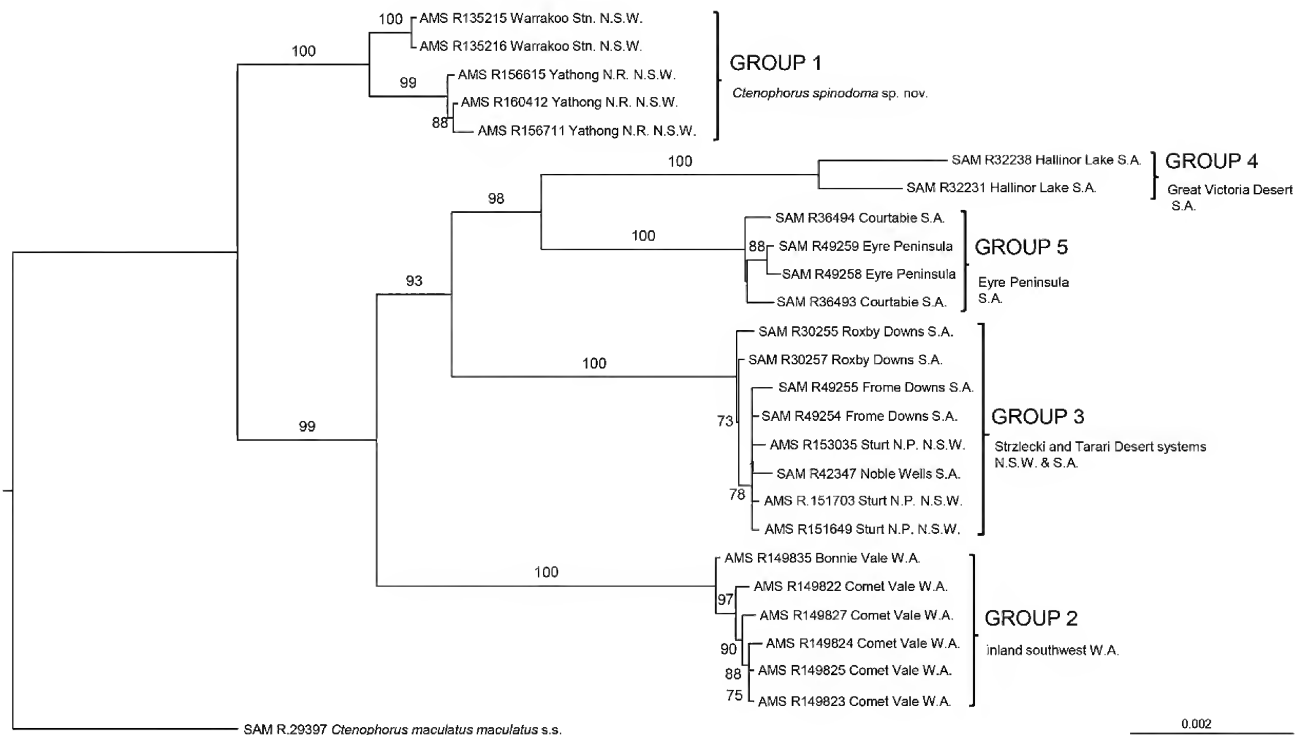


Figure 1. Phylogeny of populations from across the range formerly all included under *Ctenophorus fordi* derived from sequence data for the concatenated 12S, 16S and ND4 mitochondrial genes, maximum likelihood, partitioned analysis.

referred to as *C. fordi* s.s.) were resolved as the sister to the remaining groups that included Group 3 populations from the desert systems of inland of northeast SA and adjacent northwest NSW (hereafter referred to as *C. fordi* Strzelecki) + the Group 4 population from the Great Victoria Desert of central-west SA (hereafter referred to as *C. fordi* GVD) + the Group 5 population from the Eyre Peninsula in SA (hereafter referred to as *C. fordi* Eyre). Within this latter cluster Group 3 was retrieved as the sister to Group 4 + Group 5, with high support values at all three nodes.

The level of genetic differentiation between groups for various combinations of pairwise comparisons of groups was high (Table 1). Group 1 had an average pairwise distance of 0.057 (\pm 0.005) for all mitochondrial genes combined and 0.094 (\pm 0.010) for ND4 alone when compared to Groups 2, 3, 4 and 5 combined; Group 2 had an average pairwise distance of 0.058 (\pm 0.006) for all mitochondrial genes combined and 0.092 (\pm 0.010) for ND4 alone when compared to Groups 3, 4 and 5 combined. These levels of genetic differentiation approached that between the outgroup *C. maculatus* and all groups combined, with an average pairwise distance of 0.063 (\pm 0.006) for all mitochondrial genes combined and 0.106 (\pm 0.012) for ND4 alone. Individual average net pairwise comparisons between Groups 3, 4 and 5 for all mitochondrial genes combined and for ND4 only were in most cases only marginally different, ranging from 0.068 to 0.046 for all mitochondrial genes combined, and 0.107 to 0.065 for ND4 alone.

The level of differentiation obtained in most pairwise mitochondrial ND4 gene comparisons was equal to or greater than those reported between recognized species of Australian lizards in studies utilizing this gene to define species boundaries. McLean *et al.* (2013) cited corrected mtDNA

(ND4) net sequence divergence of 7.1–9.6% between the recently described agamid *Ctenophorus mirrityana* from far western NSW and populations of *Ctenophorus decresii* in SA. Similar levels of sequence divergence have been reported between well-established species of skinks (Stuart-Fox *et al.*, 2002), and for major clade divergence within taxa subsequently recognized to be a composite of species (Stuart-Fox *et al.*, 2002; Mousalli *et al.*, 2009). Even the lower values observed in some pairwise comparisons between our groups were of a magnitude similar to those reported for recently described species of skink in the genus *Egernia* (Doughty *et al.*, 2011).

Our results are consistent with the genetic study of Edwards *et al.* (2015) in identifying the Group 1 populations from central-west and southwest NSW as highly differentiated from all other populations currently residing under *C. fordi*, and in retrieving the remaining genetic groupings as a well-supported monophyletic group, hereafter referred to collectively as the *C. fordi* genetic lineages. However, the topology of the four lineages that remain under *C. fordi* differs between the two studies. Ours placed these four lineages in a well-supported hierarchy (Group 2 (Group 3 (Group 4 + 5))), whereas Edwards *et al.* placed these lineages within two subgroups, one comprising populations from within the geographic ranges of our Group 3 and Group 4, with a high level of support for this sister taxa relationship, the other populations within the geographic ranges of our Group 5 and Group 2, but with a low level of support for this relationship. In that study the species *Ctenophorus femoralis* from the coastal WA was retrieved as the sister to these two subgroups, but with only low-moderate support. This species was not considered in our study, and its placement, albeit tenuous, lends further support to *C. fordi* being polyphyletic. The study of Edwards *et al.* (2015) also

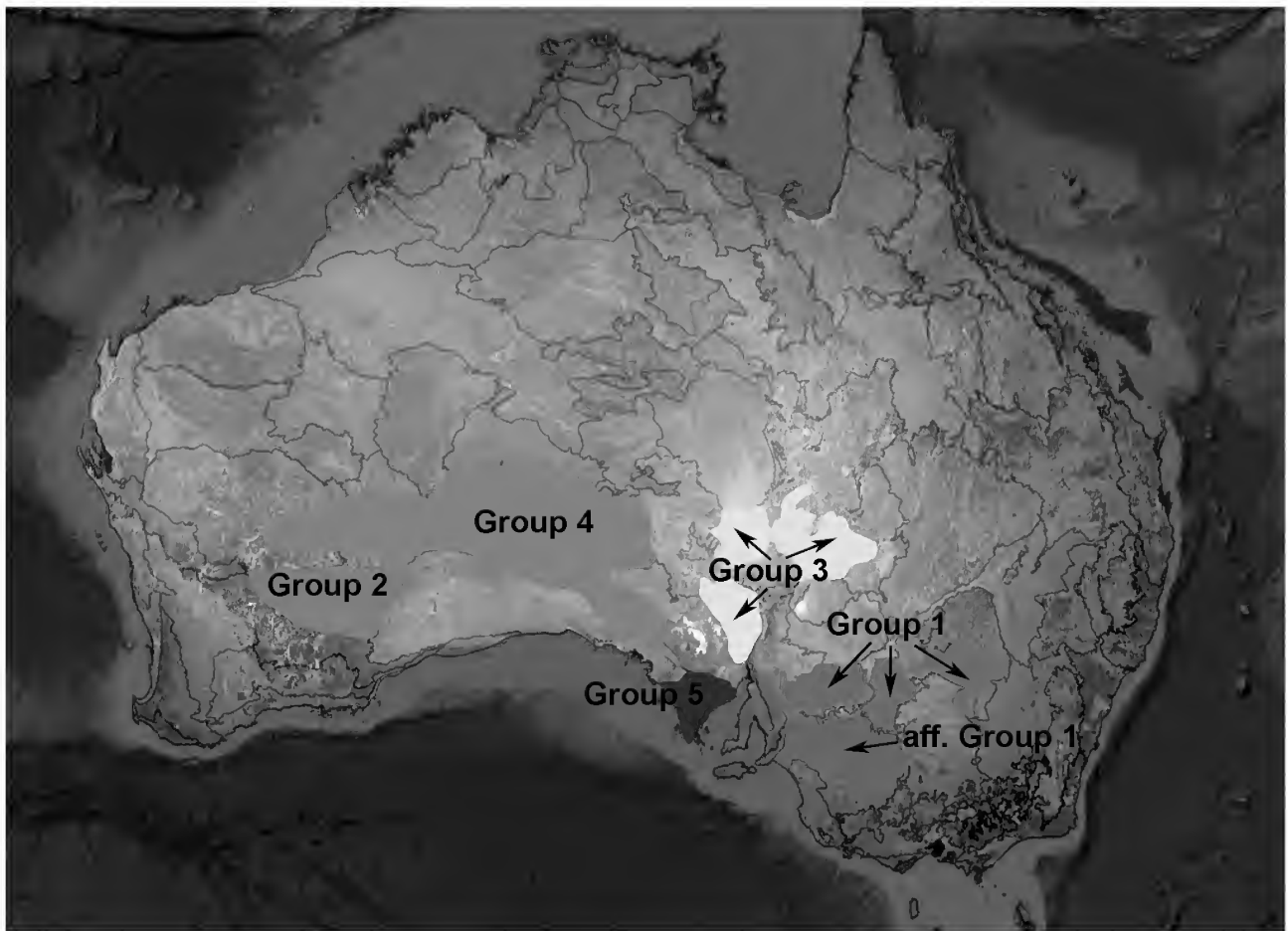


Figure 2. Generalized distribution of genetic groups identified in the phylogeny of populations formerly all included under *Ctenophorus fordi*, derived from a compilation of information from this study, the boundaries of clades identified by Edwards *et al.* (2015), and broad distribution data for specimen-based records in the Atlas of Living Australia (2019). The Group 1 genetic lineage (red) from central-west and southwest NSW, and adjacent areas of SA, representing *C. spinodomus* sp. nov. (= *C. fordi* Clade 4 of Edwards *et al.*); the Group 2 *C. fordi* genetic lineage (blue) representing *C. fordi* s.s. from inland southwest WA, (= *C. fordi* of Edwards *et al.*); the Group 3 *C. fordi* genetic lineage (cream) from the desert dunefield systems of northwest NSW, southwest Qld., and central and northeast SA (= *C. fordi* Clade 3 of Edwards *et al.*); the Group 4 *C. fordi* genetic lineage (yellow) from the Great Victoria Desert of SA (= *C. fordi* Clade 1 of Edwards *et al.*); the Group 5 *C. fordi* genetic lineage (dark grey) from the Eyre Peninsula in SA (= *C. fordi* Clade 2 of Edwards *et al.*). Also shown is the distribution of populations referred to as aff. Group 1 (brown ochre colour) from south of the Murray River (= *C. fordi* Clade 5 of Edwards *et al.*) not included the genetic study but which on morphological criteria are considered related to Group 1 *C. spinodomus* sp. nov.

included samples from populations south of the Murray in northwest Victoria and far southeast SA which our genetic study did not include, and retrieved these as the sister to populations representing our Group 1 lineage, a relationship that was well-supported. However, these populations were included in our morphological study (see Fig. 3), and found to be similar to populations from our Group 1 lineage but with differences in several key morphological traits, lending support to a sister relationship between populations either side of the Murray River as broadly suggested by the genetic study of Edwards *et al.* (2015), which are here referred to as aff. Group 1.

Morphological study. Intra-lineage differentiation in morphology within the Group 1 genetic lineage: The populations in central-west and southwest NSW referable to the Group 1 genetic lineage appear to form two metapopulations largely disjunct in distribution, with only a few records from scattered populations in intervening

areas. No differences in morphology were detected between samples from these metapopulations. Specimens from adjacent areas of southeast SA were not included in our genetic study, but no significant differences in morphology were detected between representatives of the populations from southeast SA and those from adjacent areas of southwest of NSW or those in central-west NSW. On this basis all of these populations are considered as conspecific.

Inter-lineage differentiation in morphology between the Group 1 genetic lineage and *C. fordi* genetic lineages: Populations referable to Group 1 genetic lineage from central-west/southwest NSW and populations from inland southeast SA are highly differentiated in morphology from other populations currently assigned to *C. fordi*. Differences in scalation and body proportions (refer to Table 2 and 3 for range, sd and sample size) distinguishing populations referable to the Group 1 genetic lineage from populations referable to the other *C. fordi* genetic lineages included:

Table 1. Average net pairwise distances (below diagonal axis) and standard error (above diagonal axis) between major genetic lineage “Groups” for each of the mitochondrial genes sequenced and for these genes combined.

	<i>C. spinodomus</i> sp. nov.	<i>C. fordi</i> s.s.	<i>C. fordi</i> Strzelecki	<i>C. fordi</i> GVD	<i>C. fordi</i> Eyre	<i>C. maculatus</i> s.s.
ND 4	Group 1	Group 2	Group 3	Group 4	Group 5	outgroup
Group 1		[0.011]	[0.012]	[0.014]	[0.010]	[0.012]
Group 2	0.090		[0.012]	[0.011]	[0.011]	[0.010]
Group 3	0.088	0.083		[0.015]	[0.010]	[0.013]
Group 4	0.109	0.082	0.107		[0.015]	[0.014]
Group 5	0.076	0.069	0.065	0.107		[0.010]
outgroup	0.087	0.054	0.077	0.091	0.052	
12S	Group 1	Group 2	Group 3	Group 4	Group 5	outgroup
Group 1		[0.008]	[0.011]	[0.010]	[0.012]	[0.013]
Group 2	0.025		[0.010]	[0.007]	[0.010]	[0.012]
Group 3	0.035	0.036		[0.011]	[0.012]	[0.015]
Group 4	0.031	0.015	0.036		[0.012]	[0.014]
Group 5	0.043	0.037	0.044	0.044		[0.009]
outgroup	0.049	0.043	0.054	0.050	0.027	
16S	Group 1	Group 2	Group 3	Group 4	Group 5	outgroup
Group 1		[0.005]	[0.005]	[0.006]	[0.007]	[0.007]
Group 2	0.014		[0.006]	[0.005]	[0.007]	[0.007]
Group 3	0.013	0.020		[0.007]	[0.006]	[0.006]
Group 4	0.016	0.016	0.024		[0.008]	[0.008]
Group 5	0.024	0.024	0.019	0.028		[0.008]
outgroup	0.022	0.025	0.017	0.030	0.026	
combined	Group 1	Group 2	Group 3	Group 4	Group 5	outgroup
Group 1		[0.006]	[0.007]	[0.007]	[0.006]	[0.007]
Group 2	0.051		[0.007]	[0.006]	[0.006]	[0.006]
Group 3	0.053	0.053		[0.007]	[0.006]	[0.007]
Group 4	0.062	0.046	0.065		[0.007]	[0.008]
Group 5	0.052	0.048	0.046	0.068		[0.005]
outgroup	0.057	0.042	0.052	0.062	0.038	

- from populations referable to aff. Group 1 from south of the Murray River in having: shorter hindlimbs in males** and on average fewer femoral pore scales in males ** (insufficient data for comparison of adult females).
- from populations referable to the *C. fordi* Group 2 genetic lineage (*C. fordi* s.s.) from inland southwest Western Australia in having: a significantly shorter tail in males* and females*; significantly shorter hindlimbs in males* and females*; a significantly longer body (AG) between fore and hindlimbs in males*; significantly fewer subdigital lamellae in males* and females*; significantly fewer upper labial scales in males* and females*; on average marginally more femoral pore scales in males**.
- from populations referable to the *C. fordi* Group 3 genetic lineage from the from the Strzelecki Desert system of northeast South Australia and adjacent northwest New South Wales in having: males being significantly smaller on average*, and females to a lesser extent**; in having a significantly shorter tail in males* and females*; significantly shorter hindlimbs in males* and females*; a significantly longer body (AG) between fore and hindlimbs in males*; significantly fewer subdigital lamellae in males* and females*; fewer upper labial scales in males** and significantly fewer in females*; significantly more femoral pore scales in males*.
- from populations referable to the *C. fordi* Group 4 genetic lineage from the Great Victoria Desert in having: a significantly shorter tail in males* and females*; significantly shorter hindlimbs in males* and females*; a significantly longer body (AG) between fore and hindlimbs in males*; significantly fewer upper labial scales in males* and females*; significantly fewer subdigital lamellae in males* and females*; significantly more femoral pore scales in males*.
- from populations referable to the *C. fordi* Group 5 genetic lineage Eyre Peninsula in South Australia in having: females being on average larger**; in having a marginally longer body (AG) between fore and hindlimbs in males** and females**; significantly fewer subdigital lamellae in males*; significantly fewer femoral pore scales in males*.

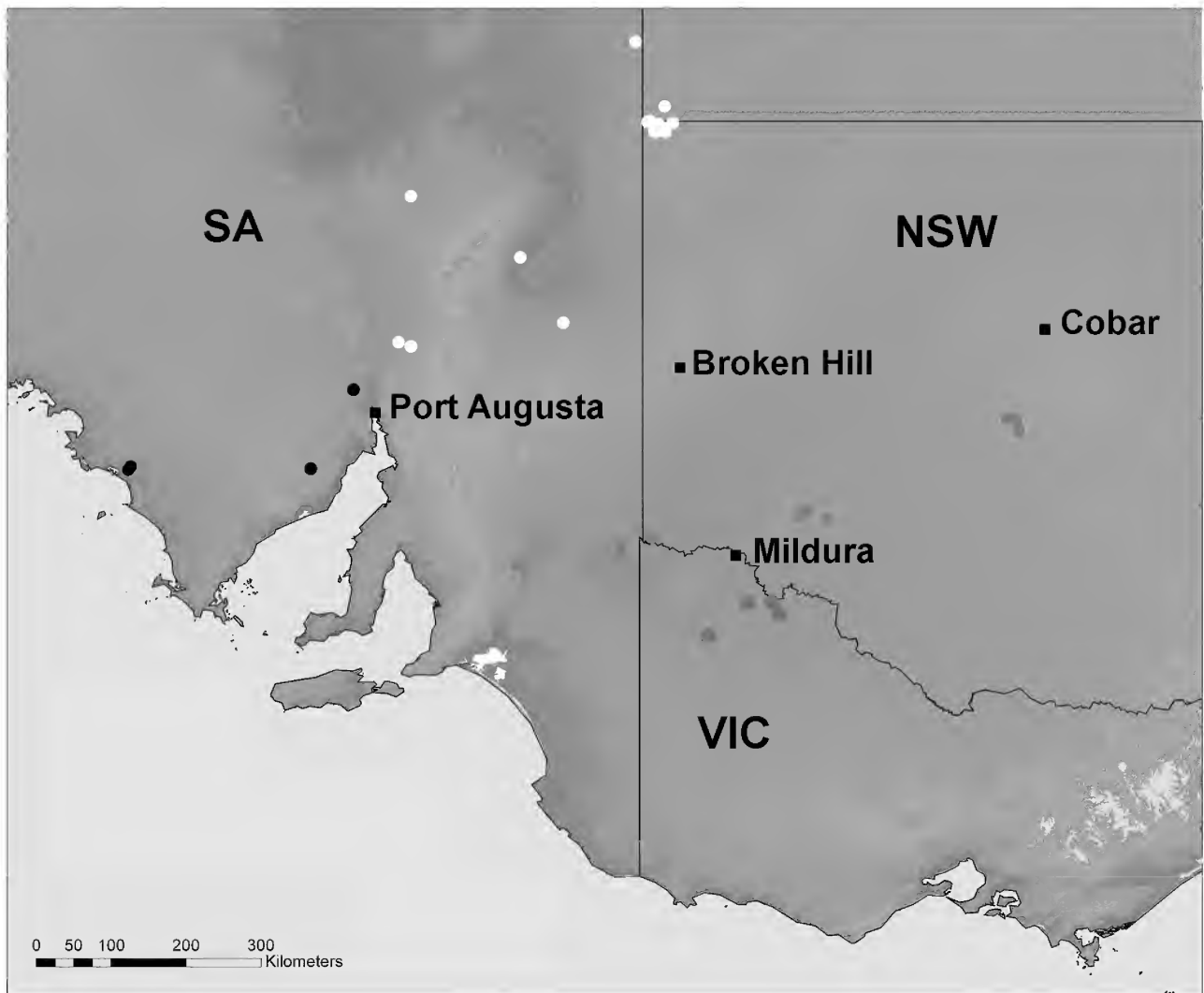


Figure 3. Distribution of specimens of Group 1 *Ctenophorus spinodomus* sp. nov. (red circles) used in morphological and genetic study relative to specimens of aff. Group 1 (brown ochre circles) from south of the Murray River used in the morphological study, and specimens of parapatric Group 3 *C. fordi* genetic lineage from the Strzelecki, Tarari and east Gawler dune systems (white circles) and Group 5 *C. fordi* genetic lineage from the Eyre Peninsula in SA (black circles).

Populations referable to the Group 1 genetic lineage (Fig. 4A) are markedly different in the expression of the dark throat and chest markings of adult males compared to populations referable to the other *C. fordi* group lineages (Fig. 4B–F), however, adult females lack these markings and cannot be readily distinguished from adult females referable to the other *C. fordi* genetic group lineages in coloration alone. The dark throat markings of Group 1 lineage adult males vary in distribution and intensity, but are usually present as obscure scattered spots and/or blotches, sometimes also tending to align either side of the midline, and only rarely forming well-defined narrow and elongate blotches which approach each other towards the chin. The dark throat markings of adult males referable aff. Group 1 (Fig. 4B) are similar in distribution to Group 1 lineage adult males but markedly more intense in colour. The throat markings of adult males referable to the *C. fordi* Group 2 (Fig. 4C) and Group 5 (Fig. 4F) genetic lineage examined were usually bold, black and coalescing to form an elongate blotch/es either side of the midline, whereas those of the *C. fordi* Group 3 and Group

4 genetic lineages (Fig. 4D, E) were typically obscure and poorly defined.

The dark chest markings of adult males referable to Group 1 genetic lineage are present variably as a few blotches medially between the forelimbs to being aligned to form a poorly defined T-shaped patch (Fig. 4A), with a narrow, occasionally broad the rearward extension. Adult aff. Group 1 males (Fig. 4B) have a similar T-shaped patch on the chest, but typically more intense in colour. The other geographically distinct genetic lineages within *C. fordi* typically have well developed dark chest patches which vary in shape and intensity, those of adult males examined referable to the *C. fordi* Group 2 (Fig. 4C) and Group 5 (Fig. 4F) genetic lineages being typically a bold, black, broadly cruciform “kite” shape (like the silhouette of a bird of prey), and those of adult males referable to the Group 3 (Fig. 4D) and Group 4 (Fig. 4E) genetic lineages also well-defined but with the pattern reduced in size.

The extent of regional differentiation in morphology, particularly that associated with throat and chest markings

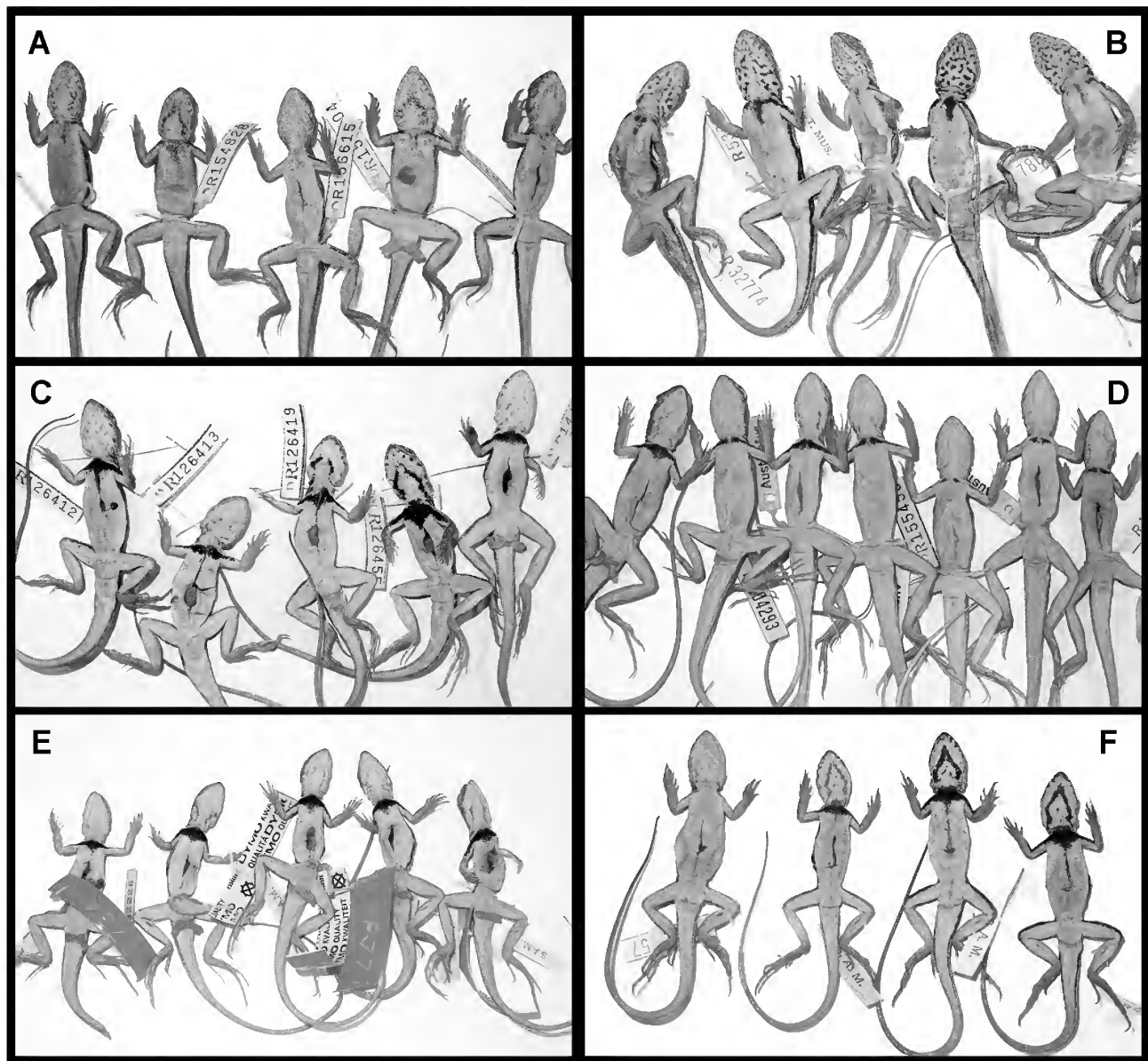


Figure 4. Comparison of dark ventral markings of adult males from groups formerly all included under *Ctenophorus fordii*: (A) Group 1 genetic lineage *C. spinodomus* sp. nov. from Yathong Nature reserve in central-west NSW; (B) aff. Group 1 from south of the Murray River; (C) the Group 2 *C. fordii* genetic lineage from Bonnie Vale in inland southwest WA; (D) the Group 3 *C. fordii* genetic lineage from Sturt National Park in the Strzelecki Desert system of northwest NSW; (E) the Group 4 *C. fordii* genetic lineage from Hallinor Lake in the Great Victoria Desert of SA; (F) the Group 5 *C. fordii* genetic lineage from near Kimba on the Eyre Peninsula in SA (photos C. Beatson).

in adult males, is consistent with the extent of geographically cohesive lineage differentiation identified by our genetic study, and with that published by Edwards *et al.* in 2015. That study regarded the species complex within which the genetic lineages of *C. fordii* reside as a group whose diversification is associated with the creation of new ecological niches in arid sand habits of southern Australia, initiated c. 3 million years ago (late Miocene). The extent of variation in the expression of throat and chest markings was interpreted as representing lineage specific visual signalling characters, with the evolution of these traits driven by interspecific interactions reinforcing boundaries between regionally distinct parapatric lineages in the arid zone where they contact. The highly divergent chest pattern of Group 1 adult males is consistent with its early divergence in the phylogeny presented here,

and with that of Edwards *et al.*, whereas the patterns of the Group 2–5 lineages are variations on a similar theme, a level of difference consistent with the more recent genetic divergence of these groups from each other.

Taxonomy

We here recognize populations from central-west and southwest NSW (our Group 1 lineage) and southeast SA as a highly differentiated, geographically defined evolutionary entity warranting recognition as a distinct species, described here as *Ctenophorus spinodomus* sp. nov. The population from south of the main Murray River channel in northwest Victoria and adjacent areas of southeast SA is similar in a number of aspects of morphology to populations from central

and southwest NSW and southeast SA north of the Murray River, but differs in several key morphological traits, and was identified as a distinct but related genetic lineage by Edwards *et al.* (2015). At this time, we recognize it as related to, but distinct from, *C. spinodomus* sp. nov., and refer to it as *C. aff. spinodomus* pending a more comprehensive investigation of these populations.

Our investigations also found significant genetic and morphological differentiation between the geographically cohesive groups of populations remaining under *C. fordii*. Our description of *C. spinodomus* sp. nov. below provides distinguishing characteristics between it and each of these geographic lineages, but the formal taxonomic treatment of these is part of a work in progress by Edwards and Hutchinson that also includes related taxa currently under *C. maculatus*.

Agamidae Gray, 1827

Ctenophorus Fitzinger, 1843

Ctenophorus spinodomus sp. nov. Sadlier, Colgan, Beatson & Cogger

<http://zoobank.org/NomenclaturalActs/47B3F6FF-A157-4C41-8070-FFE53FD36EDF>

Figs 5–7

Holotype. AMS R.156615, Yathong Nature Reserve (32.5742°S 145.3828°E) NSW, G. Swan (07 October 1999). **Paratypes.** AMS R.154827–28, Yathong Nature Reserve (32.5742°S 145.3828°E), NSW, G. Swan (12–14 October 1999); R.156647, R.156711, Yathong National Park (32.5869°S 145.4975°E), NSW, G. Swan (1999); R.156704, Yathong National Park or Yarra Property (32.58°S 145.40°E), NSW, G. Swan (1999); R.157315, Yathong Nature Reserve, 10 km NNW of Shearers Quarters (32.5864°S 145.4972°E), NSW, P. Harlow and G. Swan (07 November 1998); R.145176–77, R.145179, Yathong Nature Reserve (32.72°S 145.53°E), NSW, P. Harlow; R.114208–09, R.114211, R.114213–15, Mungo National Park, 5.0 km N of SE corner (33.77°S 143.22°E), NSW, R. Sadlier and G. Shea (02 November 1984); R.114456–57, Mungo National Park, 5.0 km N of SE corner (33.77°S 143.22°E), NSW, R. Sadlier and G. Shea (12 November 1984); R.114347–48, R.114349, Top Hut Homestead, 6.9 km S on Old Arumpo Rd. (33.73°S 142.92°E), NSW, R. Sadlier and G. Shea (17 November 1984); R.115216, Top Hut Station, 8 km NE Roys Tank (33.68°S 142.98°E), NSW, C. Tiedermann (25 November 1984); R.153214–16, Warrakoo Station (33.9858°S 141.1180°E), NSW, M. LeBreton (16 October 1998); R.7755–76, Murray Bridge (35.12°S 139.27°E), SA; R.20989, Renmark (34.17°S 140.75°E), SA; R.145481–82 Brookfield Conservation Park (34.32°S 139.50°E), SA; R.104842–43, Renmark (34.17°S 140.75°E), SA.

Etymology. The species epithet is derived from a combination of the Latin *spinosus* for spiny and *domus* for home, in reference to the species' reliance on *Triodia* grass hummocks.

The common name Mallee Dragon has been applied to "*Ctenophorus fordii*" in its broadest sense, in keeping with this concept we recommend the common name Eastern Mallee Dragon for the species described here as *Ctenophorus spinodomus* sp. nov.

Diagnosis. *Ctenophorus spinodomus* sp. nov. is diagnosed from all other species in the genus, except for the taxa currently contained within *C. maculatus* and *C. fordii*, in having a near continuous row of femoral pores either side (15–22) in adult males arranged in a row that arches forward to an apex on the midline, and a dark chest patch (although obscure) between the forelimbs in adult males. Adult female *C. spinodomus* sp. nov. can be distinguished from other regionally sympatric (*C. pictus*) or parapatric (*C. nuchalis*) species of *Ctenophorus* by the presence (vs absence) of a fine, typically uninterrupted pale dorsolateral stripe down the body from the neck to just past the hindlimbs.

Adult male *C. spinodomus* sp. nov. are diagnosed from all named subspecies of *Ctenophorus maculatus* in having fewer femoral pores in total (maximum 41 vs range of 40–57 encompassed by the *maculatus* subspecies—Storr, 1965), and in the dark markings on the throat being present as a series of dark spots and blotches either side of the midline of varying intensity and degree of coalescence vs a pattern of well-defined narrow to broad dark bars either side.

The following features of colouration and scalation in combination distinguish *Ctenophorus spinodomus* sp. nov. from taxa assignable to the other genetic lineages under *C. fordii* (see Tables 2 and 3): tail length c. 2.1–2.4 times the body length in males and c. 1.95–2.15 times in females; hindlimb length c. 82–93% SVL in males, c. 74–93% in females; upper labial scales 10–13; subdigital lamellae scales 25–31; femoral pore scales in males 16–22 either side; dark markings of the throat of adult males typically obscure and present as scattered spots and blotches, occasionally aligned either side of the midline but not coalescing to form elongate blotches; chest of adult males with a typically poorly-defined black "T" shaped patch.

Comparison with other species (Tables 2 and 3): Adult male *C. spinodomus* sp. nov. are most similar to adult male aff. Group 1 (*C. aff. spinodomus*), but differ in having shorter limbs and fewer preanal pores. Adult male and female *C. spinodomus* sp. nov. have a shorter tail length on average than adult males and females from other populations referable to the *C. fordii* Group 2 (*C. fordii* s.s.), Group 3 (Strzelecki) and Group 4 (GVD) genetic lineages, but with overlap in ranges. The tail length of adult male *C. spinodomus* sp. nov. is similar to adult males referable to the *C. fordii* Group 5 (Eyre) genetic lineage, but adult female *C. spinodomus* sp. nov. have a significantly shorter tail than Group 5 females with only minimal overlap in range. The average hindlimb length of adult male and female *C. spinodomus* sp. nov. is shorter than Group 2, Group 3 and Group 4 males and females but with overlap in ranges, though minimal to negligible respectively with Group 4 males and females. In scalation adult male and female *C. spinodomus* sp. nov. have on average fewer subdigital lamellae than adult Group 2, Group 3 and Group 4 males and females but with overlap in ranges, though minimal with respect to Group 3 females and negligible with respect to Group 4 males and females, and adult male *C. spinodomus* sp. nov. have fewer subdigital lamellae than Group 5 adult males but with overlap in range. Adult male *C. spinodomus* sp. nov. have on average more femoral pore scales than Group 3 and Group 4 males with minimal to negligible overlap respectively in range, and less than Group 5 males with minimal overlap in range.

Adult male *C. spinodomus* sp. nov. have a black "T"

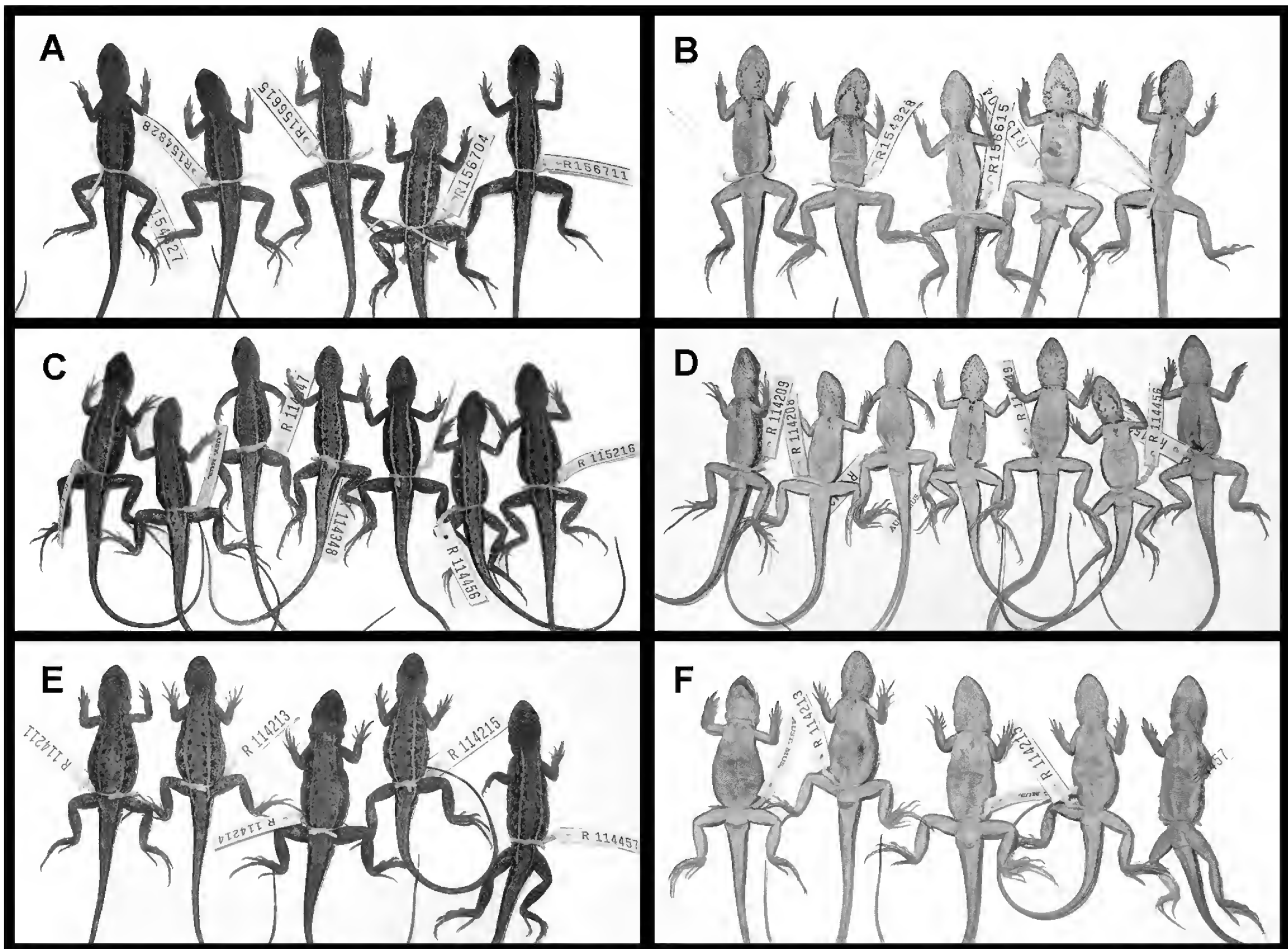


Figure 5. Types of *Ctenophorus spinodomus* sp. nov. adult males from Yathong Nature Reserve in central-west NSW (A, B), including holotype AMS R.156615 (middle specimen), and representative adult males (C, D) and females (E, F) from Mungo National Park in southwest NSW (photos C. Beatson).

shaped chest patch which is typically poorly defined. The black chest markings of aff. Group 1 and taxa assignable to the other genetic lineages under *C. fordi* are typically bold in expression and differ markedly in shape.

Description. The species is described from 17 adult males and 15 adult females regarded as representative of populations in central-west and southwest New South Wales, and southeast South Australia.

Measurements and scalation adult males: size 41.4–48.7 mm SVL (mean = 45.2); distance from axilla to groin 44.0–52.7% SVL (mean = 47.3); head length (HDL) 20.8–25.8% SVL (mean = 23.9); head width 75.4–93.4% HDL (mean = 83.9); hindlimb length (HLL) 82.1–92.6% SVL (mean = 87.3); tail length 207.1–241.5% SVL (mean = 224.1, n = 16); upper labial scales 10–13 (mean = 12.0, sd = 0.7); lamellae beneath fourth toe 25–30 (mean = 27.8, sd = 1.8); femoral pore scales 16–22 (mean = 18.6, sd = 1.42, n = 15).

Measurements and scalation adult females: size 43.6–54.5 mm SVL (mean = 48.6); distance from axilla to groin 43.9–53.6% SVL (mean = 48.1); head length (HDL) 20.8–25.4% SVL (mean = 23.4); head width 80.3–92.7% HDL (mean = 85.0); hindlimb length (HLL) 74.5–91.7% SVL (mean = 82.0); tail length 193.5–216.3% SVL (mean = 205.2); upper labial scales 10–13 (mean = 11.9, sd = 0.7); lamellae beneath fourth toe 25–31 (mean = 27.5, sd = 1.5).

Significant differences between adult males and adult females were found for body size* with adult females larger on average than adult males (SVL mean = 48.6 vs 45.2), for tail length* with adult males having longer tails (TL mean = 224.1 vs 205.2% SVL), and for hindlimb length* with adult males having longer limbs (HLL mean = 87.3 vs 82.0% SVL).

Colour and pattern: adult males (Figs 5A–D, 6A, 7A)—dorsal surface in life orange-brown and defined from the lateral surface by a narrow (2 sometimes 3 scales width), pale, dorsolateral stripe with a dark edge that extends from the nape to base of the tail ending abruptly just past the hindlimbs. Dorsal surface of the body with a series of small dark blotches adjacent to and contacting the pale dorsolateral stripe and a scattering of very fine dark flecks on the top of head and body, the extent of spotting (particularly on the head) varying from sparse to moderately dense between individuals at a location. Intrapopulation variation in definition of pattern on the lateral surface is present. Upper-lateral surface with a base colour similar (orange-brown) or marginally darker (mid brown) in tone to the dorsal surface, and dominated by a series of large dark markings (blackish blotches) of varying intensity and definition between the fore and hindlimbs, usually concordant in placement with the position of opposing small dark blotches on the dorsal surface of the body. Mid-lateral surface with a variably

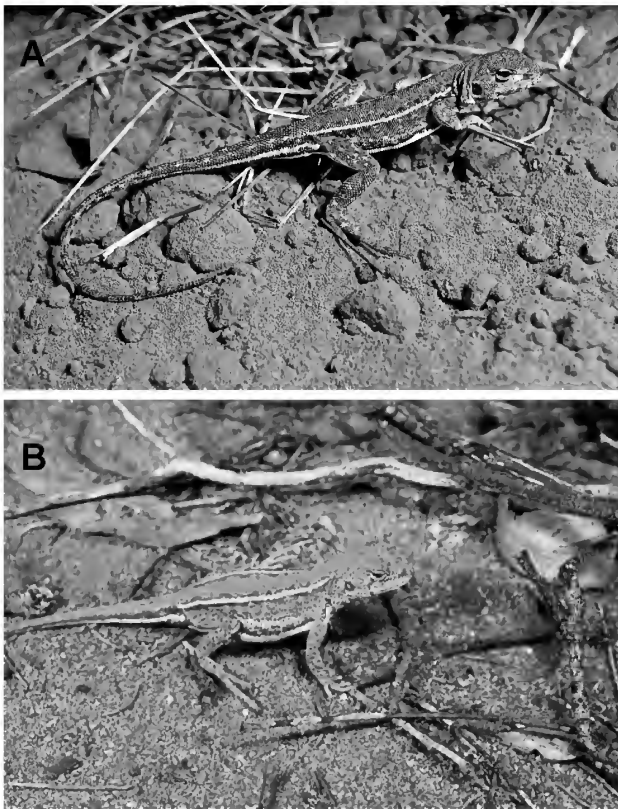


Figure 6. Live adult male (A) and female (B) *Ctenophorus spinodomus* sp. nov. from Round Hill Nature Reserve in central-west NSW (photos H. Cogger).

defined pale midlateral stripe along the side of the body between the fore and hindlimbs, distinct and defined by the dark markings (blotches) of the upper-lateral surface and a line of fine dark scattered spots along the upper and lower edges of the pale stripe, less well-defined in other individuals where the line of dark markings along the upper and lower edges of this stripe are not continuous and present only as scattered flecks. Lower surface with similar colouration to upper-lateral surface, but with the base colour tending to border the lower edge of the pale midlateral stripe and the darker markings the lateroventral margin. Tail similar in colour above to the dorsal surface of the body. The pale dorsolateral stripe of the body continues a third or less of the way along the tail as a series of faint pale spots scattered along the dorsolateral edge. Side of tail uppermost dark (an extension of the dark upper lateral markings of the body) and tending to form a distinct stripe, which in turn is bordered below by a pale stripe (an extension of the pale midlateral stripe of the body) for approximately the basal third of the tail, which in turn is defined for most of its length from the underside of the tail by a series of fine dark markings along the ventrolateral margin, usually continuous along most of its length and forming a fine dark stripe.

Ventral surface pale, white in life, with dark scattered markings on the throat and chest. Dark throat markings variable in distribution and intensity, sometimes sparse and scattered but also tending to align either side of the midline, and only rarely forming narrow and elongate blotches which approach each other towards the chin. Dark chest markings also variable in distribution and intensity, sometimes presents as a few blotches medially between the forelimbs through

to being aligned to form a poorly defined “T”-shaped patch with the lateral extensions typically narrow but the rearward extension varying from narrow to occasionally broad. Most individuals with a narrow alignment of dark markings along the anterior ventrolateral edge of the forelimbs, sometimes present as a continuous stripe at least on the humerus.

Adult females (Figs 5E–F, 6B, 7B)—dorsal and lateral surface with a similar pattern to males but overall lighter in tone. Ventral surface with the dark throat markings present as greyish specks and smudges, and chest typically without areas of dark markings.

Variation. No significant difference in scalation or body proportions were detected between populations from central-west NSW and those from southwest NSW, or with those from southeast SA west of the Murray River.

Distribution and biology. *Ctenophorus spinodomus* sp. nov. occurs on the red sandplains belonging to the Mallee dunefields (as identified by Hesse, 2010) of central-west and southwest NSW and adjacent areas of inland southeast SA that lie to the north and west of the main Murray River channel, within the IBRA bioregions of the Murray–Darling Depression (with the exception of the Darling Depression subregion) and Cobar Peneplain bioregions. Here, the distribution of populations in central-west and southwest NSW is dependent on the presence of *Triodia* hummock grass which grows as a groundcover in association with mallee woodlands (Cogger, 1974; Sadlier & Shea, 1989), termed *Triodia* Mallee habitat (Fig. 8). Extensive information on the species biology has been published by Cogger (1974, 1978) based on population studies undertaken at Round Hill Nature Reserve in central-west NSW. We present here a summary of points relevant to its reliance upon this habitat type and vulnerability to decline. The population referred to as *C. aff. spinodomus* occurs in adjacent areas of northwest Victoria to the south and east of

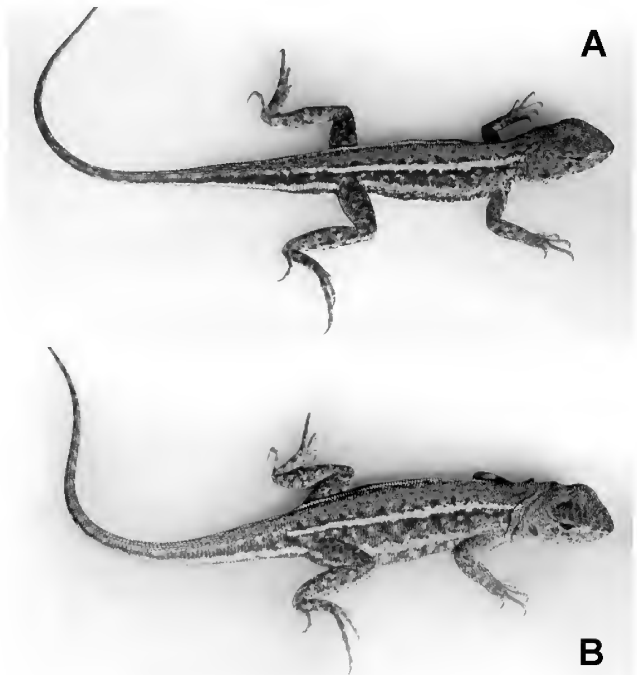


Figure 7. Live adult male (A) and female (B) *Ctenophorus spinodomus* sp. nov. from Mungo National Park in southwest NSW (photos R. Sadlier).

Table 2. Measurements and scalation values of adult males examined from populations assignable to the major “Groups”.

	Group 1 <i>spinodomus</i> sp. nov.	aff. Group 1 aff. <i>spinodomus</i>	Group 2 <i>fordi</i> s.s.	Group 3 <i>fordi</i> Strzelecki	Group 4 <i>fordi</i> GVD	Group 5 <i>fordi</i> Eyre
SVL range	41.4–48.7	43.7–50.6	42.2–51.1	42.4–55.3	40.3–53.7	42.2–49.7
mean±sd	45.2±2.24	47.4±2.8	47.2±2.5	49.5±3.3	48.4±3.1	46.4±2.9
n	17	7	13	23	18	6
TL range	207.1–241.5	203.8–235.4	231.6–262.2	243.2–294.8	217.6–291.0	196.0–243.5
mean±sd	224.1±8.4	224.2±11.7	243.7±10.1	268.9±12.3	257.9±20.6	221.5±16.0
n	16	6	13	21	18	6
AG range	44.0–52.7	39.5–48.0	39.2–47.0	39.2–48.6	38.7–47.4	42.7–46.7
mean±sd	47.3±2.3	45.4±2.8	43.4±2.8	44.1±2.6	43.1±2.5	44.8±1.5
n	17	7	13	23	18	6
HDL range	20.8–25.8	23.5–26.1	21.6–25.4	21.0–25.3	21.4–26.4	23.5–25.5
mean±sd	23.9±1.3	24.7±1.0	23.8±1.2	23.3±1.1	23.4±1.4	24.4±0.9
n	17	7	13	23	18	6
HDW range	75.4–93.4	72.3–85.8	78.2–92.1	77.2–87.1	73.4–89.3	78.6–89.5
mean±sd	83.9±4.7	80.8±4.6	85.0±3.7	81.6±2.7	82.2±4.0	84.1±3.9
n	17	7	13	23	18	6
HLL range	82.1–92.6	89.0–95.5	85.1–98.9	77.8–101.4	90.4–108.5	84.5–92.4
mean±sd	87.3±2.9	91.7±2.2	92.9±3.5	94.7±4.8	98.2±4.7	89.2±3.6
n	17	7	13	23	17	6
SDL range	25–30	25–32	28–36	27–37	31–37	29–34
mean±sd	27.7±1.8	28.0±2.3	32.5±2.4	33.6±2.3	33.9±1.5	31.2±1.7
n	17	7	13	23	18	6
ULS range	10–13	11–13	12–15	11–15	12–16	12–14
mean±sd	12.0±0.7	12.2±0.7	13.4±0.8	12.8±0.9	13.5±1.1	12.8±0.4
n	17	7	13	23	18	6
FPS range	16–22	19–23	18–21	10–18	12–16	20–23
mean±sd	18.6±1.4	20.7±1.3	17.2±2.1	14.5±1.9	14.2±1.1	21.2±1.2
n	15	7	12	23	18	6

the main Murray River channel within the Mallee dunefields, and the extent of reliance of these populations on *Triodia* Mallee habitat has yet to be established.

Ctenophorus spinodomus sp. nov. has an essentially annual life cycle, with some individuals extending into a second, rarely a third, season. Marked mortality of adults begins in late December and extends into January, with a loss of up to 85% of the population. Densities approaching 125 individuals per hectare have been found in areas regenerated 5–10 years after fire, but climax mallee communities with well-developed *Triodia* have lower densities. Males have a larger home range (mean 0.032 ha) than females (mean 0.015 ha), with juveniles a smaller range (0.007 ha) than adults, but with little shift in home range and negligible migration, and no territorial behaviour has been recorded (Cogger, 1978).

The species diel cycle revolves around utilization of *Triodia* clumps at various times of the day. During the night individuals shelter within *Triodia* and undergo pre-emergence basking amongst the spines of the clump to attain a body temperature sufficient for activity. On emergence individuals have not been observed active more than a few metres from the nearest clump of *Triodia*. During the hottest part of the day most lizards retire within the clumps of *Triodia* where summer humidity levels are higher than ambient and temperature during the hottest part of the day markedly lower than ambient and more so than substrate. However, during the winter period few individuals were found residing inactive within *Triodia*, rather, opportunistic observations suggest they dig into soil and shelter underground, but not in specially constructed burrows. It feeds almost exclusively

on small ants but will take other insects opportunistically.

The earliest recorded egg-laying in Round Hill was mid-October and the latest in late January, with a peak period for egg deposition around mid-November. Development of a clutch of eggs takes less than 8 weeks. Females deposit 2–3 eggs in a chamber that is constructed and sealed on the same day after laying. No female was recorded laying more than two clutches in a season, but given the clutch development period and length of laying season three clutches could be achieved. On average only 20% of hatchlings survive to reproductive age in the Round Hill population.

Comments. Wells & Wellington described *Phthanodon hawkeswoodi* sp. nov. in 1985. The designated holotype is a specimen (AMS R.116983) from Glenlea central fire trail Yathong Nature Reserve, NSW (collector A. B. Rose and J. Brickhill, 14 March 1981). The diagnosis presented by Wells & Wellington amounts to an extended description of the holotype that failed to provide either a “... definition that states in words characters that are purported to differentiate the taxon” or a “... bibliographic reference to such a published statement...”, as required under Article 13(a)(i–ii) of the Third edition of the Code of Zoological Nomenclature applicable at that time. As such, the description of *Phthanodon hawkeswoodi* Wells & Wellington, 1985 is unavailable for application to the species described here as *C. spinodomus* sp. nov.

Houston (1978) identified three distinct races of what was then considered *Amphibolurus fordi* in SA. One of these, his “eastern” race, was mapped as being from far southeast

Table 3. Measurements and scalation values of adult females examined from populations assignable to the major “Groups”.

	Group 1 <i>spinodomus</i> sp. nov.	aff. Group 1 aff. <i>spinodomus</i>	Group 2 <i>fordi</i> s.s.	Group 3 <i>fordi</i> Strzelecki	Group 4 <i>fordi</i> GVD	Group 5 <i>fordi</i> Eyre
SVL range	43.6–54.5	46.6–48.3	41.2–53.5	41.6–58.4	43.7–55.1	36.0–49.1
mean±sd	48.6±2.8	47.4±1.2	47.4±3.6	52.3±4.3	48.2±3.8	41.5±6.1
n	15	2	14	16	13	4
TL range	193.5–216.3	203.9–217.4	210.4–243.9	235.6–272.7	233.4–255.9	208.3–231.5
mean±sd	205.2±8.0	205.2±9.6	225.2±10.8	249.5±11.1	245.9±5.9	216.1±13.4
n	13	2	11	15	10	3
AG range	43.9–53.6	47.8–49.1	41.3–51.6	39.7–54.6	43.2–56.1	41.9–47.3
mean±sd	48.1±2.4	48.5±0.9	45.9±3.3	47.6±4.2	48.3±3.5	45.3±2.3
n	15	2	14	16	13	4
HDL range	20.8–25.4	23.4–23.6	21.9–26.2	20.3–26.2	21.4–25.5	24.2–26.2
mean±sd	23.4±1.4	23.5±0.1	23.6±1.2	22.4±1.4	23.3±1.2	25.4±0.9
n	15	2	14	16	13	4
HDW range	80.3–92.7	85.3–88.6	79.5–94.1	78.9–91.2	78.4–89.0	81.0–86.7
mean±sd	85.0±3.8	87.0±2.3	87.0±4.4	84.2±3.3	83.3±3.3	84.5±2.6
n	15	2	14	16	13	4
HLL range	74.5–91.7	80.7–81.5	84.6–99.5	82.7–101.2	91.9–101.8	82.2–88.9
mean±sd	82.0±4.6	81.1±0.6	90.4±4.0	91.2±5.5	96.6±3.4	86.4±3.0
n	15	2	14	16	13	4
SDL range	25–31	27–29	28–34	31–38	31–38	26–28
mean±sd	27.5±1.5	28±1.4	32.1±1.7	34.0±1.8	33.8±2.4	27.5±1.0
n	15	2	14	16	13	4
ULS range	10–13	11–14	11–15	11–15	13–15	11–13
mean±sd	11.9±0.7	12.5±1.4	13.4±1.2	12.9±0.8	13.6±0.5	12.1±0.6
n	15	2	14	16	13	4

**Figure 8.** *Triodia* Mallee habitat—*Triodia* hummock grass groundcover in association with mallee woodland at Round Hill Nature Reserve central-west NSW (photo H. Cogger).

SA, and by implication continuous with populations of *C. spinodomus* sp. nov. in southwest NSW. His “Eyre Peninsula” race corresponds to our Group 5 *fordi* genetic lineage from Eyre Peninsula, however, his “northern” race which included all other populations in the north and west of the state, was a composite of the Group 3 *fordi* genetic lineage from the Strzelecki and Tarari desert systems and the Group 4 *fordi* genetic lineage from the Great Victoria Desert.

Edwards *et al.* (2015) figured the distribution of populations from northwest Victoria and far southeast SA (their *C. fordii* clade 5) as extending west across the Murray River and bisecting the Group 1 populations in southeast SA and southwest NSW. Reference to the online supplementary data for this publication gives one specimen (listed as 40887) with the coordinates “-34.05 139.1833”, which would place it west of the Murray River. Presumably this is the South Australian Museum specimen R40887 which is listed in the museum database as from Morgan Conservation Park, and with those same coordinates. However, Morgan Conservation Park lies 50 km to the east of these coordinates and on the south and east side of the Murray River. On the assumption the coordinates used to map this specimen are in error, all populations identified by Edwards *et al.* as belonging to their *C. fordii* clade 5 genetic lineage actually lie entirely to the south and east of the main Murray River channel, and the distribution of this lineage is parapatric to (not bisecting) the *C. spinodomus* sp. nov. populations in southeast SA and southwest NSW—a result consistent with our morphological investigations.

Discussion

The association between a number of Australian lizard species and *Triodia* hummock grass has long been recognized, a feature attributed not only to its structural complexity (Pianka, 1969) but also to its role in providing a “microclimate refuge” (Cogger, 1984) against extremes of temperature and dryness. The extent to which different taxa utilize *Triodia* varies. For some species it represents a niche within which they exclusively reside across their range, whereas for others it is the preferred niche at certain parts of their distribution. In the interior of southeast Australia five species of lizard, the diplodactylid gecko *Strophurus elderi*, the pygopods *Delma australis* and *D. butleri*, the skink *Ctenotus atlas* and agamid *C. spinodomus* sp. nov., are obligate inhabitants of habitat with a groundcover of *Triodia*, usually on red sand soils, and typically in

association with mallee woodland (Cogger, 1984; Sadler & Shea, 1989), and referred to as *Triodia* Mallee vegetation (Bennett *et al.*, 2010). With the exception of *C. spinodomus* sp. nov., these taxa have distributions that otherwise extend west across the continent, with the populations in areas of southeast Australia representing the eastern extreme of their distribution. Of these only *C. atlas* remains an obligate to *Triodia* in mallee woodland throughout its range (Wilson & Swan, 2017). By comparison, *C. spinodomus* sp. nov. is far more limited in distribution. Not only is it restricted to those biomes in southeast Australia in which *Triodia* Mallee vegetation is present as one of its key life history traits, but also requires this habitat type be in combination with a red sand substrate which provides nesting and overwintering sites (Cogger, 1974).

The association of *C. spinodomus* sp. nov. with *Triodia* extends beyond the presence vs absence of hummock grass habitat mallee vegetation to a dependence on particular successional stages of development of *Triodia* hummocks post-fire. Bennett *et al.* (2010) identified the species as being more common in landscapes with large amounts of *Triodia* Mallee vegetation, with the “time window” for greatest cover of spinifex and presence of large healthy hummocks c. 20–50 years post-fire, with a peak at 35 years (Watson *et al.*, 2012), after which densities decline slowly. In inland southeast Australia *Triodia* Mallee habitat is fragmented, naturally and through clearing. In the Murray Mallee region large fires (> 100,000 ha) occurred on average every two decades in the period 1972–2007 (Bennett *et al.*, 2010; Haslem *et al.*, 2011). A consequence of large fires is they create an extensive single age class of regenerating *Triodia* Mallee. Situations where fragments are burnt entirely and there is no internal source for recolonization could result in local extinction of *C. spinodomus* sp. nov. The population at Round Hill Nature Reserve, studied by Cogger as part his doctoral thesis (1969) and the basis of subsequent publications (1974 and 1978), has been monitored for variations in population size at regular intervals for the past 50 years, and is the subject of an ongoing long-term monitoring of population size now into its 50th year and to be the subject of a separate publication.

The complexity of interaction of *C. spinodomus* sp. nov. with its environment clearly identify it as an extreme habitat specialist with a distribution that relies on the presence of particular attributes of *Triodia* in the mallee woodlands of the region, attributes which rise and fall with time and which rely on burning events for renewal, and which make the species highly susceptible to variations in the frequency, intensity and patterns of fire events.

ACKNOWLEDGMENT. We thank Mark Hutchinson and Carolyn Kovach (South Australian Museum) and Paul Doughty and Rebecca Bray (Western Australian Museum) for facilitating the loan of specimens used in the morphological study, Steve Donnellan (South Australian Museum) for the provision of tissue samples used in the genetic study, and Andrew Amey (Queensland Museum) and Paul Doughty for constructive reviews of the manuscript. Edwina Rickard generated the sequence data for the genetic study analyses. Timothy Cutajar produced the map of *C. spinodomus* sp. nov. presented in Fig. 3, and Corin Sadlier assisted with image 7.

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Appendix 1

Specimen voucher registration number and general location for specimens used in the genetic study, and GenBank accession numbers assigned to sequences generated for these specimens.

taxa	vouchers	locations	GenBank numbers		
			12S	16S	ND4
Group 1 <i>C. spinodomus</i> sp. nov.	AMS R.156615	Yathong NR, NSW	MN136704	MN136730	MN136678 and MN136756
Group 1 <i>C. spinodomus</i> sp. nov.	AMS R.160412	Yathong NR, NSW	MN136705	MN136731	MN136679 and MN136757
Group 1 <i>C. spinodomus</i> sp. nov.	AMS R.156711	Yathong NR, NSW	MN136703	MN136729	MN136677 and MN136755
Group 1 <i>C. spinodomus</i> sp. nov.	AMS R.135216	Warrakoo Stn., NSW	MN136701	MN136727	MN136675 and MN136753
Group 1 <i>C. spinodomus</i> sp. nov.	AMS R.135216	Warrakoo Stn., NSW	MN136702	MN136728	MN136676 and MN136754
Group 2 <i>C. fordi</i> s.s.	AMS R.149822	Comet Vale, WA	MN136692	MN136718	MN136666 and MN136744
Group 2 <i>C. fordi</i> s.s.	AMS R.149823	Comet Vale, WA	MN136693	MN136719	MN136667 and MN136745
Group 2 <i>C. fordi</i> s.s.	AMS R.149824	Comet Vale, WA	MN136694	MN136720	MN136668 and MN136746
Group 2 <i>C. fordi</i> s.s.	AMS R.149825	Comet Vale, WA	MN136695	MN136721	MN136669 and MN136747
Group 2 <i>C. fordi</i> s.s.	AMS R.149827	Comet Vale, WA	MN136696	MN136722	MN136670 and MN136748
Group 2 <i>C. fordi</i> s.s.	AMS R.149835	Bonnie Vale, WA	MN136697	MN136723	MN136671 and MN136749
Group 3 <i>C. fordi</i> Strzelecki	AMS R.151649	Sturt NP, NSW	MN136699	MN136725	MN136673 and MN136751
Group 3 <i>C. fordi</i> Strzelecki	AMS R.151703	Sturt NP, NSW	MN136700	MN136726	MN136674 and MN136752
Group 3 <i>C. fordi</i> Strzelecki	AMS R.153035	Sturt NP, NSW	MN136698	MN136724	MN136672 and MN136750
Group 3 <i>C. fordi</i> Strzelecki	SAM R49254	Frome Downs, SA	MN136712	MN136738	MN136686 and MN136764
Group 3 <i>C. fordi</i> Strzelecki	SAM R49255	Frome Downs, SA	MN136713	MN136739	MN136687 and MN136765
Group 3 <i>C. fordi</i> Strzelecki	SAM R42347	Noble Wells, SA	MN136706	MN136732	MN136680 and MN136758
Group 3 <i>C. fordi</i> Strzelecki	SAM R30255	Roxby Downs, SA	MN136708	MN136734	MN136682 and MN136760
Group 3 <i>C. fordi</i> Strzelecki	SAM R30257	Roxby Downs, SA	MN136709	MN136735	MN136683 and MN136761
Group 4 <i>C. fordi</i> GVD	SAM R32231	Hallinor Lake, SA	MN136716	MN136742	MN136690 and MN136768
Group 4 <i>C. fordi</i> GVD	SAM R32238	Hallinor Lake, SA	MN136710	MN136736	MN136684 and MN136762
Group 5 <i>C. fordi</i> Eyre	SAM R36493	Courtabie, SA	MN136717	MN136743	MN136691 and MN136769
Group 5 <i>C. fordi</i> Eyre	SAM R36494	Courtabie, SA	MN136711	MN136737	MN136685 and MN136763
Group 5 <i>C. fordi</i> Eyre	SAM R49258	Eyre Peninsula, SA	MN136714	MN136740	MN136688 and MN136766
Group 5 <i>C. fordi</i> Eyre	SAM R49259	Eyre Peninsula, SA	MN136715	MN136741	MN136689 and MN136767
Outgroup <i>C. maculatus</i>	SAM R29397	Denham, WA	MN136707	MN136733	MN136681 and MN136759

Appendix 2

Specimen voucher registration numbers and locations used in the morphological study (note pipe symbol used between specimen registration number(s) and locations).

Group 1—*C. spinodomus* sp. nov.: see type data.

aff. Group 1—*C. aff. spinodomus*: AMS R.53878 | 15 miles W of Annuello, VIC 34.78S 142.57E; AMS R.55032 | Gingimrick area, VIC 34.92S 142.65E; AMS R.68785–90 | Hattah, VIC 34.77S 142.27E; AMS R.32774 | Big Desert near Underbool ca. 30 miles along Nhill road, VIC 35.17S 141.80E.

Group 2—*C. fordi* s.s.: AMS R.149822–23 | Comet Vale, WA 29.95S 121.12E; AMS R.149824–27 | Comet Vale, sand dunes 2.5 km N Comet Vale, WA 29.92S 121.10E; AMS R.149824 | 17.6 km W Bonnie Vale Rail Stn. via road 3.8 km N Bonnie Vale, WA 30.80S 120.98E; SAM R29248–51 | 57 km S Menzies, WA 30.11S 121.10E; WAM R115156 | Bungalbin Hill, WA 30.3111S 119.7278E; WAM R126412–13, R.126419 | Bungalbin sandplain, WA 30.2975S 119.7406E; WAM R126455 | Bungalbin sandplain, WA 30.2825S 119.7603E; WAM R129294 | Bungalbin sandplain, WA 30.2975S 119.7375E; WAM R141036–39 | Bungalbin Hill, WA 30.4000 119.6328; WAM R126937, R.126940, R.126943 | Goongarrie, WA 30.0500S 121.1500E; WAM R145312 | Goongarrie Station, WA 29.9833S 121.0333E; WAM R145369 | Goongarrie Station, WA 29.9675S 121.0817E; WAM R145372 | Goongarrie Station, WA 29.9675S 121.0064E.

Group 3—*C. fordi* Strzelecki: AMS R.155335 | Sturt National Park, 1.8 km W (by road) along Whitecatch Gate road, NSW 29.1142S 141.1817E; AMS R.158938 Sturt National Park, 5.7 km W (by road) along Whitecatch Gate road, NSW 29.1311S 141.1492E; AMS R.155491 | Sturt National Park, 21.7 km (by road) W of Binerah Downs Hmstd. on Middle road, NSW 29.0256S 141.3675E; AMS R.155459 Sturt National Park, 21.7 km (by road) W of Binerah Downs Hmstd. on Middle road, NSW 29.0256S 141.3675E; AMS R.151706 | Sturt National Park, 33.1 km W Binerah Downs, NSW 29.0819S 141.2611E; AMS R.154852 Cameron's Corner region, NSW 29.0819S 141.2611E; AMS R.151721, R.154851 Sturt National Park, Cameron's Corner road, 3.4 km N Middle road turnoff, NSW 29.0356S 141.1956E; AMS R.153035 | Sturt National Park, Approx. 3 km E (by road) from Cameron's Corner road, NSW 29.0092S 141.0667E; AMS R.155453 | Sturt National Park, Cameron's Corner road, 12.3 km E Cameron's Corner, NSW 29.0017S 141.0992E; AMS R.151647 | Sturt National Park, 15.3 km S Fort Grey, NSW 29.1328S 141.2758E; AMS R.104289–91, R.104293 | Omicron Station, QLD 28.82S 141.27E. AMS R.32818–21 | approx. 23 miles north of Innamincka Bore No.2., SA 28.05S 140.92E; AMS R.70164–67 23 miles N of Innamincka Bore No.2, SA 28.05S 140.92E; AMS R.60237–38 | 27 km S of Maree on Leigh Creek road, SA 29.90S 138.22E; AMS R.64295 | near Lake Torrens Homestead, SA 31.65S 138.07E; AMS R.59874–75 | Cotabena RS. area, SA 31.70S 138.22E; SAM R42347–48, R42351 | 1 km (air) NNW of Noble Well, N3/28, SA 30.6333S 139.5333E; SAM R49253–56 | Frome Downs Stn., 1.3 km NE of Lucky Hit Bore, SA 31.4166S 140.0500E; SAM R30254–57 | Olympic Dam Roxby Downs, SA 30.4500S 136.8833E.

Group 4—*C. fordi* GVD: AMS R.7676a & b, AMS R.7677a & b, AMS R.7678a & b, AMS R.7679 | 407 miles E.W. Line, SA 30.50S 132.15E; AMS R.49578–79 | N Neale Junction Great Victoria Desert, WA 26.13S 126.52E; AMS R.49765, R.49679 | 38.1 miles N Neale Junction, WA 27.70S 125.82E; AMS R.49620 | Big Bog, WA 27.33S 126.38E; SAM R14999A–D, R.14999F–K | 7 km W Immarna RS, SA 30.4833S 132.0833E; SAM R32061, R32064, R32085 | 5.5 km S Immarna Siding, SA 30.5519S 132.1450E; SAM R32192, R32199 | 52 km N Muckera R/H, SA 29.5591S 130.1386E; SAM R32225–26, R32229 R32231 R32238 | 44 km SW Halinor Lake, SA 29.4930S 130.1641E.

Group 5—*C. fordi* Eyre: AMS R.39383 | 20 miles E Kimba-Port Augusta on Eyre Highway, SA 32.22 137.53; SAM R36493–94 | 4.5 km NW Courtabie, SA 33.1791S 134.8222E; SAM R36505 | 7.5 km N Courtabie, SA 33.1416S 134.8333E; SAM R36545, R36550 | 7 km N Courtabie, SA 33.1416S 134.8500E; SAM R49257–60 | Whyalla to Kimba road, 25 km E of Secret Rocks, SA 33.1666S 137.0166E.



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scientific publications freely accessible at
<https://doi.org/10.3853/issn.2201-4349>
ISSN 0067-1975 (print) 2201-4349 (online)