A new species of spiny-tailed gecko (Squamata: Diplodactylidae: *Strophurus*) from the mulga woodlands of inland Western Australia

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ABSTRACT – A new species of spiny-tailed gecko, *Strophurus spinula* sp. nov., is described from inland areas of southern Western Australia. Among its diagnostic features are a discontinuous mostly straight row of enlarged tubercles down either side of the body, and the caudal spines of the tail are uniformly coloured with the largest lateral spines aligned to form a laterodorsal row on either side of the tail. In these characteristics it is most similar in morphology to *Strophurus assimilis*, and to a lesser extent *S. intermedius*. Genetic information shows it is most closely related to a group of species that includes *S. intermedius*, *S. spinigerus* and *S. rankini*. *Strophurus spinula* sp. nov. is found largely within the southern mulga woodlands region of Western Australia, and at the southern margins of its range is parapatric with respect to *S. assimilis*.

KEYWORDS: Western Australia, spiny-tail, gecko

urn:lsid:zoobank.org:pub:AC759216-08B7-485B-A41B-25CEC9F58AE1

INTRODUCTION

The last comprehensive review of variation in the spiny-tailed diplodactylid geckos now assigned to the genus *Strophurus* Fitzinger, 1843 was by Kluge (1967) over half a century ago. In that review Kluge identified eight discrete and largely allopatric forms of *Strophurus ciliaris* (as *Diplodactylus ciliaris*) throughout much of inland and northern Australia, and what he then considered a hybrid zone between his 'population 5' (now = *S. ciliaris aberrans*) and *Strophurus intermedius* (then as *Diplodactylus intermedius*). Storr (1988) later reviewed the status of the *ciliaris* populations in Western Australia and formally recognised Kluge's 'population 8' as *Diplodactylus wellingtonae*, 'population 1' and 'population 5' as *D. ciliaris ciliaris* and *D. ciliaris aberrans*, respectively, and the geckos from the 'hybrid zone' as a distinct species, *D. assimilis*. Sadlier et al. (2005) later investigated the status of Kluge's *D. ciliaris* 'population 6' from Queensland using both morphological and genetic data and described it as *Strophurus krisalys*. These taxa have been widely accepted and have appeared in the herpetological literature since. However, the complexity of morphological variation in this group of geckos has not been dealt with further, and the status of various populations of *Strophurus ciliaris* remain unresolved after Kluge highlighted their existence.

Our study presents an unexpected discovery of a cryptic species previously assigned to *Strophurus assimilis* in the course of a broadscale survey of genetic variation in the genus. The molecular evidence clearly identifies *S. assimilis* as currently recognised as comprising two distantly related lineages with broadly abutting parapatric distributions, a factor that accounts to some extent for some of the variation documented in the original description by Storr (1988). Here we describe the new species and provide a revised description for *Strophurus assimilis*.

MATERIALS AND METHODS

We have used an integrative taxonomic approach (*sensu* Padial et al. 2010) in which the species recognised herein are supported by a combination of molecular data and morphology, as these two sources of data represent different lines of evidence supporting lineage independence under a general lineage species concept (de Queiroz 1999).

Acronyms: abbreviations for specimens used in the morphological and genetic studies (below) are prefixed as follows: Australian Museum, Sydney (AMS); Western Australian Museum, Perth (WAM); South Australian Museum, Adelaide (SAMA); California Academy of Sciences, San Francisco (CAS).

MORPHOLOGICAL COMPARISONS

Our sampling for the morphological study includes 22 specimens of *Strophurus assimilis*, 10 specimens of *Strophurus spinula* sp. nov., and 23 specimens of *Strophurus intermedius*. The specimens of *S. intermedius* selected were from Western Australia and South Australia, as these were considered the populations most relevant for comparisons with both *S. assimilis* and *S. spinula* sp. nov. A further 45 specimens of *S. assimilis* and 27 specimens of *S. spinula* sp. nov. from the WAM collection were examined to further assist in determining the distribution of both species (Appendix 1). The full suite of morphological characters listed below were scored where possible (bilateral scalation characters were scored on both sides and the mean value used).

Measurements: snout to vent length (SVL) — tip of snout to anterior margin of vent; axilla to groin length — measured from apex of intersection of forelimb with the body to the apex of crease of hindlimb at body and expressed as a percentage of SVL; head length — tip of snout to posterior extreme of lower jaw, expressed as a percentage of SVL; head width — width of jaw measured at labials below mid-orbit, expressed as a percentage of head length; hindlimb length — groin from apex of crease to tip of fourth toe, excluding claw, expressed as a percentage of SVL; tail length — measured from posterior margin of vent to tip of tail, on complete original tails only, expressed as a percentage of SVL.

Scalation: rostral crease — mid-dorsal groove either partially or completely dividing rostral scale (enlarged scale covering tip of snout), length of groove relative to total height of rostral scale; nasal — number of enlarged scales separating rostral from anterior margin of nostril; supranasal — number of enlarged scales bordering superior margin of nostril; postnasal — number of scales bordering posterior margin of nostril; internasal — number of scales between right and left anterior nasals, immediately posterior to rostral; supraciliary spines — number of enlarged spinose scales projecting beyond margin of dorsal eyelid; apical plates — the enlarged scales covering terminal underside of digit; fourth finger and toe lamellae — number of scales comprising much enlarged transverse scales on underside of digits (Kluge's secondaries) proximal to apical plates, and number of elliptical or round scales (in pairs) proximal to enlarged transverse scales to emergence of digit (Kluge's tertiaries); tail spines — number of enlarged scales (i.e. those modified into a spiked structure) on dorsal surface of tail in regular longitudinal rows, counted from posterior extreme of cloacal swelling to tip of tail; number of scales in a transverse line across tail between longitudinal rows of caudal spines, count taken at mid-tail length at row posterior to that bordering anterior edge of caudal spine (= intercaudals of Kluge 1967 and Sadlier et al. 2005); number of scales between (but not including the caudal spines of same longitudinal row, counts taken from caudal spine at mid-tail length to next spine immediately posterior (= intracaudals of Kluge 1967 and Sadlier et al. 2005); precloacal pores — external openings of precloacal glands in scales anterior to the vent, and are given as separate values for the left and right sides, counts are for males only; interpore scale — number of scales interrupting the precloacal pore series on midline.

GENETIC STUDY

Our genetic sampling includes 19 specimens of *Strophurus assimilis* and 9 specimens of *Strophurus spinula* sp. nov. for which we generated new mitochondrial (ND2) and nuclear (RAG1) molecular data. Genomic DNA was isolated from liver tissues subsampled from the collections of WAM, Evolutionary Biology Unit (EBU) at SAMA, and from AMS. We used a standard salt and ethanol extraction protocol, amplified following the methods of Nielsen et al. (2016) and sequenced on an ABI 3730. These samples were analysed in the context of 45 *Strophurus* samples representing 19 species within the genus, including all the relevant related 'spiny-tailed' species, and accompanied by 8 outgroup diplodactylid geckos. New sequences were added to existing mtDNA (ND2: 1497bp) and nDNA (RAG1, CMOS, PDC, PRLR: 2195bp) alignments generated by Nielsen et al. (2016) and trimmed down so that additional *Strophurus* and outgroup species were represented by a single sample. To estimate the phylogenetic relationships among *Strophurus* we used IQTREE (Nguyen et al. 2015), with separate mtDNA and nDNA alignments. The nuclear alignment was partitioned by locus. We then allowed the program to automatically pick the best fitting model of molecular evolution using Model Finder (Kalyaanamoorthy et al. 2017), then perform 1,000 ultrafast bootstraps (Minh et al. 2013). Mitochondrial and nuclear datasets were not used to jointly estimate a phylogeny due to the strongly conflicting placement of *S. assimilis.*

The sequences for *Strophurus assimilis* and *Strophurus spinula* sp. nov. generated during this study are available on GenBank under accession numbers OQ873519-OQ873542 for ND2, and OQ867145-OQ867167 for RAG1.

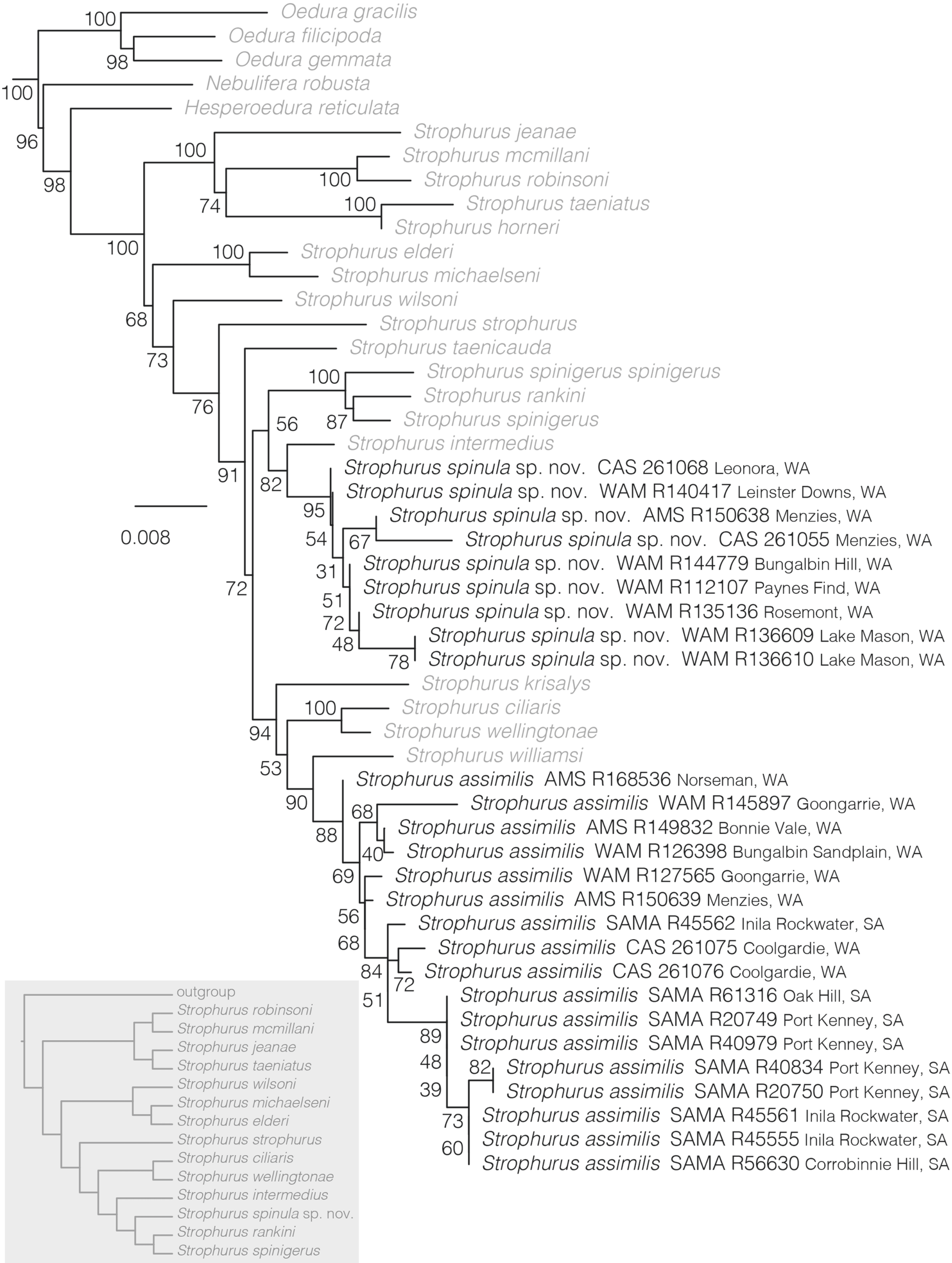

FIGURE 1 Concatenated and partitioned nuclear phylogeny with Maximum Likelihood estimates of *Strophurus* and selected outgroup taxa inferred from RAG1, CMOS, PDC and PRLR nuclear sequence data — the inset phylogram represents the relationships between the species of *Strophurus* found by Skipwith et al. (2019), but modified such that the branch represented by WAM R154745 (their *S. assimilis*) is here labelled as *Strophurus spinula* sp. nov.

RESULTS

MORPHOLOGY

Both *Strophurus spinula* sp. nov. and *Strophurus assimilis* have uniformly coloured enlarged caudal spines on the tail aligned as a dorsolateral row down either side of the tail. The spines are separated across the dorsal surface of the tail by only a few intercaudal scales (Figure 2). In *S. spinula* sp. nov. the enlarged caudal spines on the tail are typically arranged with the largest outermost and separated from each other across the dorsal surface (at midlength) by two intervening scales only slightly larger than the surrounding tail scales. In *S. assimilis* these intervening scales are markedly larger than the surrounding tail scales, and in some cases are only slightly smaller than the large spines of the laterodorsal row down either side of the tail. This can give the appearance of a row of 4 or 5 enlarged scales across the top of the tail — hence the 'whorls' described by Storr (1988).

Among the spiny-tailed members of the genus, *Strophurus wellingtonae*, *Strophurus krisalys* and several populations within *Strophurus ciliaris* (central Australia and inland north-west New South Wales and adjacent areas of inland South Australia and Queensland) also have a single row of enlarged unicoloured spines down either side of the tail. However, these are present as a single row of typically medium to short spines with the intervening scales not markedly different in size from adjacent tail scales and greater than five in number.

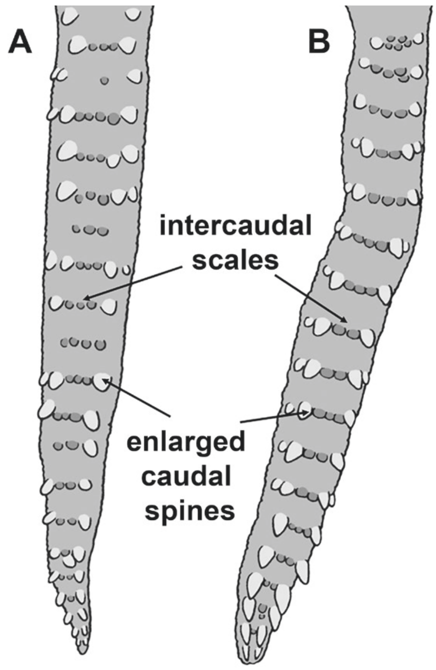

FIGURE 2 Illustration of the diagnostic tail scalation of *Strophurus spinula* sp. nov. and *S. assimilis*. A) *Strophurus spinula* sp. nov., showing the decrease in size of tail spines approaching the tip of the tail (AMS R150638 from 7 km NE of Menzies, WA); B) *S. assimilis*, showing the increase in size distally to become pronounced spines (AMS R150639 from 26.3 km SE of Menzies, WA). Also identified are the intercaudal scales which lie transversely between the enlarged caudal spines of the tail (illustration Cecilie Beatson).

TABLE 1 Comparative table of key body measurements, tail scalation and precloacal pores for *Strophurus spinula* sp. nov., *Strophurus assimilis*, and representative populations of *Strophurus intermedius* from Western Australia and South Australia.

	S. spinula sp. nov.	*S. assimilis*	*S. intermedius*
Maximum SVL (mm)	61.2	80.8	63.6
Tail length (% SVL)			
Range	47.8–64.8	49.3–66.3	41.6–56.5
Mean±SD	55.4 ± 5.7	54.9 ± 5.0	48.1 ± 4.2
N	8	17	17
Caudal spines			
Range	17–20	18–20	13–18
Mean±SD	18.5 ± 1.2	18.3 ± 0.7	15.9 ± 1.3
N	8	17	17
Precloacal Pores			
Range	11–13	12–17	9–15
Mean±SD	12.4 ± 0.9	14.9 ± 2.1	11.7 ± 1.5
N	5	11	13

TABLE 2 Net genetic distances between *Strophurus spinula* sp. nov. and *Strophurus assimilis*, and the 'spiny-tailed' group of *Strophurus* species.

	S. assimilis	*S. ciliaris aberrans*	*S. ciliaris ciliaris*	*S. intermedius*	*S. krisalys*	*S. rankini*	*S. spinigerus inornatus*	*S. spinigerus spinigerus*	*S. spinula* sp. nov.	*S. strophurus*	*S. taenicauda taenicauda*	*S. taenicauda triaureus*	*S. wellingtonae*	*S. williamsi*
S. assimilis	0	16.65	16.28	14.08	16.77	14.93	14.57	14.44	15.18	8.45	15.18	15.30	17.14	15.42
S. ciliaris aberrans	16.65	0	10.65	16.03	16.40	15.42	15.30	14.93	15.18	16.89	14.44	14.93	13.34	15.06
S. ciliaris ciliaris	16.28	10.65	0	15.06	16.40	14.81	13.71	14.32	14.57	16.40	13.10	13.10	12.73	14.44
S. intermedius	14.08	16.03	15.06	0	15.79	8.69	9.18	9.06	9.42	16.28	12.00	11.63	15.91	10.53
S. krisalys	16.77	16.40	16.40	15.79	0	16.03	15.30	15.42	15.06	16.40	14.69	15.06	16.52	14.93
S. rankini	14.93	15.42	14.81	8.69	16.03	0	7.71	7.71	8.57	16.03	12.12	12.97	16.03	10.28
S. spinigerus inornatus	14.57	15.30	13.71	9.18	15.30	7.71	0	3.67	7.96	15.54	12.24	12.00	16.16	10.77
S. spinigerus spinigerus	14.44	14.93	14.32	9.06	15.42	7.71	3.67	0	7.96	15.42	12.48	12.36	16.52	10.28
S. spinula sp. nov.	15.18	15.18	14.57	9.42	15.06	8.57	7.96	7.96	0	15.18	12.36	11.75	16.65	9.91
S. strophurus	8.45	16.89	16.40	16.28	16.40	16.03	15.54	15.42	15.18	0	14.32	14.81	17.50	15.67
S. taenicauda taenicauda	15.18	14.44	13.10	12.00	14.69	12.12	12.24	12.48	12.36	14.32	0	6.61	15.06	10.40
S. taenicauda triaureus	15.30	14.93	13.10	11.63	15.06	12.97	12.00	12.36	11.75	14.81	6.61	0	13.95	11.14
S. wellingtonae	17.14	13.34	12.73	15.91	16.52	16.03	16.16	16.52	16.65	17.50	15.06	13.95	0	15.67
S. williamsi	15.42	15.06	14.44	10.53	14.93	10.28	10.77	10.28	9.91	15.67	10.40	11.14	15.67	0

Strophurus intermedius is similar to *Strophurus spinula* sp. nov. and *Strophurus assimilis* in having enlarged uniformly coloured caudal scales on the tail. However, the expression of these enlarged tail scales in *S. intermedius* differs in that they are typically present as a pair of similarly-sized, low (somewhat flattened) tubercles on either side, separated across the dorsal surface of the tail by a few (2–3) intervening smaller scales, usually still larger than the surrounding granular scales of the tail. Occasionally, one of the paired enlarged tubercles on either side can be lost such that only a single tubercle is present, and occasionally lost to the extent that there is only a single row of enlarged tubercles on the dorsolateral alignment on either side of the tail, similar in arrangement to that seen in to *S. spinula* sp. nov. However, the enlarged caudal tubercles of *S. intermedius* decrease in size progressively over the posterior part of the tail and are barely discernible at the tip, whereas the enlarged scales (spines) of *S. spinula* sp. nov. while reduced in size at the tip are readily discernible, and those of *S. assimilis* increase in size distally to become pronounced spines towards the tip.

Strophurus spinula sp. nov. and *Strophurus assimilis* are readily differentiated from each other by the size of the tail spines on the distal part of the tail (Figure 2), and in the pattern and alignment of the dorsal tubercles on the body. In *S. spinula* sp. nov. the enlarged spines of the tail decrease in size approaching the tip of the tail whereas those of *S. assimilis* increase in size distally to become pronounced spines. *Strophurus spinula* sp. nov. and *S. assimilis* are also differentiated by pattern and alignment of dorsal tubercles on each side of the body which are typically arranged as a continuous sinuous line in *S. assimilis*, whereas the tubercles of *S. spinula* sp. nov. are arranged in a relatively straight line down the axis of the body but as discontinuous sets of 2–4 tubercles in a line.

Both *Strophurus spinula* sp. nov. and *Strophurus assimilis* differ from *Strophurus intermedius* in tail length and the number of enlarged caudal scales down the length of the original tail (Table 1). The tail of *S. intermedius* is on average shorter ($\bar{x}$ = 48.1%, 41.6–56.5%) than that of *S. spinula* sp. nov. ($\bar{x}$ = 55.4%, 47.8–64.8%) and *S. assimilis* ($\bar{x}$ = 54.9%, 49.3–66.3%), and *S. intermedius* has fewer enlarged caudal tubercules ($\bar{x}$ = 15.9, range 13–18) than the enlarged caudal spines present in *S. spinula* sp. nov. ($\bar{x}$ = 18.5, range 17–20; $p = 0.005$) or *S. assimilis* ($\bar{x}$ = 18.3, range 18–20; $p < 0.001$), but with some overlap in range. There is also a significant difference in the number of precloacal pores between *S. intermedius* ($\bar{x}$ = 11.7, range 9–15) and *S. assimilis* ($\bar{x}$ = 14.9, range 12–17; $p < 0.001$) with some overlap in range, but not with *S. spinula* sp. nov. ($\bar{x}$ = 12.4, range 11–13; $p = 0.356$) (Table 1).

GENETICS

Comparisons of the genetic distances between and within species are shown in Table 2. From our nuclear data we recover a topology that is generally congruent at the higher levels with that of Skipwith et al. (2019) — the most reliable estimate of *Strophurus* relationships to date, but with the caveat that that study lacked *S. assimilis* s.s., and as such there is some discordance with that study. Our mitochondrial data result in a topology that identifies similar major clades of species in agreement with the nDNA tree except for the strong and conflicting placement of *S. assimilis* as sister to *S. strophurus*. Our mtDNA topology is more similar to the concatenated tree presented by Nielsen et al. (2016). Here we present the nDNA tree (Figure 1) to avoid the potentially artifactual representation of *S. assimilis* and *S. strophurus* as sister taxa. We agree with the suggestion of Nielsen et al. (2016) that the pairing of these species in mitochondrial data is likely the result of historical introgression.

TAXONOMY

The genetic data clearly indicates *Strophurus assimilis* as currently conceived is polyphyletic, comprising two species of spiny-tailed gecko. The morphological assessment further supports the differentiation of these lineages as distinct taxa, one of which is here described as a new species.

Genus *Strophurus* Fitzinger, 1843

Strophurus spinula sp. nov.

Lesser Thorn-tailed Gecko

(Figure 3)

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MATERIAL EXAMINED

Holotype

Australia: *Western Australia*: WAM R135136 Rosemont (27.9308°S, 122.3181°E), collected by Paul West (HGM Environmental Services), 15–22 September 1998.

Paratypes

Australia: *Western Australia*: WAM R112107 Paynes Find, 20 km SW (29.2858°S, 117.4808°E), G. Harold, 10 October 2003; WAM R144778 Bungalbin Hill area (30.3333°S, 119.6833°E), Ecologia, 11 December 2000; WAM R144779 Bungalbin Hill area (30.3333°S, 119.6833°E), Ecologia, 11 December 2000; WAM R136609, R136610 Lake Mason Station (27.5650°S, 119.4297°E), M.A. Cowan, 15 September 2004; WAM R136771 Lake Mason Station (27.5275°S, 119.4722°E) M.A. Cowan, 28 November 2004; AMS R150638 Menzies, 7 km NE of Menzies (29.65°S, 121.05°E); WAM R117157 Dead Horse Rocks, 6.5 km N Menzies (29.3666°S, 121.2833°E), G. Thomson, 20 July 1993; WAM R140417 Leinster Downs Station (28.1561°S, 120.6931°E), G. Harold and R. Hart, October 1999.

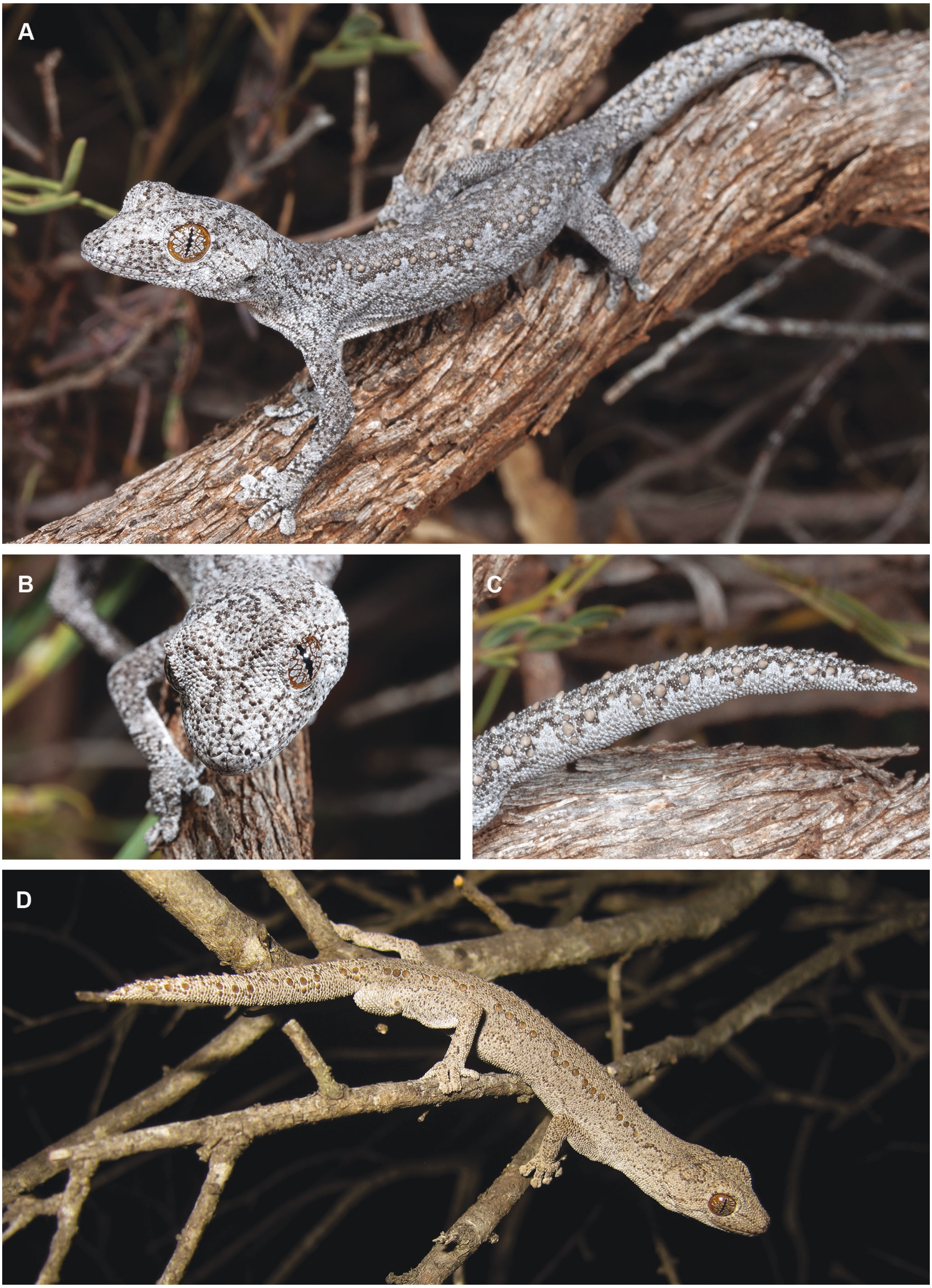

FIGURE 3 Two individuals of *Strophurus spinula* sp. nov. from Mt Gibson in Western Australia. A and D) aspects of the whole body and the straight-line and broken arrangement of tubercles along the dorsolateral axis of the body; B) the head; C) arrangement of enlarged spines along the tail (photos: A–C Anders Zimny; D Ray Lloyd).

Referred Material

See Appendix 1.

DIAGNOSIS

Strophurus spinula sp. nov. can be distinguished from other members of the genus by the following combination of characters: a relatively straight and discontinuous row of enlarged unicoloured tubercles along the dorsolateral margin of the body; tail with a single row of enlarged unicoloured spines on either side of the original tail, progressively decreasing in size towards the distal part of the tail; scales in a transverse line across the tail between longitudinal rows of enlarged caudal spines scales 2–3 in number at mid-tail and larger than surrounding tail scales.

Of the species likely to be confused with *Strophurus spinula* sp. nov. only *Strophurus assimilis* and some populations of *Strophurus ciliaris* have a single row of enlarged, unicoloured, spines on either side of the tail. *Strophurus spinula* sp. nov. can be distinguished from populations of *S. ciliaris* with unicolored, spines on either side of the tail (those listed as *S. ciliaris* 'population 7' — Sadlier et al. 2005), in having 2–3 intervening scales in a transverse line across the tail between longitudinal rows of enlarged caudal spines at mid-tail vs 4–7, and in these being larger vs similar in size to the surrounding tail scales. *Strophurus spinula* sp. nov. can be distinguished from *S. assimilis* in having the distal tail spines reducing in size towards the tail tip, whereas *S. assimilis* has the distal tail spines increasing in size towards the tail tip. *Strophurus spinula* sp. nov. can be further distinguished from *S. assimilis* in having the enlarged tubercles along the dorsolateral margin of the body present as a straight, but discontinuous, row vs a more or less continuous wavy row of enlarged tubercles down the body.

DESCRIPTION

Measurements: Maximum SVL 61.2 mm ($\bar{x}$ = 51.9, range 40.8–61.2, n = 10); tail length 47.8–64.8% of SVL ($\bar{x}$ = 55.4%, n = 8); axilla to groin length 40.2–50.8% of SVL ($\bar{x}$ = 45.2% n = 8); head length 25.0–30.1% SVL ($\bar{x}$ = 26.7%, n = 10); head width 66.2–74.4% of head length ($\bar{x}$ = 71.4%, n = 10); hind limb length 38.6–46.7% SVL ($\bar{x}$ = 42.4%, n = 10).

Scalation: Nostril surrounded by rostral, single supranasal, two postnasals, and first labial. Rostral divided by a median groove. Internasals 1–3 (mode 2). Enlarged ciliary spines 1–3 (mode 1), and low (length 1.5 times greater than that of adjacent scales). Underside of digits of forelimbs with single pair of large apical plates, followed on fourth digit by 4–5 (mode 4) transverse lamellae and proximally by 1–2 (mode 2) pairs of elliptical or circular scales. Underside of digits of hind limbs with pair of large apical plates, followed on fourth digit by 4–6 (mode 5) transverse lamellae and proximally by 0–3 (mode 2) pairs of elliptical or circular scales. Precloacal pore row in males 11–13 (mode 13) in total, interrupted medially by 1–2 poreless scales. Cloacal spurs two either side.

Enlarged dorsal tubercles of the body arranged in a single parallel row each side of the dorsal midline, tending to be in a straight alignment down the paravertebral axis of the body, but usually broken at intervals along its length. Enlarged dorsal spines of original tail 17–20 ($\bar{x}$ = 18.5 ± 1.2, n = 8) down either side of the tail. At mid-distance along tail these spines are separated (transversely) by two (rarely three) scales in a transverse line across the tail between the longitudinal rows of enlarged caudal spines, and by 4–5 intervening scales between the enlarged spines down the tail.

Colour and pattern: Dorsal surface mid-grey, and on well-patterned individuals contained within a wavy dorsolateral edge that defines it from the lighter-coloured lateral surface of the body. Dorsal surface of body relatively uniform or with scattered dark markings, these being concentrated along the dorsolateral edge. Dark dorsal colour converging at the shoulders and then extending forward over the neck and head variably as irregular broad blotches, or as scattered markings and forming a coarse dark temporal streak to the back of the eye and a pattern of dark reticulating markings on top of the head. Dorsal tubercles of the body uniformly grey to light to dark tan in colour and aligned along the outer (convex) inflexions of the dark wavy dorsolateral edge. Lateral surface of the body light grey, relatively uniform or variably with darker blotches similar in tone to dorsal surface and/or with dark markings, these tending to be aligned along the midlateral axis in a wavy pattern and forming a pattern of connected pale grey blotches along the side of the body. Ciliary spines usually grey, sometimes darker. Tail light grey with an extension of darker markings from the wavy dorsolateral edge extending as irregular markings down either side of the tail in the intracaudal spaces between the enlarged tail tubercles.

The reticulated part of the iris is ringed in orange-brown in the images of the only two live individuals photographed from Mt Gibson (Figure 3). Colour of mouth lining unknown.

DISTRIBUTION

Strophurus spinula sp. nov. has been recorded as for north as Yalgoo (28.35°S), Lake Mason Station (27.5275°S) and Rosemont (27.9308°S), south to Mt Gibson (29.575°S), Bungalbin (30.333°S) and Menzies (29.65°S), and east to Laverton and White Cliffs (Figure 4A). Most of its distribution lies within the southern part of the Mulga (*Acacia aneura*) woodlands of Western Australia, extending peripherally into adjacent vegetation types in the south of its range.

The distribution of *Strophurus spinula* sp. nov. broadly overlaps with *Strophurus strophurus*, though the latter is more widespread, and to a lesser extent in the east of its range with *Strophurus wellingtonae*. *Strophurus spinula* sp. nov. and *Strophurus assimilis* are largely parapatric in distribution, with minimal overlap in the Bungalbin Hill area and Mount Manning.

HABITAT

Data associated with records of *Strophurus spinula* sp. nov. in the WAM collection note it as being recorded in the north of its range from 'open mulgas on red rocky soil' and 'mulga on red loam' at White Cliffs (R53335, R56011, R85442–44), 'mulga below a breakaway' at Leinster Downs Station (R140417), 'mulga/shrubs' at Yuinmery (R74699), 'low shrubland with acacia emergence' on Mount Wardiacco (R49283), and in 'sparse eucalypts open acacia on stony red soil' (R60922–23) and 'eucalypts over mixed acacias on stony red-brown loam' (R112107) near Paynes Find. In the south of its range, it was found in 'mallee with dense mixed understory' near Bungalbin Hill (R144778–79). A single specimen recorded from Rosemont by HGM Environmental Services in 1998 (as *Strophurus assimilis*) which presumably represents the holotype, was from a site located on a saline alluvial plain with scattered halophytic shrubland (HGM 1999).

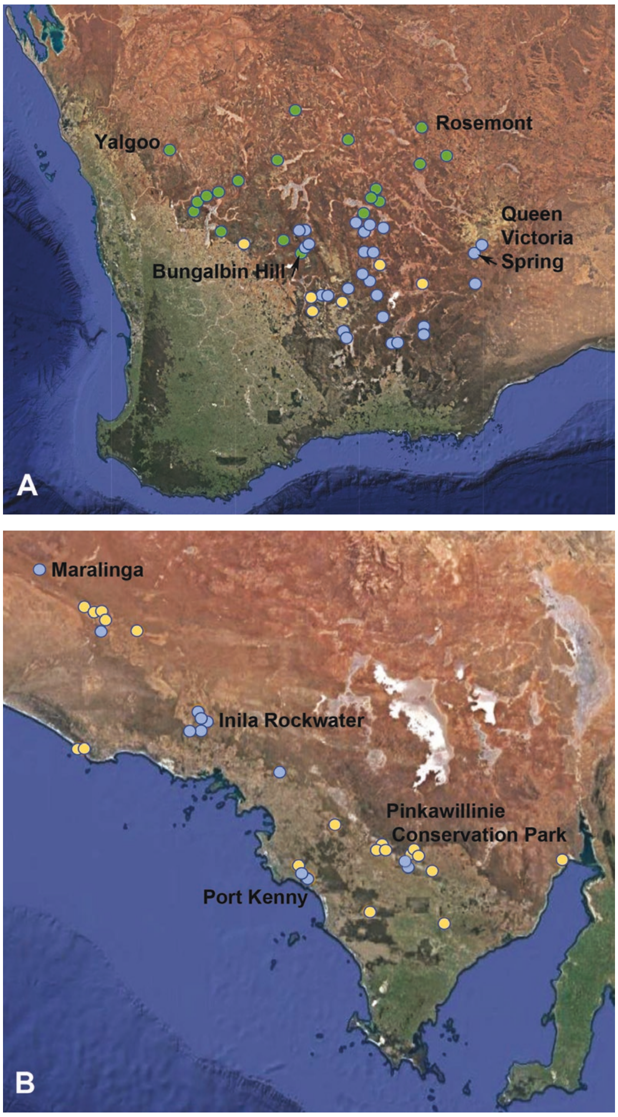

FIGURE 4 A) Distribution of *Strophurus spinula* sp. nov. (green) and *Strophurus assimilis* (blue) in Western Australia; B) distribution of *Strophurus assimilis* (blue) in South Australia based on locations given in Appendix 1. Note: yellow dots represent records previously assigned to *Strophurus assimilis* which are represented by observations or museum specimens whose identity was uncertain, or which were not included in the material examined.

ETYMOLOGY

The species name 'spinula' is the Latin for 'little thorn' in reference to the comparatively small size of the tail spines, a feature which distinguishes it from regionally parapatric *Strophurus assimilis* which has more pronounced spines on the tail and bears the common name the 'Thorn-tailed Gecko'. The specific epithet is constructed as a noun in apposition.

Strophurus assimilis **Storr, 1988**

Figures 5–7

With the description of *Strophurus spinula* sp. nov. a revised description and distribution for *Strophurus assimilis* is provided here.

DIAGNOSIS

Strophurus assimilis can be distinguished from other members of the genus by the following combination of characters: a continuous to near continuous (sometimes broken) wavy row of enlarged unicoloured tubercles along the dorsolateral margin of the body (Figures 5, 7A–B); tail with a single row of enlarged unicoloured spines on either side of the tail that progressively increase in size and become more spinose approaching the distal part of the tail (Figures 6A, 7A, 7C); scales in a transverse line across the tail between longitudinal rows of enlarged caudal spines scales mid-tail 2–3 in number at mid-tail, and typically significantly larger than surrounding tail scales; colour of mouth lining deep blue.

Of the species likely to be confused with *Strophurus assimilis*, only *Strophurus spinula* sp. nov., some populations of *Strophurus ciliaris*, and *Strophurus wellingtonae* have a single row of enlarged, unicolored, spines on either side of the tail. *Strophurus assimilis* can be distinguished from populations of *S. wellingtonae* and *S. ciliaris* with unicolored spines on either side of the tail in having the 2–3 vs 7–11 and 4–7 scales, respectively, in a transverse line across the tail between the longitudinal rows of enlarged caudal spines at mid-tail, and in these being larger vs similar in size to the surrounding tail scales. Further, *S. assimilis* can be distinguished from *S. ciliaris* in having a blue vs yellow mouth colouration. *Strophurus assimilis* can be distinguished from *S. spinula* sp. nov. in having the distal spines of the tail increasing is size compared to those preceding, whereas

S. spinula sp. nov. has the distal tail spines decreasing in size. *Strophurus assimilis* can be further distinguished from *S. spinula* sp. nov. in having the enlarged tubercles along the dorsolateral margin of the body present as a more-or-less continuous wavy row of enlarged tubercles down the body row vs straight but discontinuous row.

DESCRIPTION

Measurements: Maximum snout-vent length (SVL) 80.8mm (adults $\bar{x}$ = 67.0, range 53.7–80.8, n = 22); tail length 49.3–66.3% of SVL ($\bar{x}$ = 54.9%, n = 17); axilla to groin length 41.9–51.3% SVL ($\bar{x}$ = 46.4, n = 22); head length 23.9–28.3% SVL ($\bar{x}$ = 26.2%, n = 22); head width 62.6–78.6% of head length ($\bar{x}$ = 70.2%, n = 22); hind limb length 36.7–48.8% SVL ($\bar{x}$ = 41.7%, n = 22).

Scalation: Nostril surrounded by rostral, single supranasal, usually two postnasals (occasionally three), and first labial. Rostral divided by a median groove. Internasals usually one (rarely two). Enlarged ciliary spines 2–7 (mode 5), and moderate in length (2 times that of adjacent scales). Underside of digits of forelimbs with single pair of large apical plates, followed on fourth digit by 3–5 (mode 4) transverse lamellae and proximally by 1–3 (mode 2) pairs of elliptical or circular scales. Underside of digits of hind limbs with pair of large apical plates, followed on fourth digit by 4–5 (mode 4) transverse lamellae and proximally by 1–3 (mode 2) pairs of elliptical or circular scales. Precloacal pores in males 12–17 in total, separated medially by 1–2 (rarely 3) poreless scales. Cloacal spurs 2–3 either side (mode 2).

Enlarged dorsal tubercles of the body arranged as a single, parallel row on each side down the paravertebral axis of the body, wavy in alignment and typically continuous over most of its length, but broken anteriorly at and just posterior of the forelimbs in some individuals. Enlarged dorsal spines of original tail in a regular arrangement of 18–20 ($\bar{x}$ = 18.3 ± 0.7, n = 17) rows down either side of the tail. At mid-distance along tail these spines are separated (transversely) by 2–4 scales across the tail, these intervening scales consisting of an enlarged tubercle with or without an additional smaller enlarged scale (also typically larger than the adjacent granular tail scales), and by 5 (rarely 4) intervening scales between the enlarged spines down the tail.

Colour and pattern: Dorsal surface light to mid grey, occasionally darker, and contained within a dorsolateral series of enlarged, tan to dull orange-coloured tubercles that form a wavy edge down either side of the body. Dorsal surface of body relatively uniform but sometimes with irregular dark markings anteriorly concentrated as a wavy dorsolateral edge along the underside of the enlarged tubercles, and extending anteriorly as a wavy margin to the top of the eye. Base colour of the lateral surface of the body usually similar to the dorsal surface. Some individuals darker in tone and with a pattern of elongate and irregular (sometimes diamond-shaped) and variably connected paler blotches on the lateral surface, aligned and variably continuous with a pale temporal streak along the side of the head to the back of the eye. A variably defined pale canthal stripe along the snout, and in some more or less extending along the side of the tail. Individuals with this pattern (Figure 6A) present a two-toned (darker dorsal/lighter lateral) appearance by virtue of the paler lateral markings dominating the surface appearance. The dark dorsal colouration of two-toned individuals extends across the top of the head uniformly or broken into large blotches. Ciliary spines usually grey-brown to tan, occasionally lighter grey or

FIGURE 5 Holotype of *Strophurus assimilis*, Storr (WAM R72164) from near Bungalbin Hill in Western Australia. Note: the well-defined wavy and continuous row of enlarged tubercles along the dorsolateral axis of the body.

brown to dark brown. Tail similar in colour and pattern to body, with the enlarged tail tubercles similar in colour to those on the body, and in some individuals the enlarged intercaudal scales similarly coloured.

The reticulated part of the iris in the image of both live individuals from the Coolgardie and Norseman area in Western Australian (Figure 6) and from Eyre Peninsula in South Australia (Figure 7A) is ringed in dark brown.

Variation: There is variation in the extent of enlarged dorsal tubercles down each side of the paravertebral axis of the body between the insertions of the limbs. In Western Australia, this row is typically continuous and wavy over most of its length (Figure 5) in populations in the north-west (Bungalbin Hill area) and south-west of its range (i.e., Yellowdine and Southern Cross), but can be broken and discontinuous anteriorly at and just posterior of the forelimbs (Figure 6) in some populations

FIGURE 6 *Strophurus assimilis.* A) Jimberlana Hill near Norseman (AMS R168536); B) near Coolgardie (CAS 261076). Note: lack of continuity anteriorly of enlarged tubercles along dorsolateral axis of the body (photos Ross Sadlier).

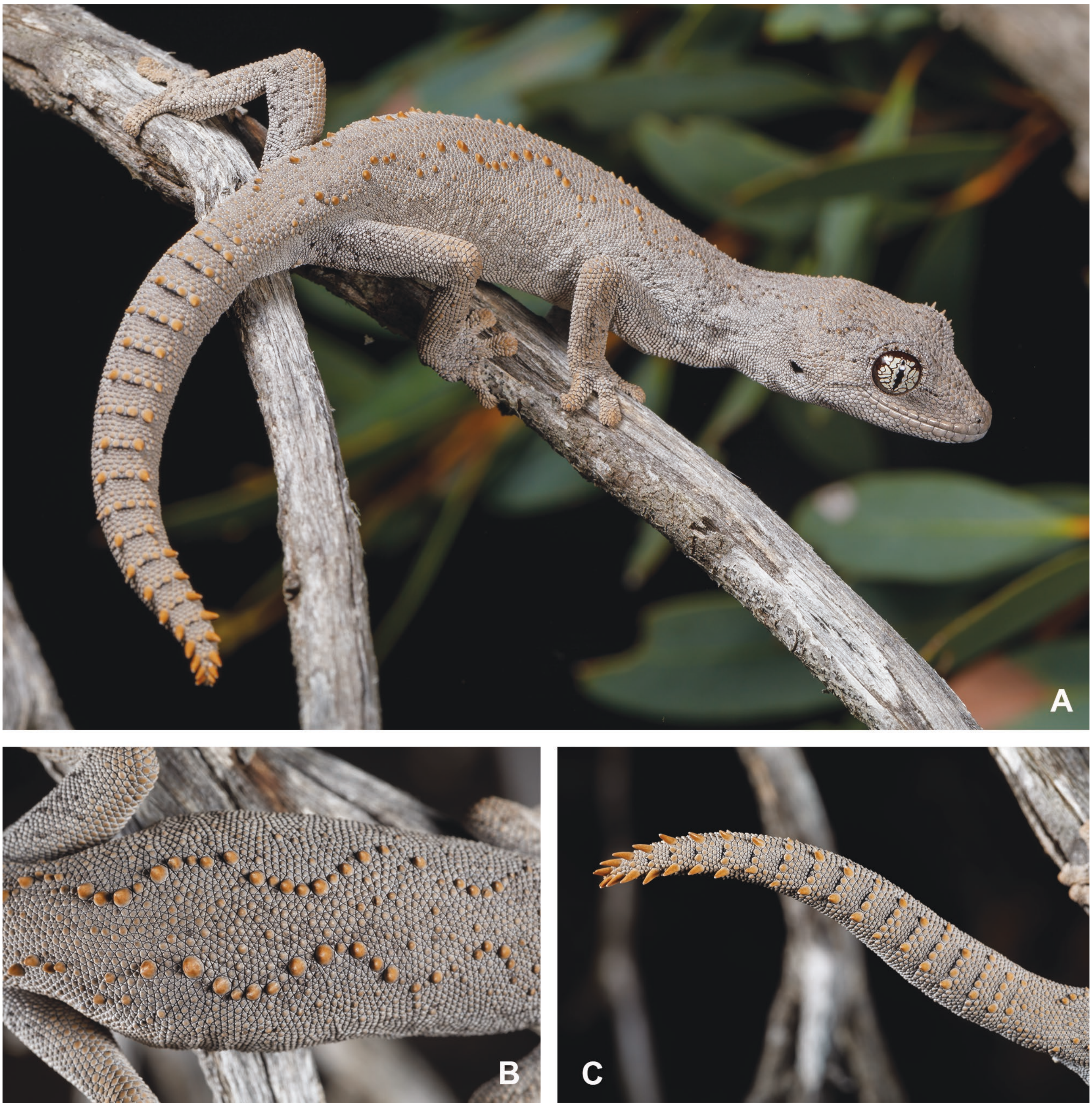

FIGURE 7 *Strophurus assimilis*. A) Port Kenny in South Australia; B) the well-defined wavy and continuous row of tubercles along the dorsolateral axis of the body; C) the particularly pronounced tail spines of the Eyre Peninsula population as they increase in size distally (photos Jules Farquhar).

in the east of its range in Western Australia (i.e., Coolgardie and Norseman). Those individuals with the enlarged dorsal tubercles broken or reduced in number anteriorly and lacking an original tail can be difficult to distinguish from *Strophurus spinula* sp. nov.

In the Queen Victoria Springs area at the eastern extremity of the species distribution in Western Australia, several specimens (WAM R15213, R58709, R99605, R99606 R100621) had the enlarged dorsal tubercles down each side of the body, wavy in alignment over most its length, in some broken and discontinuous anteriorly, and three had an original tail with the distal spines increasing is size — these could be unequivocally assigned to *Strophurus assimilis*. Other specimens from the area Queen Victoria Springs (WAM R15214, R48652, R48657, R48658) had the enlarged dorsal tubercles down each side of the body broken and discontinuous anteriorly, and to some extent posteriorly, and one had the row of tubercles broken and discontinuous over much its length down the body — all did not have original tails and could not be unequivocally assigned to *S. assimilis* and are here listed as incertae sedis. The extent of variation observed at this location in the presence and alignment of the enlarged dorsal tubercles of the body highlights the difficulty in determining the identity of individuals on this character alone where the original tail has been lost.

Conversely, most of the specimens and images of individuals from the population in the Eyre Peninsula and adjacent areas in South Australia have the line of enlarged dorsal tubercles between the insertions of the limbs continuous and wavy over most its length (Figure 7A–B), and the enlarged dorsal tubercles of the tail spinose in appearance (Figure 7A and C). Images of live individuals of this population typically have a light to mid ground colour with enlarged dorsal tubercles of the body and tail tan to dull orange.

Populations in Western Australia have fewer enlarged ciliary scales (2–5, mode 3) than those on the Eyre Peninsula (4–7, mode 5) and in the eastern Great Victoria Desert region (5–6, mode 5) of South Australia.

DISTRIBUTION

Strophurus assimilis has been recorded in Western Australia as far north as Mount Manning Range (29.9833°S), Bungalbin Hill area (30°S) and the vicinity of Menzies (29.916°S), south to McDermid Rock (32.0555°S) and Norseman area (32.147°S), and east to Queen Victoria Spring (123.6833°E) and Zanthus (123.56677°E) (Figure 4A). In South Australia it been recorded from sites on the western coast and adjacent interior of Eyre Peninsula, extending into the Queen Victoria Desert as far east as the Kimba area and as far west as Maralinga (131.58719°E) (Figure 4B).

HABITAT

Data associated with records of *Strophurus assimilis* in the WAM collection note it as being recorded from the following habitats. In the north of its range in Western Australia from 'mallee with spinifex on red brown sand' at Goongarrie Station (R145897), 'red sand dunes spinifex shrublands' just south of Menzies (R100520), whereas the population from further west just north-east of Bungalbin Hill occurred in 'heath/banksia' (R76141, R76218–19, R76226–27) and 'heath/mallee' (R76195). The population from the more arid interior to the east near Queen Victoria Spring was recorded from 'mallee with spinifex on red brown sand' (R48652), 'mallee spinifex' on 'red brown sand' (R48657–58), 'open marble gum woodland over *Triodia basedowii*' (R100621), and — '*Acacia helmsii*, *Hakea francisiana*, *Grevillea* spp., *Allocasuarina* spp., some *Eucalyptus mannensis* and *E. gonglyocarpus*' (R99605–06).

Further south in its range the species has been recorded from a 'callitris heath isolate' near Boorabbin (R72267, R74418–20), 'low heath on yellowish soil' near Yellowdine (R61322), 'open sedges and grasses on granitic soils' at Boodarding Rock (R78765–66), 'acacia shrubland near granite outcrop' near Woolgangie (R78724), '*E. salmonophloia* woodland' near Heartbreak Ridge (R72362), and 'samphire' (R74295) and '*C.* [= *Allocasuarina*?] *campestris* heath' (R74294) near McDermid Rock.

DISCUSSION

Two recent phylogenetic studies, one by Nielsen et al. (2016) investigating the evolution of defensive strategies in *Strophurus* and the other by Skipwith et al. (2019) on the relationships of diplodactylids and carphodactylids, included samples of *Strophurus assimilis* as it was conceived then.

Nielsen et al. (2016) included five samples of our redefined *Strophurus assimilis*, but no samples of *Strophurus spinula* sp. nov. Their study recovered a well-supported sister relationship between *S. assimilis* s.s. and *Strophurus strophurus* in their phylogenetic analysis based on a concatenated mitochondrial (mtDNA) and nuclear (nDNA) data set. However, this result was not recovered in any analyses of nuclear data alone and was regarded as indicative of mtDNA introgression between the two species, which were then regarded as overlapping geographically. Our study also found a sister relationship between *S. assimilis* and *S. strophurus* in the analysis of the concatenated ND2 mtDNA and RAG1 nDNA data set, and for ND2 alone, but not for RAG1 alone, also supporting the potential introgression between the two species. However, our revised *S. assimilis* is largely parapatric with *S. strophurus*, rather than overlapping with it in distribution as stated by Nielsen et al. (2016).

Skipwith et al. (2019) used a similar suite of *Strophurus* species in their study based on Ultra Conserved Elements, but their sample of *Strophurus assimilis*, a specimen (WAM R154745) from Mt Gibson, is here recognised as *Strophurus spinula* sp. nov. That study placed *S. spinula* sp. nov. (as *S. assimilis*) within a group that also included *Strophurus intermedius*, *Strophurus spinigerus* and *Strophurus rankini*, a result consistent with our study (Figure 1). Further, Skipwith et al. (2019) also found the spineless *Strophurus strophurus* to be the sister to the 'spiny-tailed' species, a result also consistent with our study, and consistent with its similarities to other 'spiny-tailed' species in overall appearance, colour and behaviour, despite lacking tail spines.

ACKNOWLEDGEMENTS

We are grateful to Paul Doughty (WAM) for assistance with images that assisted in defining the distributions of *Strophurus spinula* sp. nov. and *Strophurus assimilis*, to Anders Zimny and Ray Lloyd for the use of images of *Strophurus spinula* sp. nov., and to Jules Farquhar for images of *Strophurus assimilis* from Eyre Peninsula. Aaron Bauer was supported by the Lemole Endowed Chair Funds through Villanova University.

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MANUSCRIPT RECEIVED 15 DECEMBER 2022; ACCEPTED 29 MARCH 2023.

APPENDIX 1

Specimens used in compiling the description *Strophurus spinula* sp. nov. and redescription of *Strophurus assimilis* are marked with a single asterisk (*), specimens used in the genetic analysis only with a double asterisk (**), and those used in both morphological study and genetic analysis by a triple asterisk (***) – the remaining specimens of these species listed were examined for key diagnostic features only and were used in compiling the distribution map (Figure 4). Specimens of *Strophurus intermedius* examined in the morphological study are listed below, as are other species used in the genetic analysis. Western Australia is abbreviated to WA, and South Australia to SA.

Strophurus spinula sp. nov.

Type material (all WA): WAM R135136*** (holotype) Rosemont (27.9308°S, 122.3181°E); WAM R112107*** (paratype) Paynes Find, 20 km SW (29.2858°S, 117.4808°E); WAM R144778* (paratype) Bungalbin Hill area (30.3333°S, 119.6833°E); WAM R144779*** (paratype) Bungalbin Hill area (30.3333°S, 119.6833°E); WAM R136609***, R136610*** (paratypes) Lake Mason Station (27.5650°S, 119.4297°E); WAM R136771* (paratype) Lake Mason Station (27.5275°S, 119.4722°E); AMS R150638*** (paratype) Menzies, 7 km NE of Menzies (29.65°S, 121.05°E); WAM R117157* (paratype) Dead Horse Rocks, 6.5 km N Menzies (29.3666°S, 121.2833°E); WAM R140417*** (paratype) Leinster Downs Station (28.1561°S, 120.6931°E).

Other material WAM (all WA): R1304 Laverton (28.6333°S, 122.4000°E); R20652–53 White Cliffs (28.4333°S, 122.9500°E); R48340 48 km N Beacon (30.0000°S, 117.8333°E); R49283 (paratype) SW slope of Mount Wardiacco (28.9833°S, 118.2167°E); R53290 10 km SW Kookyne (29.4000°S, 121.4167°E); R53335 White Cliffs HS (28.4333°S, 122.9500°E); R60922–23 (paratypes) Paynes Find (29.2500°S, 117.6833°E); R67122 12 km NNE Bungalbin Hill (30.3000°S, 119.7167°E); R69068–70 1 km N Yuinmery HS (28.5500°S, 119.0167°E); R75576 Yalgoo (28.3500°S, 116.6833°E); R76034–35, R76044–47 4 km NNE Mount Jackson (30.2166°S, 119.2667°E); R85442–43 White Cliffs HS (28.4333°S, 122.9500°E); R86639 28 km S Leonora (29.1333°S, 121.3333°E); R117157 Dead Horse Rocks, 6.5 km N Menzies (29.3666°S, 121.2833°E); R131632 Ninghan Station [Wangarra Rock] (29.4169°S, 117.2828°E); R1366368 Lake Mason Station (27.5275°S, 119.4722°E); R154745 Mount Gibson (29.5750°S, 117.1603°E).

Other material CAS (all Western Australia): 261055** Menzies, 2.9 km S (29.71472°S, 121.04283°E); 261068** Leonora, 42.2 km S (29.26392°S, 121.29036°E).

Strophurus assimilis

Referred material WAM (all WA): R15213 Queen Victoria Spring (30.4333°S, 123.5667°E); R17859 Coolgardie (30.9500°S, 121.1667°E); R26755–56 Dedari (31.0833°S, 120.6833°E); R58709 4 km S Queen Victoria Spring (30.4666°S, 123.5667°E); R64783 Mount Manning Range (29.9833°S, 119.6000°E); R65322 3.7 km SW McDermid Rock (32.0486°S, 120.7111°E); R65901–02 3.5 km NE Comet Vale (29.9000°S, 121.5000°E); R67109 (paratype) 16 km NE Bungalbin Hill (30.2666°S, 119.7333°E); R67124, (paratype) 12 km NNE Bungalbin Hill (30.3000°S, 119.7167°E); R67174, 72165, 72167–70, R72213 (paratypes) 15 km NE Bungalbin Hill (30.2930°S, 119.7333°E; R67184 (paratype) 20 km NE Bungalbin Hill (30.2500°S, 119.7667°E); R72164 (holotype) 15 km NE Bungalbin Hill (30.2930°S, 119.7333°E); R72267 near Boorabbin (31.2500°S, 120.2333°E); R74294–95 6.3 km SW McDermid Rock (32.0555°S, 120.7111°E); R74418–21 23 km SSW Boorabbin (31.2500°S, 120.0667°E); R76218–19, R76226–27 (paratypes) 15 km NE Bungalbin Hill (30.2833°S, 119.7333°E); R78694 (paratype) 10 km ENE Mount Manning Range (SE Peak) (29.9666°S, 119.7500°E); R87863 Wanaway Well, 15 km SW Widgiemooltha (31.6000°S, 121.466°E); R99605–06 Queen Victoria Spring Nature Reserve (30.2333°S, 123.6833°E); R99895 Bungalbin Hill (30.4000°S, 119.6333°E); R100520*** 15 km SW Menzies (29.8333°S, 120.9167°E); R100621 25 km NNE Queen Victoria Spring (30.2333°S, 123.6833°E); R111224 Bungalbin Hill (30.2833°S, 119.7500°E); R112874 Ora Banda (30.3994°S, 121.1239°E); R121224 Bungalbin (30.2833°S, 119.7500°E; R126363 Bungalbin Sand Plain (30.2950°S, 119.7419°E); R126392, R126398**, R126402, R126404 Bungalbin Sand Plain (30.2950°S, 119.7419°E); R127565*** Goongarrie (29.9633°S, 121.0750°E); R132865 5 km NE Dedari (31.9500°S, 120.6167°E); R135205 10 km NW Norseman (32.1602°S, 121.7417°E); R144128 7 km NW Broad Arrow (30.4275°S, 121.2600°E); R145897*** Goongarrie Station (29.9680°S, 121.0250°E).

Referred material SAMA (all SA): R20749–50*** Port Kenny (33.17°S, 134.68°E); R40834*** 8 km NW of Port Kenny (33.12°S, 134.61°E); R40834* 8 km NW of Port Kenny (33.1167°S, 134.6125°E); R40835* 1.5 km NW of Port Kenny (33.16°S, 134.67°E); R40979** 5 km NW of Witera, on Flinders H/way; R42982* 5 km NW of Port Kenny (33.13°S, 134.63°E); R43033* 5 km NW of Port Kenny (33.13°S, 134.63°E); R45555*** 16.5 km NNE of Inila Rockwater (31.63°S, 133.45°E); R45561*** 16 km NNE of Inila Rockwater (31.65°S, 133.49°E); R45562*** 26 km N of Inila Rockwater (31.54°S, 133.40°E); R52627* Pinkawillinie Conservation Park (33.06°S, 135.79°E); R56630*** 1.2 km E (92 Deg) Corrobinnie Hill (32.99°S, 135.75°E); R61316*** 8.2 km NNW Oak Hill (32.13°S, 134.33°E); R61578* 16.2 km NE Pinbong Trig, Pinkawillinie Conservation Park (32.86°S, 135.50°E); R65776* 1 km E Maralinga (30.16°S, 131.59°E); R67583* 20.6 km N Koonibba Community (31.72°S, 133.44°E); R68101* 57.45 km SW Ooldea (30.78°S, 132.30°E).

Referred material AMS (all WA): R149832*** 17.6 km W Bonnie Vale Rail Stn. via road 3.8 km N Bonnie Vale (30.80°S, 120.98°E); R150639*** Menzies, 26.3 km SSE Menzies (29.92°S, 121.12°E); R150641* Dedari (31.08°S, 120.68°E); R168536*** Jimberlana Hill, 7 km E of Norseman (32.147°S, 121.81122°E).

Referred material CAS (all WA): 261075** 11 km E of Barra Road junction and Spargoville Road (31.18243°S, 121.21506°E); 261076** 21.4 km east of Barra Road junction and Spargoville Road (31.19257°S, 121.32133°E).

Strophurus intermedius

Material examined SAMA: R5956A, 5956B, 5956C Fraser Range WA (31.97°S, 122.87°E); R63254 Eyre Highway at Fraser Range WA (31.02°S, 122.82°E); R46265 Whyalla Conservation Park SA (32.95°S, 137.56°E); R47557 2 km NW of Iron Chieftain SA (33.17°S, 137.13°E); R61335 2.7 km ESE Wiabuna SA (31.97°S, 133.56°E); R61434 15.0 km NNE Coorabie SA (31.81°S, 133.10°E); R61528–29 23.1 km WSW Coorabie SA (31.90°S, 132.05°E); R68181 23 km NW Whyalla SA (32.89°S, 137.39°E); R26483 67.5 km NW Cook SA (30.07°S, 130.07°E); R63073 8.5 km N Peelunibee Water SA (31.36°S, 131.18°E); R63094 1 km NE Peelunibee Water SA (31.43°S, 131.18°E); R63099 3.4 km N Peelunibee Water SA (31.41°S, 131.20°E); R63372 16.6 km ENE Colona SA (31.59°S, 132.23°E); R63454 35.9 km WSW Yalata Roadhouse SA (31.56°S, 131.44°E); R63467 22.0 km NNE Nundroo SA (31.60°S, 132.29°E).

Material examined AMS: R100544 Newman Rocks WA (32.12°S, 123.17°E); R115725 Pt. Parham SA (34.43°S, 138.27°E); R168533–35 Newman Rocks WA (32.12°S, 123.98°E).

Incertae sedis

Material examined WAM (all WA): R15214 '10 miles' E Zanthus (31.0333°S, 123.5667°E); R48652 1–3 km N Queen Victoria Spring (30.4166°S, 123.5667°E); R48657–58 2–4 km N Queen Victoria Spring (30.4000°S, 123.5667°E); R72112 12 km NNE Bungalbin Hill (30.3000°S, 119.7167°E); R72166 15 km NE Bungalbin Hill (30.2930°S, 119.7333°E; R121235, Bungalbin (30.2833°S, 119.7500°E; R130847 Beacon Area (30.2375°S, 118.3028°E).