



<http://dx.doi.org/10.11646/zootaxa.3878.1.3>

<http://zoobank.org/urn:lsid:zoobank.org:pub:9D0BF37E-B384-46A1-A9E5-10412F70D208>

A new phasmid gecko (Squamata: Diplodactylidae: *Strophurus*) from the Arnhem Plateau: more new diversity in rare vertebrates from northern Australia

PAUL M. OLIVER¹ & TOM PARKIN^{2,3}

¹Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia; Museum Victoria, GPO Box 666, Melbourne, Victoria 3001, Australia; Australian National University, Research School of Biology, Acton, Australian Capital Territory, 2061.

E-mail: paul.oliver@anu.edu.au

²Museum & Art Gallery of the Northern Territory, GPO Box 4646, Darwin, Northern Territory 0801, Australia.

E-mail: elapideco@gmail.com

³Corresponding author

Abstract

The Arnhem Plateau is a rugged expanse of sandstone escarpment in the Australian Monsoonal Tropics with a highly endemic biota. Here we describe a new species of small spinifex dwelling *Strophurus* (phasmid gecko) that also appears to be endemic to this region. *Strophurus horneri* sp. nov. can be diagnosed from all congeners by aspects of size, coloration and scalation. Even with the description of this new species, however, levels of morphological and genetic diversity within *Strophurus* from the stone country of the Northern Territory suggest additional divergent lineages are present. A number of recent studies have now provided preliminary evidence of evolutionary diversity within the Arnhem Plateau, but data remains scant and almost nothing is known about how topography and historical processes have shaped the endemic biota of this region.

Key words: Australian Monsoonal Tropics, endemism, lizard, Kakadu National Park, sandstone, spinifex

Introduction

The Arnhem Plateau is a rugged, spectacular and iconic block of deeply dissected sandstone escarpment that extends over an area of approximately 32,000 km² in the ‘Top End’ region of the Australian Monsoonal Tropics (AMT). The plateau is composed of geologically stable sandstones of varying height (100–400 m a.s.l.) and is environmentally and geologically distinct from surrounding landscapes (Nott 1995, Fig. 1). This unique geology and its associated microclimates has shaped a distinctive biota including numerous endemic taxa (e.g. 2 amphibians, 11 reptiles, 4 birds, 2 mammals and nearly 170 plants) (Woinarski *et al.* 2009). However, the region still remains very poorly documented by scientists—little is known about the history and origin of endemic lineages, and almost nothing is known about intraregional patterns of phylogeographic diversity.

Strophurus Fitzinger is an Australian endemic genus of climbing geckos characterised by unique caudal glands with the ability to exude a viscous distasteful substance (Greer 1989; Melville *et al.* 2004; Wilson & Swan 2013). Five species of *Strophurus* (*S. elderi* (Stirling & Zeitz), *S. jeanae* (Storr), *S. mcmillani* (Storr), *S. robinsoni* (Smith), and *S. taeniatus* (Lönnberg & Anderson)) appear to exclusively occupy spinifex (*Triodia* spp.) hummock grass clumps in arid, semi-arid, and monsoon tropical landscapes spanning the northern half of Australia (Storr 1978; How *et al.* 1986; Wilson & Swan 2013). The last four of these form a natural group (S. Nielsen, unpub. data) that is colloquially referred to as ‘phasmid geckos’ owing to their resemblance to stick insects (Phasmatidae) in their elongate and gracile proportions, camouflage and movement.

Phasmid geckos have also been known from the Arnhem Plateau for over a decade (I. Morris, pers. comm.), but have not been considered in recent popular guides (e.g., Wilson & Swan 2013). Given their apparent disjunction from other phasmid geckos, and the high endemism on the Plateau, it has been suspected that these

animals might represent a distinct taxon. Here we present genetic and morphological evidence for the presence of a distinct lineage and formally describe it as a new species.

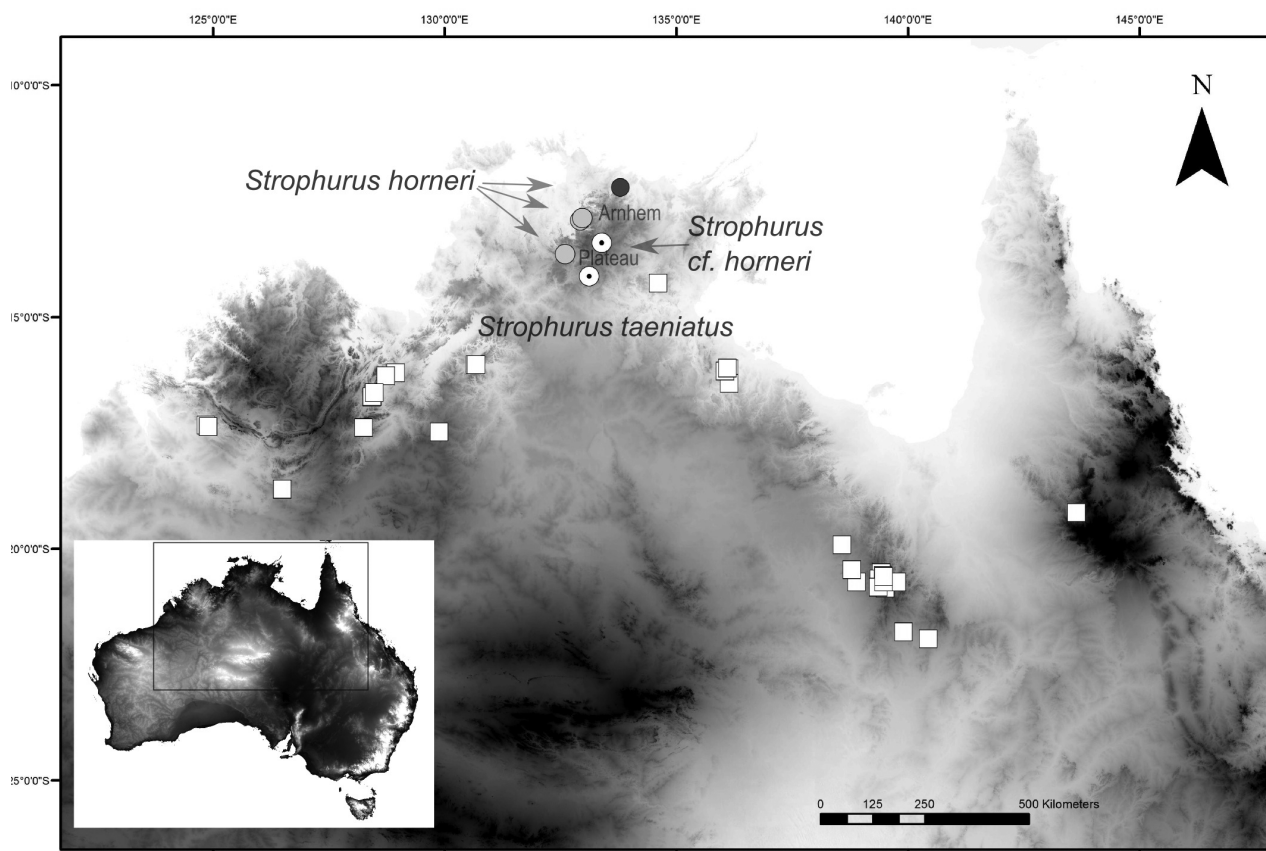


FIGURE 1. Map of northern Australia showing position of the Arnhem Plateau (dark grey region at centre top of Australia), and localities for the single voucher of *Strophurus horneri* sp. nov. (dark grey circle), sites for additional material of *Strophurus horneri* sp. nov. (grey circles) and *Strophurus cf. horneri* (white circles with central dot), and museum records for *Strophurus taeniatus* (white squares) from across northern Australia.

Materials and methods

Genetics. As part of broader investigations into the systematics and diversity of *Strophurus* (R. Laver, S. Nielsen unpub. data) we amplified sequence data including samples of all recognised species of phasmid geckos, including two samples of *Strophurus* sp. from the Arnhem Plateau (NMV D72591, and a tail from a specimen collected and released at Namarragon Gorge; see below), four samples of *Strophurus taeniatus* (NTM R36750–51, SAMA R55298, WAM R162452), and a single exemplar of *Strophurus robinsoni* (WAM R156743) (Genbank numbers KMO16842–8). Data for other recognized taxa (*S. jeanae*, originally mislabelled as *S. taeniatus*, and *S. mcmillani*) was downloaded from GenBank (Melville *et al.* 2004).

New samples were extracted using Qiagen high throughput extraction robot at Museum Victoria. A 900–1200 bp region of the *ND2* gene and surrounding tRNAs was amplified using one of the following two combinations of primers: 1) AAG CTT TCG GGG CCC ATA CC (L4437; Macey *et al.* 1997) and CTA AAA TRT TRC GGG ATC GAG GCC (Asn-tRNA; Read *et al.* 2001); or 2) GCC CAT ACC CCG AAA ATS TTG and TTA GGG TRG TTA TTT GHG AYA TKC G (Oliver *et al.*, 2007). PCR products were amplified for 40 cycles at an annealing temperature of 55°C. Unpurified products were sent to a genetic services company (Macrogen, Korea) and sequenced in both directions. These data were aligned with sequence data published by Melville *et al.* (2004) and downloaded from GenBank. Our final alignment included 867 bp of data and was aligned using the MUSCLE algorithm (Edgar 2004) implemented in Geneious version 6.0.5 (Biomatters 2012), and subsequently checked by

eye and translated to check for misplaced stop codons and reading frame shifts. We calculated genetic distance data using MEGA v5.0 (Tamura *et al.* 2011).

Morphology. We examined material in the Australian Museum (AMS), Museum and Art Gallery of the Northern Territory (MAGNT), Museum Victoria (NMV), Queensland Museum (QM), and Western Australian Museum (WAM). Measurements were recorded to the nearest 0.1 mm using digital calipers as follows: snout-vent length (SVL), total length from tip of snout to the anterior edge of vent; head width (HW), maximum transverse width of the head between eyes and ears; head depth (HD), maximum depth of the head just posterior to the orbitals; head length (HL), from anterior edge of ear to tip of snout; eye to naris distance (EN), from anterior corner of eye to posterior edge of naris; internarial distance (IN), from the inner edges of the nares; transverse length of eye (EYE); axilla to groin distance (Trk), from the posterior edge of the forelimb insertion to the anterior edge of the hindlimb insertion; length of lower arm (Crus), from bent elbow to bent wrist; length of lower leg (Tibia), from bent knee to bent heel; tail length (TL); maximum tail width (TW) and depth (TD); and maximum width of the 3rd finger (3FW) and 3rd toe (3TW) on the left side.

The following scalation data was also recorded: number of supralabials (SuL), to rictus of jaw and midpoint of eye (on left and right side); infralabials (InL), to rictus of the jaw; length of rostral crease (RC), as a percentage of rostral height; number of postocular spines on left and right (PS); total number of enlarged cloacal spurs (CS), on left and right side; and total number of rows of enlarged lamellae (more than twice the width of surrounding scales) under the the third left finger (FL3) and third left toe (TL3).

Results

Genetic divergences. Mean uncorrected genetic divergence (p-distances) between the two genetic samples of Arnhem Plateau *Strophurus* and their closest relative (*S. taeniatus*) was 13.2% (range 12.5–13.6%). Disjunct samples of *S. taeniatus* from localities spanning Western Australia, the Northern Territory and western Queensland were more closely related to each other (0.2–8.4%) than they were to *Strophurus* from the Arnhem Plateau. The other recognized taxa of phasmid gecko (*S. jeanae*, *S. mcmillani* and *S. robinsoni*) were more highly divergent (19.5–23.1%). Genetic divergence between the two samples from the northern Arnhem Plateau was also quite high (8.8%).

Morphology. The single whole and genotyped specimen of *Strophurus* from the Arnhem Plateau (Figures 2–3) could be distinguished from all other named spinifex *Strophurus* (including *S. taeniatus*) by the combination of its very small size (SVL < 40 mm), rostral separated from the nostril by an internasal scale, rostral not divided by a strongly defined medial groove, its high number of relatively small supralabials (13–15), and very weakly striped venter.

Life photographs of the holotype (Fig. 3), a further specimen photographed in southern Kakadu (Fig. 4A) and the genotyped but uncollected specimen from Namarragon Gorge (Fig. 4B), show that they all have a similar colour pattern of four broad yellow longitudinal stripes on a darker greyish or brown background. This pattern is not observed in *Strophurus taeniatus*, which is variable, but usually has greyish base colouration with three wide brownish stripes (two lateral, one dorsal) and much thinner yellow stripes (Fig. 4C). This yellow pigmentation is not apparent in preservative.

Two additional specimens of *Strophurus* from the southern and central Arnhem Plateau (held at MAGNT) differ in having a short rostral crease and a distinct plain brownish colouration with very weak lateral longitudinal striping. No photographs of these specimens in life are available and it is difficult to assess if their plain colouration is an artifact of preservation. These specimens also do not conform with *S. taeniatus* (they lack a complete rostral crease, have no or very weak dorsal and ventral striping and have a high number of relatively small supralabials) (Table 1).

TABLE 1. Meristic and mensural data of museum material of phasmid geckos, *Strophurus*, from the Arnhem Plateau, Northern Territory, Australia.

	<i>S. horneri</i> sp. nov.	<i>S. cf. horneri</i>	<i>S. cf. horneri</i>
	NMV D72591	NTM R29670	NTM R26152*
	Holotype		
Sex	F	M	F
SVL	35.7	43.0	34.7
HW	5.6	7.0	5.2
HD	3.6	4.9	3.8
HL	8.8	10.0	8.1
EN	3.3	3.8	2.9
IN	1.5	2.2	1.8
EYE	2.1	2.4	2.4
Trk	17.5	21.0	18.9
Crus	5.2	6.3	5.2
Tibia	6.0	7.8	5.6
TL	24.2	14.3	20.9
TW	3.2	2.0	3.0
TD	2.7	2.0	2.4
3FW	0.7	0.6	Na
3TW	0.8	0.8	Na
SuL-R	13(11)	13(11)	13(11)
SuL-L	15(11)	14(11)	14(11)
InL-R	14	12	14
InL-L	15	14	13
RC	0%	50%	60%
PS	5/3	4/4	3/2
CS	Na	2/3	Na
FL3	4,5,5,6,5	4,6,6,7,5	4,4,6,_,5
TL3	4,4,4,5,5	4,5,6,6,6	Na
HW/SVL	0.16	0.16	0.15
HD/HW	0.64	0.70	0.73
Trk/SVL	0.49	0.49	0.54
EN/EYE	1.57	1.58	1.21
Crus/SVL	0.15	0.15	0.15
Tibia/SVL	0.17	0.18	0.16
TW/TD	1.19	1.00	1.25
TL/SVL	0.68	0.33	0.60

*Specimen in poor condition, hence some characters impossible to accurately score.

Systematics

The single specimen from the northern edge of the Arnhem Plateau is genetically divergent and morphologically distinctive, and on this basis we describe it as a new species below. The other specimens from the southern and central Arnhem Plateau show evidence of potentially significant morphological variation and further material and genetic data is required to resolve the taxonomic placement of these populations (listed in Appendix 1.).

Strophurus horneri sp. nov.

Arnhem Phasmid Gecko

Figs. 2–4B

Holotype. NMV D72591, female, Yirrkakak, west Arnhem Land, Northern Territory, Australia (12°12'14"S, 133°48'03"E), collected by P. Horner, J. Melville & R. Glor, 9 November 2004.

Additional material. Tail tips in ethanol, all from Kakadu National Park, Northern Territory: MAGNT TS0053, Namarragon Gorge, (12°54'39.42"S, 132°56'01.28"E); CCM2502 (13°38'20.67"S, 132°36'17.54"E) and CCM 2572 (12°51'41.40"S, 132°58'45.84"E), both held at the Australian National University, Canberra.

Diagnosis. A very small (SVL ~ 36 mm) and slender-bodied *Strophurus* with a narrow head (HW/SVL 0.15–0.16), no caudal spines or tubercles, rostral separated from the nostril by an internasal scale, a high number of relatively small supralabials (13–15), and body coloration in life consisting of four broad yellow longitudinal stripes on a greyish or brown background. As more specimens of this species are examined it may be confirmed that rostral not or only partially divided by a strongly defined medial groove is another useful diagnostic character. Males of all related taxa (*S. jeanae*, *S. robinsoni*, *S. taeniatus* and *Strophurus* cf. *horneri* from elsewhere on the Arnhem Plateau) also lack post-cloacal or femoral pores, and it is presumed that this species also shares this character state.

Description of holotype. Female with following dimensions (mm): SVL 35.7; HW 5.6; HD 3.6; HL 8.8; EN 3.3; IN 1.5; EYE 2.1; Trk 17.5; Crus 5.3; Tibia 6.0; TL 24.2; TD 2.7; TW 5.6; 3FW 0.7; 3TW 0.8.

A very small (SVL < 40 mm) and slender gecko (Fig. 2). Head wide (HW/SVL 0.16) and flattened (HD/HW 0.64), much wider than body and distinct from neck; snout broadly rounded in dorsal profile, acute in lateral profile, longer than eye (EN/EYE 1.6), loreal region slightly concave, interorbital region and top of snout nearly flat, canthus rostralis indistinct. Eyes large, pupil vertical, fringe of projecting ciliaries extending from anteroventral to posterodorsal edge of eye, longest and distinctly acute at the anterodorsal corner, small slightly recurved postocular spines on right (5) and left (3) sides of the orbital. Ear opening on left near circular, slightly wider than high, opening on right obscured by folded skin. Rostral hexagonal, very flattened, approximately four times as wide as high, without a distinct medial groove, bordered dorsally by two semilunate nasals and two small granular internasals. Nares not in contact with rostral, bordered by semilunate nasal, first supralabial, and two enlarged postnasals; enlarged supralabials 13 on right and 15 left, 11 to midpoint of eye; first supralabial squarish, others tend to be rectangular or oval and somewhat wider than deep, generally no more than twice the height of dorsally adjacent scales. Head, temporal, and nuchal scales very small and granular, dorsal scales on snout noticeably larger. Infralabials 14 on right, 15 on left, all bordered ventrally by 3–4 rows of slightly enlarged scales grading into small granular gular scales, anterior infralabials rounded, as wide as deep, more than twice the depth of adjacent scales, medial and posterior infralabials somewhat rectangular, much wider than high and no deeper than adjacent scale series. Mental rounded, slightly deeper than wide, similar in shape and size to first infralabials, bordered posteriorly by two rounded postmentals.

Body slender and long (TrL/SVL 0.49), near circular in cross-section; ventrolateral folds clearly apparent behind forelimbs, present but less prominent along remainder of torso; body scalation small and granular, dorsum with larger rounded or triangular scales interspersed with much smaller intervening scales, ventral scales relatively homogenous, grading larger medially, medial ventral scales up to twice width of lateral ventral scales.



FIGURE 2. Dorsal and ventral view of holotype of *Strophurus horneri* sp. nov. NMV D72591. Scale bar =1cm. Photograph courtesy Museum Victoria.

Forelimbs moderately long and slender (Crus/SVL 0.15), hindlimbs slightly longer and also slender (Tibia/SVL 0.17). Digits moderately long and well developed, some outer digits on hands and feet have preserved folded inwards making lamellae counts difficult; all digits with expanded subdigital lamellae, 4–5–5–6–5 on left hand, 4–4–4–5–5 on left foot, terminal lamellae paired and distinctly separated from penultimate lamellae, subsequent 2–3 subterminal lamellae much wider than deep, undivided although often with distinct posterior and anterior notches, proximal lamellae smaller and rounded; claws present on all digits, minute, not extending beyond terminal lamellae.

Tail original, broken along dorsal edge of autonomy plane, narrower and shorter than body (TL/SVL 0.68), distinctly inflated, widest around midpoint, slightly flattened (TW/TD 1.2). Caudal scales granular, heterogeneous, consisting of large round scales and much smaller intervening near triangular scales, arranged in relatively distinct segmented rows, much larger ventrally. Cloacal opening with no spurs or swellings.

Colouration in preservative. Base colouration medium to light brownish-grey (Fig. 2); overlain by several darker stripes extending from the base of neck to tip of tail - a broad darker grey vertebral stripe, a pair of very thin brownish-grey paravertebral lines, a pair of broad light grey lateral stripes with distinctly darker edges, and a pair of indistinct thin lower lateral stripes. Head base colouration dark brownish-grey, slightly darker on crown than snout, with indistinct brown flecking and longitudinal lines on the snout, extensive light brown maculations around the supralabials, and a series of postorbital stripes that merge with lateral stripes on the torso. Venter greyish-cream with a few indistinct light brown longitudinal stripes on the anterior torso and numerous brownish spots or flecks on the throat. Limbs distinctly darker than torso on both dorsal and ventral surfaces, with scattered indistinct darker flecks, and faint broad striping on the ventral surface of the hindlimbs. Dorsal and lateral pattern of tail similar to torso with alternating wide vertebral, thin paravertebral and wide lateral stripes on a grey background; ventral surfaces light creamish-grey with three thin darker grey stripes.

Colouration in life. A photograph of the holotype in life (Fig. 3) shows the areas of the dorsum and tail that are very light in preservative have a very clear yellowish wash and form four distinct longitudinal stripes that



FIGURE 3. *Strophurus horneri* sp. nov. in life. Holotype NMVD72591 photographed at Yirrkakak. Photograph courtesy Rich Glor.

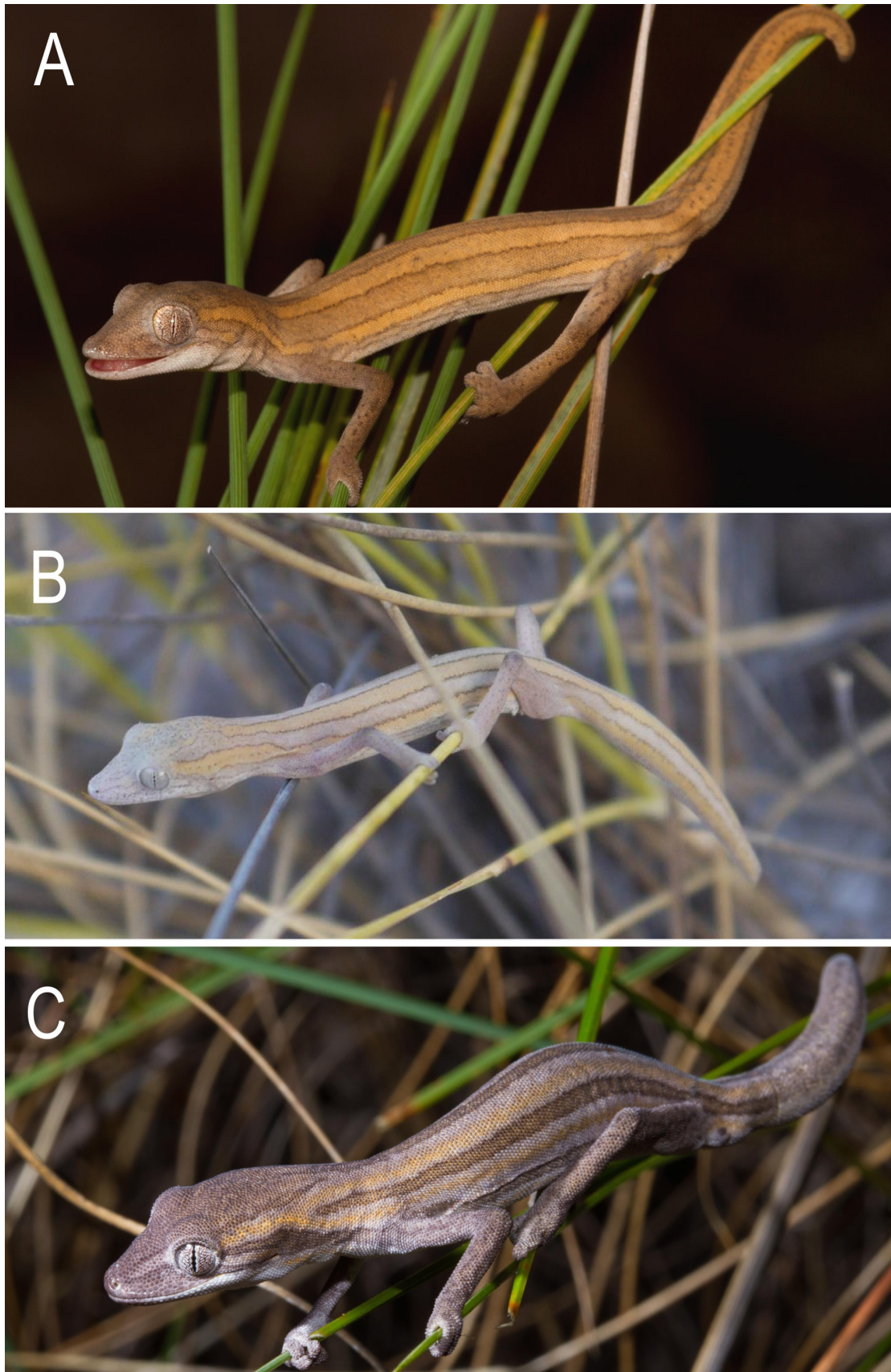


FIGURE 4. A) *Strophurus horneri* sp. nov. seen and photographed in southern Kakadu National Park. Note prehensile tail and pink tongue. Photograph courtesy Brendan Schembri. B) *Strophurus horneri* sp. nov. captured and released at Namarragon Gorge, Kakadu NP. Photograph courtesy Stuart Young. C) *Strophurus taeniatus* from Wongalara Sanctuary. Note thinner yellow lateral stripes. Photograph courtesy Stephen Zozaya.

contrast strikingly against the bordering areas which are light to almost bluish grey with very fine light brown flecking. The iris is light grey with extensive very fine light brown vermiculations, while the pupil is elliptical with distinctly scalloped edges.

Variation. Photographs of additional specimens were kindly provided by Stuart Young and Brendan Schembri (Figs. 4A–B). Both have the same basic dorsal pattern of four yellow longitudinal stripes on a medium grey background. The yellow stripes on these specimens are slightly brighter and their edges are more strongly defined than on the holotype. The posterior dorsum of the head in one specimen also has distinct large yellow maculations (Fig. 4A). The tongue is pink (Fig. 4B).

Comparisons with other taxa. *Strophurus horneri* **sp. nov.** is distinguished from most *Strophurus* (*S. assimilis* (Storr), *S. ciliaris* (Boulenger), *S. intermedius* (Ogilby), *S. krisalys* Sadlier, *S. rankini* (Storr), *S. spinigerus* (Gray), *S. strophurus* (Duméril & Bibron), *S. taenicauda* (De Vis), *S. wellingtonae* (Storr) and *S. williamsi* (Kluge)) by its smaller size (SVL < 50mm) and further differs from most of these species by lacking distinctive rows of tubercles or spines on the tail. It also presumably further differs in lacking post-cloacal or femoral pores, however this needs to be confirmed.

Of the six remaining species of *Strophurus* which lack caudal spines and are generally also found in association with spinifex or other grasses, *Strophurus horneri* **sp. nov.** can be distinguished from *S. elderi*, *S. jeanae*, and *S. michaelseni* (Werner 1910) by the presence of an internasal scale separating the rostral scale from the nostril (vs rostral in contact with the nostril); from *S. mcmillani* by its smaller size (adult SVL ~ 36.0 mm vs 40.3–49.1 mm) and less robust build (HW/SVL ~ 0.15 vs 0.17–0.19); and from *S. robinsoni* by its smaller adult size (SVL ~36.0 mm vs 53.0–56.0 mm), less robust build (HW/SVL ~ 0.15 vs 0.17–0.19), and dorsal pattern consisting of alternating yellow and grey stripes (vs very thin discontinuous dark grey longitudinal striations on a light grey background).



FIGURE 5. Habitat of *Strophurus horneri* **sp. nov.** at Namarragon Gorge, Kakadu National Park. The specimen in Fig. 4B was captured at night in a spinifex clump at this locality. Photograph courtesy Stuart Young.

It differs from its geographically proximate sister species *S. taeniatus* in having smaller and more numerous supralabial scales (13–15 vs 10–12) and four wide yellow longitudinal stripes on a greyish or brown background (vs usually a more complicated pattern of three wide brown stripes and four much thinner yellow stripes). It also tends to have a relatively plain venter and throat pattern of small brown flecks or at most a single very thin continuous longitudinal stripe (vs usually three pairs of near continuous, thin greyish stripes). Some or all populations of *S. horneri* **sp. nov.** may also differ from *S. taeniatus* in having the rostral not or only partially divided by a clear crease, but more material is required to confirm this.

Distribution and habitat. *Strophurus horneri* **sp. nov.** is known only from the Arnhem Plateau region in the Top End of the Northern Territory. The holotype was collected on the northern edge of the Arnhem Plateau in the vicinity of Yirrkakak. Other specimens have been observed at other localities along the western edge of the Arnhem Plateau (Brendan Schembri, Mitchell Scott pers. comm.), and this species may occur throughout the western and northern Arnhem Plateau (Fig. 1).

Where data is available, all specimens were found in well developed spinifex patches on or at the base of large sandstone escarpment or boulders (Fig. 5). The longitudinal striped patterning evident in life provides excellent camouflage in this habitat. Brendan Schembri (pers. comm.) reports that this species was comparatively easy to find in long unburnt spinifex in a sheltered gully in southern Kakadu. The potential role of fire frequency in shaping the distribution and abundance of this taxon warrants further investigation.

Etymology. Named in honor of Dr. Paul Horner, Emeritus Curator of the Museum and Art Gallery of the Northern Territory, in recognition of his significant contributions to Australian reptile systematics.

Discussion

It has not been widely recognised that phasmid geckos occur in the Arnhem Plateau, and the total number of specimens from this area available for research remains very small (Storr 1978; How *et al.* 1986; Wilson & Swan 2013). Recent work elsewhere in northern Australia has also revealed previously undetected populations and cryptic taxonomic diversity in phasmid geckos, and another ecologically similar lineage of very small geckos (*Crenadactylus* Gray) (Oliver *et al.* 2012, Vanderduys *et al.* 2012). These small and relatively secretive taxa seem to be easy to overlook – but also show a propensity for diversifying within the Australian Monsoonal Tropics. Even in this case, the morphological and genetic variation shown by our limited sample of phasmid geckos from the Arnhem Plateau indicates more material and research is certainly required to properly resolve taxonomic boundaries.

This rugged and distinctive sandstone escarpment of the Arnhem Plateau has potentially offered protection to biodiversity from threatening processes such as fire and aridification over evolutionary timescales (Woinarski *et al.* 2009). *Strophurus horneri* **sp. nov.** is the twelfth species of reptile known only from this region (Wilson & Swan 2013) and museum collections indicate that additional unrecognized lizard species are present (P. Horner, pers. comm.). Recent work on two other gecko lineages associated with the plateau has also revealed some evidence of deep intraspecific coalescence times [Oliver 2014 a, b]). These data suggest that not only does species diversity in this region remain underestimated, but also that intraregional processes may have shaped localised patterns of persistence and diversification within the extremely complex topography of the Plateau itself. However, overall patterns of genetic diversification within the escarpment still remain very poorly resolved.

The paucity of genetic material from taxa endemic to the Arnhem Plateau reflects the extreme difficulty in accessing much of this region. However, although remoteness has impeded understanding of regional biogeography, it has not insulated the biota from threatening processes; most notably many mammals have recently undergone severe declines (Woinarski *et al.* 2011). Some large reptiles also appear to have declined – the formerly locally abundant Arnhem Plateau endemic skink *Bellatorias obiri* was last seen by scientists nearly a decade ago even though there have been several targeted surveys (Armstrong & Dudley 2004). A suite of synergistic factors may be involved in these declines. Within the Arnhem Plateau, cessation of traditional Aboriginal burning practices over the last century, and concomitant increases in the frequency and intensity of fire regimes is believed to be a particularly important threat (Russel-Smith *et al.* 2003; Woinarski *et al.* 2009), but introduced predators, herbivores and plants may also be significant (Woinarski *et al.* 2011). The ongoing discovery of endemic diversity

and intraregional genetic variation (such as that shown by the phasmid geckos) suggests that an improved understanding of intraregional biogeography may provide an important context for efforts to conserve the evolutionary diversity of this increasingly threatened region.

Acknowledgements

We thank Andrew Amey, Patrick Couper, Ross Sadlier, Jane Melville, Gavin Dally and Katie Smith for facilitating the loan and examination of specimens, Katie Smith, Rebecca Laver and Stuart Nielsen for providing sequence data, Katie Smith for taking high resolution photographs of the holotype, Rich Glor and Jane Melville for generously allowing us to work on material they collected and for providing a photograph of the holotype in life, Stuart Young, Brendan Schembri and Mitchell Scott for photographs and additional information about the specimens captured in life, Stephen Zozoya for photographs of *Strophurus taeniatus*, and Paul Horner, Ray Lloyd, Dane Trembath, Brendan Schembri for useful discussions. We thank Paul Doughty and an anonymous reviewer for their comments on the manuscript. This work was supported by a linkage grant from the Australian Research Council to Paul Oliver, Michael Lee and Paul Doughty, and a McKenzie Postdoctoral fellowship to Paul Oliver from Melbourne University. All material examined was collected under the relevant state permits and ethics approvals. Recent surveys in Kakadu were supported by the Australian Government funded Long Term Ecological Research Network (LTERN).

References

- Armstrong, M. & Dudley, A. (2004) *The Arnhem Land Egernia, Egernia obiri in Kakadu National Park. Report to Parks Australia North*. Northern Territory Department of Infrastructure Planning and Environment, Darwin. [unknown page number]
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
<http://dx.doi.org/10.1093/nar/gkh340>
- Greer, A. (1989) *The Biology and Evolution of Australian Lizards*. Surrey Beatty and Sons, Sydney, New South Wales, Australia, 264 pp.
- How, R.A., Dell, J. & Wellington, B.D. (1986) Comparative biology of eight species of *Diplodactylus* gecko in Western Australia. *Herpetologica*, 42, 471–482.
- Macey, J.R., Larson, A., Ananjeva, N.B., Fang, Z. & Papenfuss, T.J. (1997) Two novel gene orders the role of light-strand replication in the rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution*, 14, 91–104.
<http://dx.doi.org/10.1093/oxfordjournals.molbev.a025706>
- Melville, J., Schulte, J.A. & Larson, A. (2004) A molecular study of phylogenetic relationships and evolution of antipredator strategies in Australian *Diplodactylus* geckos, subgenus *Strophurus*. *Biological Journal of the Linnean Society*, 82, 123–138.
<http://dx.doi.org/10.1111/j.1095-8312.2004.00324.x>
- Nott, J. (1995) The antiquity of landscapes on the north Australian craton and the implications for theories of long-term landscape evolution. *The Journal of Geology*, 103, 19–32.
- Oliver, P.M., Hugall, A.H., Adams, M.A., Cooper S.J.B. & Hutchinson, M.N. (2007) Genetic elucidation of cryptic and ancient diversity in a group of Australian diplodactyline geckos; the *Diplodactylus vittatus* complex. *Molecular Phylogenetics and Evolution*, 44, 77–88.
<http://dx.doi.org/10.1016/j.ympev.2007.02.002>
- Oliver, P.M., Palmer, R. & Doughty, P. (2012) Hidden biodiversity in northern Australia, the case of the Kimberley clawless geckos (*Crenadactylus*). *Wildlife Research*, 39, 429–435.
<http://dx.doi.org/10.1071/wr12024>
- Oliver, P.M., Smith, K.L., Bauer, A.M. & Laver, R. (2014a) Long-term persistence and vicariance within the Australian Monsoonal Tropics: the case of the Giant Cave and Tree Geckos (*Pseudothecadactylus*). *Australian Journal of Zoology*, 61, 462–468.
- Oliver, P.M., Smith, K.L., Laver, R.L., Doughty, P. & Adams, M. (2014b) Contrasting patterns of persistence and diversification in vicars of a widespread Australian lizard lineage (the *Oedura marmorata* complex). *Journal of Biogeography*. 41 (11), 2068–2079.
<http://dx.doi.org/10.1111/jbi.12364>

- Read, K., Keogh, J.S., Scott, I.A.W., Roberts, J.D. & Doughty, P. (2001) Molecular phylogeny of the Australian frog genera *Crinia*, *Geocrinia* and allied taxa (Anura: Myobatrachidae). *Molecular Phylogenetics and Evolution*, 21, 294–308. <http://dx.doi.org/10.1006/mpev.2001.1014>
- Russell-Smith, J., Yates, C., Edwards, A., Allan, G.E., Cook, G.D., Cooke, P. & Smith, R. (2003) Contemporary fire regimes of northern Australia, 1997–2001: change since Aboriginal occupancy, challenges for sustainable management. *International Journal of Wildland Fire*, 12, 283–297. <http://dx.doi.org/10.1071/wf03015>
- Storr, G.M. (1978) Seven new gekkonid lizards from Western Australia. *Records of the Western Australian Museum*, 6, 337–352.
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution*, 28, 2731–2739. <http://dx.doi.org/10.1093/molbev/msr121>
- Vanderduys, E.P., Kutt, A.S. & Perkins, G.C. (2012) A significant range extension for the northern Australian gecko *Strophurus taeniatus*. *Australian Zoologist*, 36, 20–21. <http://dx.doi.org/10.7882/az.2012.003>
- Wilson, S. & Swan, G. (2013) *A Complete Guide to Reptiles of Australia*. 4th Edition. New Holland Publishers, Sydney, 592 pp.
- Woinarski, J.C., Russell-Smith, J., Andersen, A.N. & Brennan, K. (2009) Fire management and biodiversity of the western Arnhem Land Plateau. In: Russell-Smith, J., Whitehead, P. & Cooke, P. (Eds.), *Culture, Ecology and Economy of Fire Management in North Australian Savannas: Rekindling the Wurrk Tradition*. CSIRO Publishing, Canberra, Australian Capital Territory, pp. 201–228.
- Woinarski, J.C., Legge, S., Fitzsimons, J.A., Traill, B.J., Burbidge, A.A., Fisher, A., Firth, R.S.C., Gordon, I.J., Griffiths, A.D., Johnson, C.N., McKenzie, N.L., Palmer, C., Radford, I., Rankmore, B., Ritchie, E.G., Ward, S. & Ziembecki, M. (2011) The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters*, 4, 192–201. <http://dx.doi.org/10.1111/j.1755-263x.2011.00164.x>

APPENDIX 1. Specimens included in morphological comparative analyses.

Strophurus mcmillani (n = 10): WAM R28186; WAM R43039–41; WAM R43076; WAM R43078; WAM R43226; WAM R43229; WAM R56188; WAM R57323 (all paratypes).

Strophurus robinsoni (n = 4): WAM R67960; WAM R108645; WAM R108647; WAM R156743 (all paratypes).

Strophurus taeniatus (n = 30): AMS R17642; AMS R28435; AMS R48640; AMS R48652; AMS R53390; AMS R53392; AMS R53397; AMS R53439; AMS R53761; AMS R56895–9; AMS R72477; AMS R73059; AMS R125953; NTM R36343; NTMR36750–1; QM J39029; QM J39032; QM J47580; QM J47581; QMJ64459; QM J64483; QM J81097; QM J87493; QM J88151.

Strophurus cf. horneri (n=2): MAGNT R29670; MAGNT R26152.