



Ctenotus rungulla sp. nov. (Scincidae; Sphenomorphinae), a new sandstone-associated skink that highlights reptile endemism in Queensland's Gregory Range



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Abstract

We describe a new sphenomorphine skink, *Ctenotus rungulla* sp. nov., currently known only from sandstone habitats in the Gregory Range of inland northern Queensland. *Ctenotus rungulla* sp. nov. would be identified as *C. brevipes* or *C. terrareginae* using keys available at the time of publication. The new species differs most obviously from the regionally sympatric *C. brevipes* in having 5–6 distinct ear lobules, which are entirely absent in *C. brevipes*. The new species differs from the allopatric *C. terrareginae* in being smaller and in various aspects of colour-pattern. Mitochondrial DNA sequence data, however, indicate that *C. rungulla* sp. nov. is most closely related to the allopatric *C. ingrami*, from which the new species differs in being smaller, lacking a vertebral stripe, possessing a red-orange flush on the hindbody, and in having a higher midbody scale row count. *Ctenotus rungulla* sp. nov. is now the fourth reptile species known to be endemic to the Gregory Range, highlighting the biodiversity values of this remote rocky region.

Key words. *Ctenotus rungulla* sp. nov.; *Ctenotus brevipes*; *Ctenotus ingrami*; Einasleigh Uplands; Gregory Range; sandstone; Queensland.

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<https://zoobank.org/References/AFC2E084-AB29-4956-AD36-BAC635622104>

Introduction

With 109 species recognised at the time of writing (ASH 2023), *Ctenotus* Storr, 1964, (Scincidae; Sphenomorphinae) is the most species-rich genus of terrestrial Australian vertebrates. The number of valid species-level taxa in *Ctenotus*, however, remains uncertain as dense

geographic sampling combined with genome-wide molecular data indicate that some recognised species are conspecific with other nominal taxa, while others likely contain undescribed "cryptic species" (Rabosky et al. 2014; Prates et al. 2023). Reflecting trends in Australian reptile taxonomy generally, taxonomic research on

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Ctenotus since 2010 has largely involved revision of species complexes through detailed genetic analysis of nominal taxa (Rabosky et al. 2014; Kay & Keogh 2012; Rabosky et al. 2017; Prates et al. 2022; Prates et al. 2023). In contrast, here we evaluate, recognise, and describe a new and distinct *Ctenotus* from the Gregory Range of northern Queensland.

The Gregory Range of northern Queensland — part of Australia's Great Dividing Range — stretches from Croydon in the north-west to north of Hughenden in the south-east, forming the southern boundary between the Gulf Plains (GUP) and Einasleigh Uplands (EIU) bioregions (IBRA 2012). Most of the Gregory Range is dominated by sandstone outcrops and escarpments of the Hampstead, Loth, and Gilbert River formations (Foley et al. 2020), with peripheral areas of granite and basalt. These sandstone escarpments follow the edge of the Gilberton Plateau in the southern half of the Gregory Range, becoming more fragmented and dissected to the north. Endemic reptiles have long been known from other sandstone regions in northern Australia, such as the escarpments of the Kimberley and Arnhem plateaus (Wilson & Swan 2021). By contrast, descriptions of reptile species endemic or near endemic to the Gregory Range are recent. At the time of publication, these species are *Lerista vanderduysi* Amey, Couper and Worthington Wilmer, 2016 (in Couper et al. 2016); *Oedura argentea* Hoskin, Zozaya, and Vanderduys 2018; and *Lucasium iris* Vanderduys, Hoskin, Kutt, Wright, and Zozaya 2020. Here we add to this list with the description of a new skink species, *Ctenotus rungulla* sp. nov., so far known only from the sandstones of Queensland's Gregory Range.

An unusual looking *Ctenotus* has been known from the Gregory Range for some time, with Keith McDonald observing individuals in the Rungulla region in the early 2000's, and subsequent observations at Cobbold Gorge (authors pers. obs.), in the vicinity of Agate Creek (M. Anthony pers. comm.), and at Gilberton Station (J. Wright pers. comm.). These observations were generally assigned to *Ctenotus brevipes* Storr, 1981, the only other *Ctenotus* in the area that could be confused with the new species based on colour-pattern and body size. But given the speed and evasive nature of *Ctenotus*, specimens of this putatively undescribed species have, until recently, evaded collection. The first specimen was collected by one of the authors (D. Case) in 2022 on a rocky mesa near Agate Creek, south-west of Forsayth. This specimen (Qld Museum accession [QM] J97908) keyed out to *C. terrareginae* Ingram & Czechura, 1990, using the key available in Wilson (2022) and to *C. brevipes* using the key in Cogger (2014). Preliminary mitochondrial DNA (mtDNA) sequencing of this individual, however, indicated the putative new species to be more closely allied to *C. ingrami* Czechura & Wombey, 1982. This raised questions regarding the identity of the *C. ingrami* paratype WAM R56322 from near Croydon, which is

in the same general region as the new taxa but from woodland rather than rocky habitat and is much further northwest than the nearest *C. ingrami* record (Fig. 1). This highlighted the need for increased survey efforts, additional DNA sequencing, and assessments of morphology to determine the identity of the northern *C. ingrami* and to assess if and how the putative new species differs from *C. ingrami*. Here we recognise and describe *C. rungulla* sp. nov. based on the results of these efforts.

Methods

Targeted field surveys and sampling

Targeted active searches were performed at several sites across the Gregory Range and nearby areas to collect specimens, habitat information, and distributional data on the putative new species. Surveys included areas where the putative new species had been previously observed (e.g., Gilberton Station and the vicinity of Agate Creek) and at several new localities (Table S1; <https://doi.org/10.6084/m9.figshare.25803070>). Searches largely targeted accessible sandstone habitats, but also included nearby open woodland and *Acacia shirleyi* thickets. Several sites of varying habitat types in the vicinity of Croydon were searched to detect and capture putative *C. ingrami* or *C. rungulla* sp. nov., including at a site matching the locality and habitat description of the *C. ingrami* paratype WAM R56322 near Croydon ("*Eucalyptus miniata* – *Acacia* sp. association on a gravelly substrate"). Our goal was to collect fresh tissues to determine the affinities of this presumably outlying population of *C. ingrami*. Specimens were fixed in either 10% buffered formalin (QM J97908–97911) or 100% ethanol (QM J97917–J97918), followed by storage in 70–75% ethanol. Livers were taken as tissue samples prior to fixation and stored in 100% ethanol.

Mitochondrial DNA sequencing and phylogenetics

We sequenced ~700 base pairs (bp) of the mitochondrial DNA (mtDNA) locus coding for the *NADH dehydrogenase subunit 4* protein (*ND4*) for newly collected *Ctenotus* specimens and additional tissue samples obtained from the Queensland Museum (QM) and Sebastian Hofer (James Cook University). The *ND4* protein-coding gene was amplified using the forward primer *ND4*: 5'-TGA CTA CCA AAA GCT CAT GTA GAA GC-3' (Forstner et al. 1995) and the reverse primer *tRNA-Leu*: 5'-TAC TTT TAC CTT GGA TTT GCA CCA-3' (modified from Arévalo et al. 1994). Each PCR occurred in a total volume of 30 µL that included: 15 µL Promega GoTaq G2 Colorless Master Mix, 11 µL MilliQ H₂O, 1 µL of each primer (total 2 µL) at 10 µM concentration, and 2 µL genomic DNA. We used the following protocol for PCR amplification: 95°C 3 min; 10 cycles of 94°C 30 s, 50°C 30 s, 68°C 45 s; 25 cycles of 94°C 30 s, 48°C 30 s, 68°C 45 s; 68°C 3 min; final rest at 10°C. PCR products were sequenced on an AB 3730xl DNA Analyzer at the Genome Discovery Unit, ACRF Biomolecular Resource Facility, John Curtin School

of Medical Research, Australian National University. The resulting chromatograms were trimmed in Geneious Prime 2021.2.2 based on a 0.05 error probability threshold followed by pairwise alignment of the forward and reverse reads to produce a consensus sequence for each sample. The 19 newly sequenced samples (GenBank: PP788563–PP788581) were then aligned to 25 additional *Ctenotus ND4* sequences obtained from GenBank, in addition to one *Lerista bipes* to serve as the outgroup (GenBank: AY169666). Alignment was done using Clustal Omega 1.2.3 implemented in Geneious 2021.2.2 with default settings. The final sequence alignment consisted of 668 bp and included 27 recognised *Ctenotus* species, with a focus on species in north-eastern Australia, especially those morphologically similar to *C. rungulla* sp. nov. All sequences and their associated GenBank accessions (Table S2) are available on Figshare: <https://doi.org/10.6084/m9.figshare.25803070>.

Using this alignment, we performed a maximum-likelihood phylogenetic analysis using IQ-TREE version 2.2.0 (Minh et al. 2020). ModelFinder (Kalyaanamoorthy et al. 2017) was used to determine the best substitution model (TPM2+F+I+G4). Branch support was obtained via 1000 ultrafast bootstrap (UFB) replicates (ufboot2; Hoang et al, 2018). Pairwise sequence distances were calculated across all samples by dividing the pairwise number of nucleotide differences by the total alignment length (668 bp).

Morphology

Morphometric and scalation data were taken from the six preserved specimens of what we herein describe as *C. rungulla* sp. nov. (QM J97908–97911; J97917–97918) and the *C. ingrami* paratype WAM R56322 from near Croydon. Colour-pattern was assessed visually using photographs of specimens in life and in preservative, with a focus on the presence, number, and position of stripes and spots. Comparisons with other species were done using information available in published taxonomic works (i.e., Ingram 1979; Czechura & Wombey 1982; Ingram & Czechura 1990; Horner 2007; Couper et al. 2002).

Morphometrics. One of us (SMZ) recorded the following linear measurements using Mitutoyo digital callipers to the nearest 0.1 mm: snout-to-vent length (SVL), from the tip of the snout to the posterior edge of the cloaca (which was also confirmed using a clear plastic ruler); tail length (TL; done using ruler), from the posterior edge of the cloaca to the tip of the tail; trunk length (TrunkL), from the posterior insertion of the forelimb to the anterior insertion of the hindlimb; head length (HL), from the tip of the snout to the anterior edge of the ear opening; head width (HW), measured as the widest point of the head posterior to the eyes and anterior to the ear opening; head depth (HD), the deepest point of the head, approximately in line with the eyes,

measured transversely; snout length (SnL), from the tip of the snout the anterior margin of the orbit; forelimb length (FLL), measured from the elbow to wrist with each of these bent to a 90° angle; hindlimb length (HLL), similar to FLL, with knee and ankle bent; length of the fourth toe (4TL), measured from the tip of the claw to the corner between the third and fourth toes. Limb length in *Ctenotus* typically measured from the insertion of the limb to the tip of the longest digit (e.g., Prates et al. 2022), which reflects the entirety of the limb. In attempting this, however, we found it difficult to keep limbs sufficiently straight and could not closely replicate this measurement multiple times on the same individual. For this reason, we use ilio-tibia length as a proxy for hindlimb length, and radio-ulna length as a proxy for forelimb length. Measurements were taken on the right side, where relevant.

Scalation. We recorded the following scale counts and character states: mid-body scale rows (MBSR); the number of individual nuchal scales (rather than nuchal pairs); the number of supralabial scales; the number of infralabial scales; the supralabial scale present immediately below the eye; the number of supraoculars; the number of supraciliaries; whether the parietals are in contact; interparietal free or fused; the presence and number of pre-suboculars; paravertebral scale rows, counted from the first nuchal to the last paravertebral scale in line with the posterior margin of the hindlimb; number of lamellae on the underside of the fourth toe; whether and to what extent scales on the top of the fourth toe are divided by oblique sutures; the degree to which lamellae on the fourth toe are keeled, with or without a fine distal point; number of ear lobules, their relative size, and the degree to which they are blunt or pointed. Scale names are as defined in Horner (1991).

Results

Targeted field surveys

Outcomes of targeted *Ctenotus* searches are listed in Table S1, including locality and habitat details. Note that these were active searches (in daytime) rather than trapping surveys. Details of localities, habitat descriptions, and overall distribution (Fig. 1) for the new species are detailed in the species description below. A total of six specimens of what we describe herein as *C. rungulla* sp. nov. were vouchered from three localities: Gilbert River Reserve for Natural Resource Management, near Agate Creek ($n = 3$, including the original specimen); Gilberton Station ($n = 1$); and Hampstead Springs Station ($n = 2$). These cover three of the four known localities for this species, with no specimens collected from Cobbold Gorge Nature Refuge. All specimens originated from areas of sandstone escarpment in open woodland (Fig. 2). Notably, surveys near Croydon did not yield any *Ctenotus* matching the appearances of either *C. ingrami* or *C. rungulla* sp. nov., despite high *Ctenotus* activity (*C. spaldingi* & *C. brevipes*; Table S1). These searches includ-

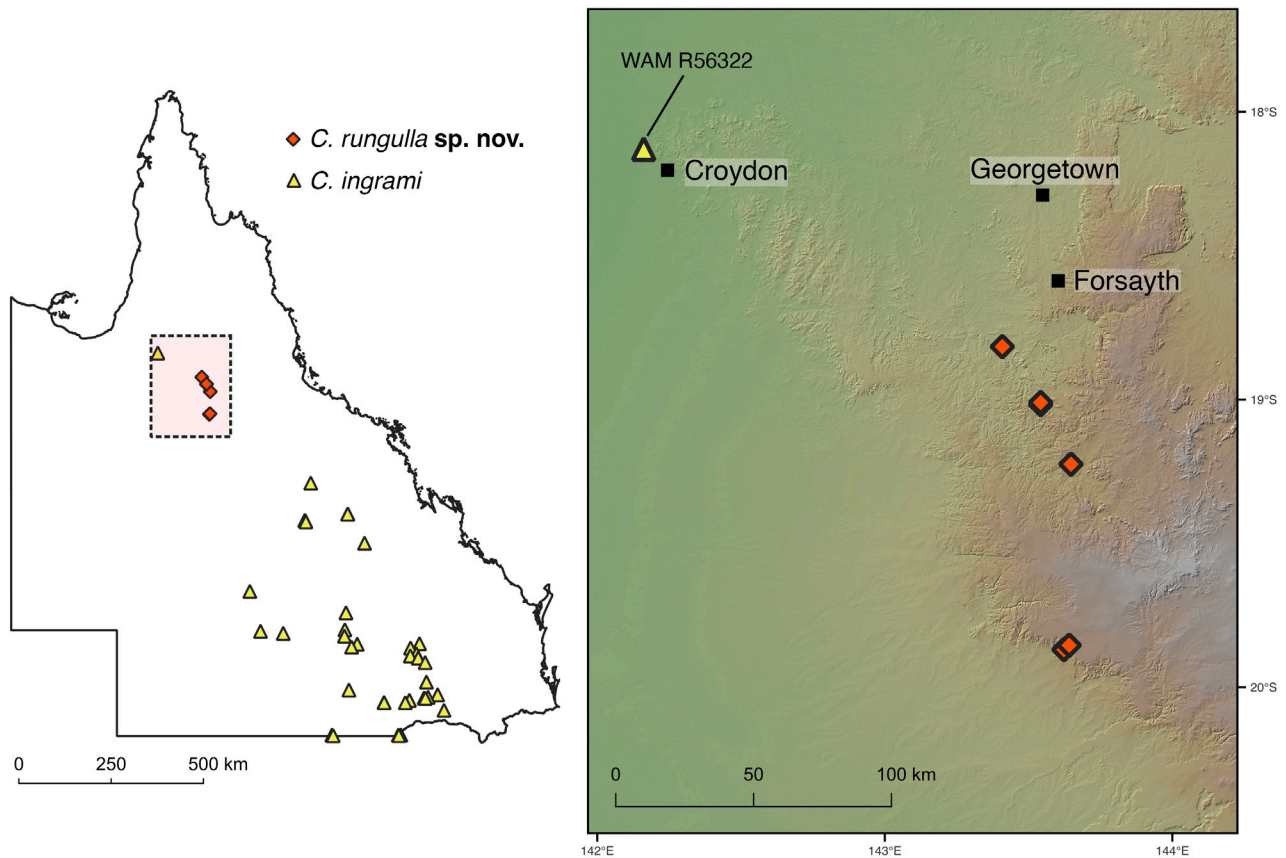


Figure 1. Geographic records of *Ctenotus rungulla* sp. nov. and *C. ingrami* across Queensland (left) and centred on the Gregory Range in central-northern Queensland (right). The map on the right uses hill-shading and an elevational colour gradient to illustrate the topographic complexity of the Gregory Range and neighbouring areas. The northernmost point for *C. rungulla* sp. nov. reflects observational records at Cobbold Gorge with no associated specimens or samples.

ed two active surveys at a site ca. 12 km west of Croydon in Woollybutt-*Acacia* woodland on gravelly soil matching the collection site description for *C. ingrami* paratype WAM R56322, and at several other nearby sites listed in Table S1.

mtDNA divergence and relationships

Figure 3 shows the results of maximum-likelihood phylogenetic analysis via IQ-TREE. The six sequenced individuals of *C. rungulla* sp. nov. form a fully supported, monophyletic lineage that is recovered as sister to *C. ingrami* with strong support (UFB = 97). Branches deeper in the tree are generally recovered with low to modest support. Curiously, but not strictly relevant to our study, *C. nullum* is recovered within *C. inornatus* — possibly indicating the taxonomy of the *inornatus* group is even more complicated than previously shown (see Prates et al. 2023).

Pairwise sequence divergence between *C. rungulla* sp. nov. and *C. ingrami* ranges from 10.03–10.93% (mean 10.53%) for the *ND4* locus. This is greater than or similar to average levels of sequence divergence observed for several other species pairs, for example: *quinkan* vs. *rawlinsoni* (6.59%); *eutaenius* vs. *lateralis* (7.54%); *superciliaris* vs. *inornatus* (8.98%); *eutaenius* vs. *inornatus* (9.58%);

burbidgi vs. *superciliaris* (10.18%); *arcanus* vs. *terrareginae* (10.4%). Pairwise sequence dissimilarity among samples of *C. rungulla* sp. nov. is low, ranging from 0–1.05% (mean 0.55%). The full dissimilarity matrix is available on Figshare (<https://doi.org/10.6084/m9.figshare.25803070>).

Morphology

In concordance with mtDNA data, the overall appearance of what we herein describe as *C. rungulla* sp. nov. is similar to *C. ingrami*. The new species, however, is different and diagnosable with respect to body size, colour-pattern, and the number of midbody scale rows. *Ctenotus rungulla* sp. nov. would be identified as *C. brevipes* using the key in Cogger (2014) but differs from this species in having 5–6 distinct ear lobules, which are absent in *C. brevipes*. The key in Wilson (2022) would identify the new species as *C. terrareginae*, which is larger and differs in various aspects of colour-pattern (see 'Comparison with nearby congeners' section below). Data on morphometrics and scale counts for the six specimens of *C. rungulla* sp. nov. and *C. ingrami* WAM R56322 are listed in Table 1; these data and further information on colour-pattern, scale characters, and comparisons with other species appear in the species description below.



Figure 2. Habitat at the three sites from which *Ctenotus rungulla* sp. nov. were collected: (a,b) Hampstead Springs Station; (c) Gilberton Station; and (d) the Gilbert River Reserve for Natural Resource Management (holotype capture site). Photos: (a–c) S. Zozaya; (d) D. Case.

Despite its geographic proximity to the Gregory Range, *C. ingrami* paratype WAM R56322 (Fig. 4) from near Croydon is morphologically consistent with the variation reported for *C. ingrami* (unsurprising given it is a paratype) but not *C. rungulla* sp. nov. (Table 1). Specifically, WAM R56322 has the following character states that have not been observed in *C. rungulla* sp. nov. so far: obvious vertebral stripe present; SVL = 82 mm; MBSR = 26; subdigital lamellae = 24. We thus conclude that WAM R56322 is not a specimen of *C. rungulla* sp. nov., although we concede that fresh tissue samples are required to fully resolve the affinities of this apparently disjunct *C. ingrami* population.

Taxonomic decision

Here we recognise species in the spirit of the Biological Species Concept (Mayr 1963). Because we cannot assess reproductive isolation directly in our case, we use heuristics from multiple lines of evidence (integrative taxonomy; Padial et al. 2010) to delineate what are likely to be reproductively isolated species — i.e., species hypotheses that can be further tested as new data is generated. Specifically, we consider divergence for a given data type to support species status if it is equal to or exceeds the divergence observed for other species pairs

(ideally, those for which there is good evidence of reproductive isolation).

We recognise and describe *Ctenotus rungulla* sp. nov. as a distinct species based on several lines of evidence that indicate species-level divergence from *C. ingrami*, its putative sister species: mtDNA sequence divergence (10.03–10.93%) matching or exceeding that seen among several other species pairs (see above); body size divergence (max SVL 67 mm *versus* 84 mm in *C. ingrami*); several distinct and diagnosable colour-pattern differences (detailed under 'Comparison with nearby congeners' below); non-overlapping variation in MBSR counts (*C. rungulla* sp. nov. 28–30; *C. ingrami* 25–27); and ecological divergence (*C. rungulla* sp. nov. is associated with sandstone outcropping, while *C. ingrami* is associated with woodlands on heavy soils [Wilson & Swan 2021; S. Zozaya pers. obs.]).

Discussion

The recent trend in Australian reptile taxonomy has been the recognition of new species through the revision of widespread 'species' using detailed genetic and morphological assessment (e.g., Oliver et al. 2020; Pavón-Vázquez et al. 2022; Hoskin & Couper 2023). In

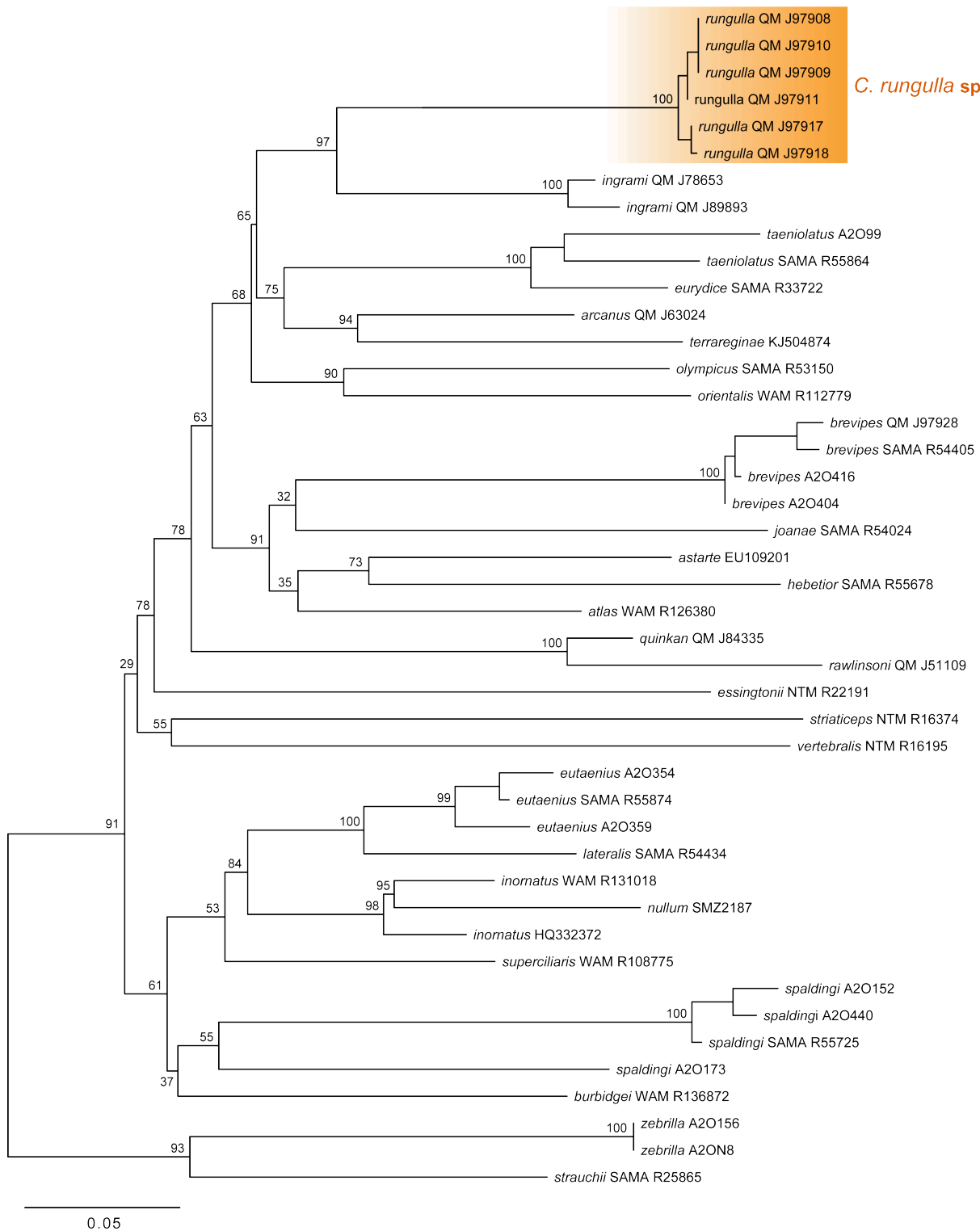


Figure 3. Mitochondrial DNA relationships among 44 samples across 27 *Ctenotus* species inferred from 668 bp of the *ND4* protein-coding gene using IQ-TREE. *Ctenotus rungulla* sp. nov. forms a deeply divergent, monophyletic lineage that is recovered here as sister to *C. ingrami*. The divergence between these two species is similar to, or greater than, levels observed among several other recognised species. Ultrafast bootstrap (UBS) support values are shown for major branches. The scale bar represents the average number of substitutions per site. The holotype of *C. rungulla* sp. nov. (QM J97909) appears in bold. The tree was rooted with *Lerista bipes*, which is excluded here for graphical purposes.

contrast, the savannas of north-eastern Australia — especially the EIU and adjacent areas of the GUP and Cape York Peninsula — have been yielding obviously new species across several groups. These include

gekkonids (Zozaya et al. 2019), diplodactylid geckos (Vanderduys 2016; Hoskin et al. 2018; Vanderduys et al. 2020), and skinks (Amey et al. 2019). Herein we have added a *Ctenotus* to that list. *Ctenotus rungulla* sp. nov.



Figure 4. Paratype of *Ctenotus ingrami* (WAM R56322) with reported locality 11 km west of Croydon, Queensland, much further north than other *C. ingrami* records and geographically close to the distribution of *C. rungulla* sp. nov. Its relatively large size (SVL = 82 mm), obvious vertebral stripe, and comparatively lower midbody scale row (26) and lamellae counts (24) are inconsistent with the range of variation observed for *C. rungulla* sp. nov. Photo: Stephen Zozaya.

is the fourth described reptile species thought to be endemic to the Gregory Range and, along with *Oedura argentea* and *Lucasium iris*, is the third of these that appears restricted to sandstone habitats. As highlighted previously, the description of reptile species endemic to this region only started in 2016 (*Lerista vanderduysi*; Couper et al. 2016) despite the proximity of the Gregory Range to Townsville and Cairns, northern Australia's two largest cities. It is becoming apparent that the Gregory Range is a hotspot of reptile endemism, with more endemic species awaiting description (e.g., *Heteronotia* geckos; S. Zozaya et al. in progress).

While we consider the data presented here — including diagnostic differences in body size, scale counts, ecology, and colour-pattern — to strongly support recognition of *C. rungulla* sp. nov. as a distinct species from *C. ingrami*, denser geographic sampling combined with genome-wide data for both species will be necessary to test species hypotheses more rigorously. Further survey work is especially needed to acquire new specimens and fresh tissue of the Croydon area *C. ingrami* to better resolve their affinity to *C. rungulla* sp. nov. and *C. ingrami* more broadly. Recent genomic work across the *C. inornatus* group has shown that colour-pattern characters can be unreliable when delineating *Ctenotus* species (Prates et al. 2023). While *C. rungulla* sp. nov. is diagnosable across several traits in addition to colour-pattern, it is worth acknowledging that colour-pattern variation in some *Ctenotus* is better explained by local adaptation than by species boundaries. Curiously, the colouration

of *C. rungulla* sp. nov. is very similar to *C. quinkan* and *C. coggeri*, two other sandstone-specialist *Ctenotus*. These species lack a vertebral stripe and upper-lateral spots and become flushed with red or orange on the hindbody. While anecdotal, this observation suggests that adaptation to sandstone habitats might strongly influence colour-pattern evolution in *Ctenotus*.

Taxonomy

***Ctenotus rungulla* Zozaya, Case & Hoskin, sp. nov.**

Figures 5–8, 9a, 9b

<https://zoobank.org/NomenclaturalActs/BDD141C8-766D-4C8E-BC12-5E34FF64F090>

Holotype. QM J97909 (Fig. 5; GenBank accession PP788571), Gilbert River Reserve for Natural Resource Management (19.0175°S, 143.5420°E), approximately 2.5 km southwest of Agate Creek Fossicking Area, collected by D. Case 08 September 2022.

Paratypes. QM J97908 & J97910, locality and collector details as for holotype; QM J97911, Gilberton Station, (19.2167°S, 143.6413°E), collected by N.P. Gale, W.J. Read, and J.M. Wright; QM J97917 & J97918, Hampstead Springs Station (19.8542°S, 143.6411°E), collected by S.M. Zozaya, W.J. Read, and S.A. Macor.

A medium-sized *Ctenotus* species (maximum SVL in type series = 67 mm; mean = 56 mm) distinguished from con-

Table 1. Morphometric and meristic data for the type series of *Ctenotus rungulla* sp. nov. and the *C. ingrami* paratype from Croydon. Where bilateral counts differ within an individual (QM J97908), counts are given as left/right. Empty values for WAM R56322 are because the specimen was too damaged for accurate measurement. Abbreviations: SVL—snout-to-vent length; TrunkL—trunk length (posterior insertion of forelimb to anterior insertion of hindlimb); TL—tail length; HL—head length (tip of rostral to anterior margin of ear); HW—head width (widest point posterior to eyes); HD—head depth (deepest point posterior to eyes); SnL—snout length (tip of rostral to anterior margin of orbit); HLL—Hindlimb length (from knee to heel); FLL—forelimb length (from elbow to wrist); 4TL—length of the fourth toe; MBSR—midbody scale rows.

Accession	QM J97908	QM J97909	QM J97910	QM J97911	QM J97917	QM J97918	WAM R56322
Species	rungulla	rungulla	rungulla	rungulla	rungulla	rungulla	ingrami
Type status	paratype	holotype	paratype	paratype	paratype	paratype	paratype
Latitude	19.0175°S	19.0175°S	19.0175°S	19.2167°S	19.8542°S	19.8542°S	ca. 18.12°S
Longitude	143.5420°E	143.5420°E	143.5420°E	143.6413°E	143.6411°E	143.6411°E	ca. 142.16°E
SVL	67	60	62	52	47.5	47	82
TrunkL	34.7	31.9	31.3	25.7	23.5	23.5	49.9
Tail state	regrown	original	original	tip regrown	original	regrown	broken
TL	103	138	158	93	109	84	-
HL	12.1	10.9	12.5	10.9	10	10.3	15.5
HW	7.8	7	7.8	7.1	6	6.2	10.3
HD	6.9	6.2	6.2	5.9	4.9	5.1	9.1
SnL	5.6	5.4	5.9	5.2	4.9	5.1	7.2
HLL	10.1	9.7	10.2	8.8	7.2	7.7	13
FLL	6.4	6	6.6	5.4	4.7	4.6	-
4TL	11.5	11.8	12.7	10.3	10	9.7	12.7
MBSR	28	30	28	28	30	30	26
Paravertebrals	57	56	53	56	55	57	48
Nuchals	7	7	6	6	6	7	4
Supralabials	8	7	7	8	8	8	8
Infralabials	6	6	6	6	6	6	6
Lamellae 4th toe	26	25	26	27	26	28	24
Supraoculars	4	4	4	4	4	4	4
Supraciliaries	10/9	9	9	9	9	10	10
Ear lobules	6/5	5	6	5	5	5	5

genera by the unique combination of: 28–30 midbody scale rows; presubocular single; nasals narrowly separated; prefrontals narrowly to moderately separated; frontoparietals paired; four supraoculars, with second being wider than first or third, and first three of which contact the frontal; 5–6 bluntly pointed lobules on anterior margin of ear opening; middle ear lobules largest; laterally compressed, keeled or narrowly callous subdigital lamellae, most of which terminate in a point; oblique sutures dividing supradigital scales along basal third to half of fourth toe; colour-pattern of longitudinal, black and white ventrolateral to laterodorsal stripes; vertebral stripe absent, or at most a faint dark line along nape; broad, solid black upper lateral stripe lacking distinct pale spots; ground colour fades from grey or grey-brown anteriorly to red-orange or copper-orange posteriorly, with reddish flush strongest across hips and hindlegs; relatively well-defined, dark lateral stripe extends at least 75% along the length of original tails.

Description of type series. Measurements and scale counts for each of the type series are given in Table 1. Data that follow are presented as range (min–max) fol-

lowed in brackets by mean (\bar{x}) for linear measurements and proportions, or mode for counts. Where specific scale counts are split evenly among the six specimens, the number of specimens with each count is given instead of a mode. Sample sizes are six unless otherwise stated. Measurements are rounded to nearest 0.1 mm; proportions are rounded to nearest 0.1%, or to nearest 1% when greater than 100%.

Measurements and proportions (Table 1). Snout-to-vent length (SVL) 47–67 mm (\bar{x} = 56 mm). Tail length 84–158 mm (\bar{x} = 114 mm); length of original tails 229.5–254.8 mm (\bar{x} = 238.1%; n = 3) of SVL. Trunk length 23.5–34.7 mm (\bar{x} = 28.4 mm), 49.3–53.2% (\bar{x} = 50.7%) of SVL. Head length 10.0–12.5 mm (\bar{x} = 11.1 mm), 18–21.8% (\bar{x} = 20%) of SVL. Head width 6.0–7.8 mm (\bar{x} = 7.0 mm), 60–66% (\bar{x} = 63%) of head length. Head depth 4.9–6.9 mm (\bar{x} = 5.9 mm), 49.2–57.5% (\bar{x} = 52.9%) of head length. Snout length 4.9–5.8 mm (\bar{x} = 5.3 mm), 46.6–49.4% (\bar{x} = 48.1%) of head length. Hindlimb length 7.2–10.2 mm (\bar{x} = 8.9 mm), 15–16.9% (\bar{x} = 16%) of SVL. Forelimb length 4.5–6.6 mm (\bar{x} = 5.6 mm), 9.5–10.7% (\bar{x} = 10%) of SVL. Length



Figure 5. Preserved holotype of *Ctenotus rungulla* sp. nov. (QM J97909), collected from Gilbert River Reserve for Natural Resource Management, Queensland. Photos: S. Zozaya.

of fourth toe 9.7–12.7 mm (\bar{x} = 11 mm), 115–139% (\bar{x} = 124%) of hindlimb length.

Scale characters (Fig. 6). Midbody scales in 28 (n = 3) - or 30 (n = 3) rows. Paravertebral scales in 53–57 rows (bimodal mode = 56 & 57). Supraoculars four, the first three contacting frontal, and with the second wider than the first or third. Supraciliaries 9–10 (mode = 9), the first of which is largest and contacts the prefrontal, first supraocular, second loreal, and both preoculars (contact with lower preocular narrow). Supraciliary counts in QM J97908 are asymmetric: left = 9, right = 10. Supral-

abials seven (n = 2) or eight (n = 4), with either 5th (when seven supralabials) or 6th (when eight supralabials) immediately below eye (subocular supralabial). Infralabials six. Presubocular single, contacting lower preocular and both the subocular supralabial and the next anterior supralabial. Loreals two, second largest. Nasals narrowly separated. Prefrontals narrowly to moderately (e.g., Figs. 5, 6) separated. Parietals in broad contact. Interparietal free. Frontoparietals paired. Nuchals six (n = 3) or seven (n = 3). One primary (upper) temporal, two secondary (lower) temporals. Large, ver-

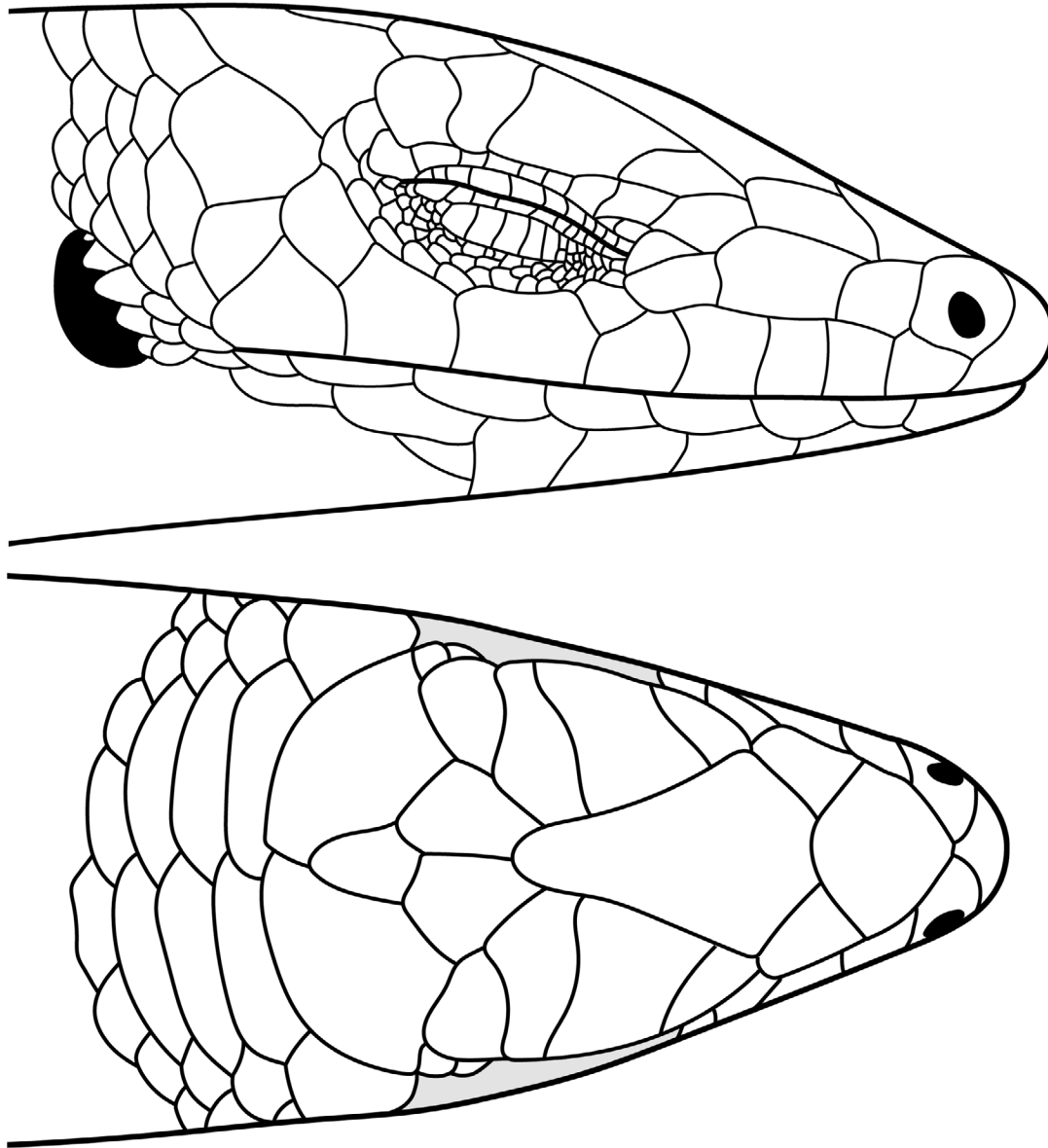


Figure 6. Typical head scalation of *Ctenotus rungulla* sp. nov. in lateral and dorsal view. Illustrations are based on paratypes QM J97917 (lateral view) and QM J97911 (dorsal view).

tically elliptical ear opening with 5–6 (mode = 5) bluntly pointed lobules along the anterior margin (Figs. 6, 7, 9). Ear lobule counts in QM J97908 are asymmetric: left = 6, right = 5. Lobules smallest near the top and bottom margins of ear opening, becoming largest toward the middle. Toes laterally compressed; subdigital lamellae on fourth toe 25–28 (mode = 26); lamellae keeled to narrowly callous, most of which terminate distally in a point, with proximal lamellae near base of toe often forming an acute spine. Supradigital scales on the fourth toe are divided by oblique sutures along basal third to half of digit length (Fig. 5).

Colour and pattern in life (Figs. 7, 9a, 9b). Simple longitudinally aligned body pattern of seven alternating black (= 4) and white (= 3) ventrolateral to laterodorsal stripes. Dorsal body surface immaculate and lacking vertebral

stripe or, at most, with a narrow dark line along midline of neck, extending no more than 10 paravertebral scale rows from parietals. Dorsal ground colour grey to grey-brown anteriorly, fading to red-orange or copper-orange posteriorly, with red-orange flush strongest across hips and hindlimbs, then fading to olive-yellow or yellow-brown on original tails. Pale dorsolateral stripe narrow ($\frac{1}{2}$ scale width) bordered above by similarly narrow, black laterodorsal stripe, both of which extend posteriorly from the supraoculars as well-defined stripes that become increasingly indistinct posteriorly, often having faded entirely on the hindquarters. The pale dorsolateral stripe is bordered below by a broad (2–2.5 scales wide), solid black upper lateral stripe extending from the nasal or loreals, through the eye, along the entire body, becoming narrower above the hindlimbs and extending along ~50–90% the length of original



Figure 7. Photographs of *Ctenotus rungulla* sp. nov. in life. (a) Holotype QM J97909 from Gilbert River Reserve for Natural Resource Management. (b) QM J97911 from Gilberton Station. (c) QM J97917 and (d) QM J97918 from Hampstead Springs Station. Photos: (a) C. Hoskin; (b-c) W. Read; (d) S. Zozaya.

tails, where the stripe gradually becomes narrower and less distinct. A poorly defined, white to pale-brown spot often present behind eye on upper temporal scale, set within black upper lateral stripe. White mid-lateral stripe (*ca.* 1 scale wide) extends from supralabials, through the ear, above the forelimb and along body, where it is interrupted by the hindlimb but then continues along original tails to a similar distance as the black upper lateral stripe. White mid-lateral stripe bordered below by black stripe (1–2 scales wide) that starts near posterior edge of ear opening — sometimes as a loosely aligned series of dark marbling from neck to axilla, where it coalesces into a stripe — extending onto forelimb and along body where it is interrupted by the hindlimbs but then continues along tail to similar distance as black upper lateral stripe but becoming more indistinct earlier on, often forming a series of aligned spots on the posterior 50–90% of original tails. White lower-lateral stripe (*ca.* 1–1.5 scales wide) below — often poorly defined anteriorly when the neighbouring black stripes are marbled and discontinuous — extends from near lower posterior margin of ear opening onto forelimb and onto body, losing definition posteriorly due to the fading away of the narrow, black ventrolateral stripe that borders it below. This narrow (*ca.* ½ scale width), black ventrolateral stripe (the lower-most stripe) is often poorly defined, forming a thin line extending from below ear opening

— sometimes only a series of aligned spots and blotches, as for black mid-lateral stripe — onto forelimbs and along flanks, gradually losing definition along the body and fading away entirely by mid-trunk to groin. Forelimbs with pale and black stripes; pale stripes white on upper forelimb, becoming flushed red-orange distally. Hindlimbs red-orange to copper-orange with obscure black stripes or blotches. Dorsal surfaces of head often with obscure dark flecks, spots, and reticulations. Supralabials and infralabials white with black bars or blotches. Ventral surfaces white, often with diffuse grey to blue-grey scale margins of varying intensity (from obvious to absent), particularly on the throat and chest.

Colour and pattern in spirit (Figs. 5, 8). Pattern as described above, although colouration differs in preservative. Dorsum uniform grey or light orange-brown, losing the distinct reddish-orange flush on hindquarters seen in-life. Limbs and tails also light orange-brown, with colouration on tail often lighter and more vibrant than is observed on the body or limbs. The two specimens fixed in ethanol, rather than formalin, have scattered blue-green patches of discolouration (QM J97917 & J97918).

Etymology. Named for Rungulla National Park, in the traditional lands of the Agwamin people (also spelled "Ewamian"). Used as a noun in apposition. While the

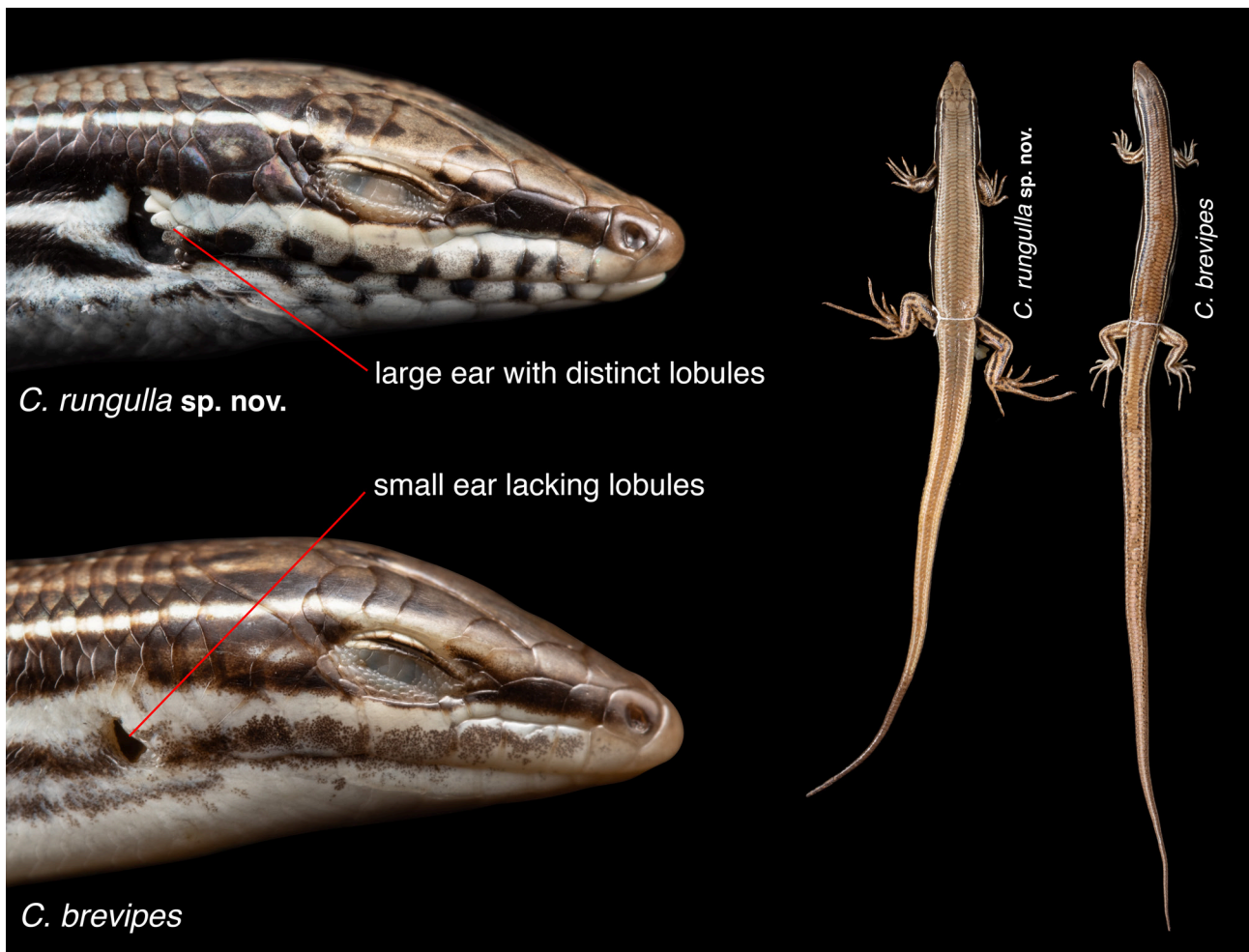


Figure 8. Comparison of *Ctenotus rungulla* sp. nov. with the regionally sympatric and superficially similar *C. brevipes*. The absence of ear lobules immediately differentiates *C. brevipes* from all other described *Ctenotus*. Among other differences, *C. brevipes* also has a more elongate, gracile body compared to *C. rungulla* sp. nov. Specimens of *C. rungulla* shown are QM J97917 (head photo) and QM J97911 (dorsal photo); the *C. brevipes* specimen is QM J97928 in both photos. Photos: S. Zozaya.

species has not been collected from what is now Rungulla NP, it was observed in the area by Keith McDonald in the early 2000's, and two of the three collection sites — Gilbert River Reserve for Natural Resource Management and Gilberton Station — occur very nearby the Rungulla NP border (1.5 km north and 3.1 km east of the border, respectively).

Proposed common name. Rungulla Rock Ctenotus.

Comparison with nearby congeners. Previous sightings of *C. rungulla* sp. nov. have most often been attributed to the regionally sympatric *C. brevipes* (Fig. 8), which *C. rungulla* sp. nov. would be identified as using the dichotomous key in Cogger (2014). The two species differ most obviously in that *C. rungulla* sp. nov. have a large ear opening with 5–6 distinct ear lobules *versus* a small ear opening with no ear lobules in *C. brevipes* (a character state unique among *Ctenotus*; Fig. 8).

Ctenotus rungulla sp. nov. would be identified as *C. terrareginae* (Fig. 9c, 9d) using the dichotomous key in Wilson (2022) but is also very similar in overall appearance to *C. quinkan* (Fig. 9e, 9f) — another sandstone-dwelling

Ctenotus from north-eastern Australia. Neither *C. terrareginae* nor *C. quinkan* are known from the vicinity of the Gregory Range, with *C. terrareginae* occurring in the wet sclerophyll forests of the Townsville–Cardwell region and *C. quinkan* known only from sandstone habitats in the Laura–Cooktown region. Nevertheless, *C. rungulla* sp. nov. differs from both *C. terrareginae* and *C. quinkan* in its smaller size (maximum recorded SVL = 67 mm, *versus* 91 mm in *C. terrareginae* and 81 mm in *C. quinkan*) and lower lateral zone patterned with distinct black and white stripes, including a distinct white lower-lateral stripe, with black mid-lateral stripe only sometimes interrupted by white blotching on the neck and axilla (*versus* lower lateral zone of black and white marbling always present from ear opening to at least mid-body in both *C. terrareginae* and *C. quinkan*, with no distinct white lower-lateral stripe). It further differs from *C. terrareginae* in lacking a vertebral stripe (sometimes present in *C. terrareginae*) and having dorsal colouration that transitions from grey or grey-brown anteriorly to reddish-orange or copper-orange posteriorly (*versus* uniform brown in *C. terrareginae*). It also differs further



Figure 9. *Ctenotus rungulla* sp. nov. (a,b) compared to three similar Queensland species: *C. terrareginae* (c,d), *C. quinkan* (e, f), and *C. ingrami* (g,h). With respect to colour-pattern, *C. rungulla* sp. nov. is differentiated from some or all these species by the absence of a vertebral stripe (vs. d,g,h), red-to-orangish flush on the hindbody (vs. c,d,g,h), well-defined mid-lateral and lower-lateral stripes (vs. c–f), and the absence of yellowish flush laterally on the forebody and neck (vs. g,h). Photos of *C. rungulla* sp. nov. are holotype QM J97909 (a) and QM J97918 (b). Remaining photos are of unvouchered animals: *C. terrareginae* from the Paluma Range (c,d); *C. quinkan* from Isabella Falls (e,f); and *C. ingrami* from Yuleba (g) and Bowra Sanctuary (h). Photos: C. Hoskin (a); S. Zozaya (b,c,g); R. Lloyd (e); N. Gale (d,f); A. Zimny (h).

from *C. quinkan* in that the supradigital scales of the fourth toe are divided by oblique (*versus* transverse) sutures along only one-third to half the digit length (*versus* along entire digit in *C. quinkan*).

Ctenotus rungulla sp. nov. appears genetically most similar to *C. ingrami* (Figs. 4, 9g, 9h), from which it differs in: lacking a dorsal stripe (at most a narrow stripe on the nape, versus a continuous or near continuous stripe down the entire dorsum in *C. ingrami*); its smaller body size (maximum recorded SVL = 67 mm, versus 84 mm in *C. ingrami*); lack of yellow flush on the neck and forebody (sometimes present in *C. ingrami*; Figs. 9g, 9h); dorsal colouration transitioning from grey or grey-brown anteriorly to reddish-orange or copper-orange posteriorly (*versus* uniform brown in *C. ingrami*); a solid black upper lateral zone (*versus* brown ground colour often bleeding into upper lateral zone in *C. ingrami*); and higher midbody scale row count (28–30, *versus* 25–27 in *C. ingrami*).

Ctenotus rungulla sp. nov. can be differentiated from all other Queensland *Ctenotus* species in having a lateral body pattern of longitudinal black and white stripes, entirely lacking distinct vertebral or paravertebral stripes, with no distinct pale blotches or spots through the dark upper lateral zone.

Distribution and habitat. The type series of *C. rungulla* sp. nov. were collected from three localities: Gilberton Station (QM J97911); the Gilbert River Reserve for Natural Resource Management, near Agate Creek (QM J97908–97910); and Hampstead Springs Station (QM J97917 & J97918). The species has also been observed at Cobbold Gorge Nature Refuge (C. Hoskin pers. obs. 2013; S. Zozaya pers. obs. 2017). These localities span a 244 km line from Cobbold Gorge in the north to Hampstead Springs in the south (Fig. 1). All known sites are from sandstone escarpments in the central to southern Gregory Range. The Cobbold Gorge site lies within the Kidston subregion of the Einasleigh Uplands bioregion (EIU), while the remaining sites are all from the Gilberton Plateau subregion of the Gulf Plains bioregion (GUP) — although the Gilberton Station and Agate Creek sites are essentially on the boundary of the EIU and GUP, which in this area follows the eastern escarpments of the Gilberton Plateau. Despite having only been recorded at four localities, *C. rungulla* sp. nov. is almost certainly more widespread through the rugged sandstone habitats of the Gregory Range, most of which is inaccessible by road.

Habitats where *C. rungulla* sp. nov. were collected or observed are similar, consisting of sandstone outcroppings — especially sandstone pavements with exfoliating caprock, typically on top of escarpments — among dry woodland with *Acacia* trees and shrubs (often lancewood, *A. shirleyi*) and occasional large Bloodwood (*Corymbia* sp.) and Woollybutt (*Eucalyptus miniata*) trees (Fig. 2). They appear to use a variety of microhabitats

and have been observed using *Chleistochoa* sp. grasses and spinifex hummocks (*Triodia bitextura*) common in these areas, in addition to fallen logs and leaf-litter. In these habitats we have observed *C. rungulla* sp. nov. in syntopy with *C. spaldingii*, *C. zebrilla*, and *C. eutaenius*.

Remarks. Colouration and patterning for all observed individuals was consistent, with reddish-orange flush on the limbs and hindbody, transitioning to olive-yellow to olive-brown on the tail, and a pattern of lateral stripes and no distinct vertebral stripe. At the Agate Creek sites, specimen QM J97908 was the largest individual sighted, with most others noticeably smaller (D. Case pers. obs.). Similarly, at Hampstead Springs most individuals seen were relatively small compared to QM J97908; however, some large individuals were observed but evaded capture.

Conservation status. *Ctenotus rungulla* sp. nov. is currently known from four general localities, with an estimated Extent of Occurrence (EOO) of 1,075 km² and Area of Occupancy (AOO) of 24 km² following IUCN guidelines (IUCN 2019). Its true distribution, however, is certainly much more widespread. The sandstone habitats of the Gregory Range are extensive and relatively well protected in Rungulla National Park, Littleton National Park, parts of Blackbraes National Park, and in several Nature Refuges (e.g., Gilberton, Cobbold Gorge, Bellfield, Esmeralda, North Head). While various land use activities and planned developments might impact parts of this species' range, it is likely secure throughout much of its rugged and inaccessible distribution. We therefore recommend the species be listed as *Least Concern*.

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Supplementary Data

The following files are available on Figshare: <https://doi.org/10.6084/m9.figshare.25803070>.

Supplementary_tables.docx – Table S1 and Table S2. Table S1 shows sites where targeted searches for *Ctenotus* were performed, brief habitat descriptions, and the species detected. Table S2 shows the 44 *Ctenotus* samples included in mtDNA phylogenetic analysis and their respective GenBank accession numbers.

Morphology.csv – Morphological data for *C. rungulla* sp. nov. and *C. ingrami* specimen WAM R56322.

ND4_alignment.fasta – Alignment of the 45 ND4 sequences used in phylogenetic analysis.

Dissimilarity_matrix.csv – Pairwise sequence dissimilarity among samples for the ND4 locus.

ND4_iqtree_phylogeny.tree – Newick file of ND4 phylogeny inferred using IQ-TREE.

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