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The last piece of the puzzle: Detection of an extremely rare lizard in the Kimberley completes the phylogeny of Australian dragons (Agamidae)

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Abstract

Although the phylogeographic relationships of Australian agamids are well-understood, an important lineage has been conspicuously missing from all phylogenies of this group to date: the mysterious and monotypic *Cryptagama aurita* (Storr, 1981). Prior to this study, *C. aurita* was known from only four specimens, all collected in the 1990s before tissue sampling for genetic analyses became standard practice. From 2011–2023, over 60 individuals were observed and photographed across five sites in the remote central Kimberley: 24 of these were also tissue-sampled and 6 individuals were collected from one site for museum specimens. Detailed morphometric measurements were recorded for the 6 specimens and a released individual. Using these data we confirm the central Kimberley specimens and observed individuals are *C. aurita*, more than tripling the estimated extent of occurrence for this elusive species. The central Kimberley discoveries have provided significant insight into the distribution and ecology of *C. aurita* and completed the phylogeny of Australian agamids. Using tissue samples of *C. aurita* we provide the first complete multi-gene genus-level phylogeny of Australian dragon lizards and discover that the formerly monotypic *C. aurita* is nested within *Ctenophorus*. For this reason we provide an expanded description of this species as *Ctenophorus aurita* and a suggested common name of 'hidden dragon'.

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Introduction

Dragon lizards (family Agamidae) are arguably the most conspicuous and well-known reptile group in Australia's arid and tropical regions (Melville & Wilson 2019). All 86 species of Australian agamids are members of the Amphibolurinae sub-family (Pyron et al. 2013). This includes iconic species such as *Chlamydosaurus kingii* (frilled lizard), *Pogona* spp. (bearded dragons) and the distinctive *Moloch horridus* (thorny devil). Genetic analyses indicate that the Australian agamid lineage entered Australasia from the mesic north approximately 30 million years ago (Mya) and diversified extensively in Australia from approximately 20 Mya as aridity increased (Honda et al. 2000; Hugall et al. 2008).

Australian agamids are popular study organisms across the fields of ecology, evolution, and behaviour because of their wide diversity of size, colour, morphology, behaviour, and ornamentation (e.g. Stuart-Fox & Ord 2004; Chen et al. 2013; Edwards et al. 2015; Ramos & Peters 2016; Littleford-Colquhoun et al. 2019). Since the early 2000s, extensive genetic analyses have provided a clear understanding of phylogeographic patterns for many Australian agamid species-groups and bioregions (see Melville et al. 2001, 2008, 2016; Shoo et al. 2008; Edwards & Melville 2010). Virtually complete phylogenies are now available across two genes (Schulte et al. 2003; Hugall et al. 2008). Despite this detailed understanding of agamid evolution, there is a lineage that has been conspicuously missing from all Australian agamid genetic phylogenies to date: the monotypic genus *Cryptagama* Witten, 1984 containing a single species *C. aurita* (Storr, 1981).

Prior to 2011, *Cryptagama aurita* was only known from four specimens at three sites in the remote east Kimberley, Western Australia (WA) and in the Northern Territory (NT). The first two specimens – both juveniles – were collected from Kandimalal/Wolf Creek Meteor Crater in the Kimberley in April 1979. In September 1979, a third specimen (the holotype) was collected approximately 80 km north, near the town of Halls Creek (**Figure 1**). Storr (1981) used these three specimens to describe *C. aurita* as *Tympanocryptis aurita* based on similarities with *T. cephalus* and other pebble-mimic dragons, i.e. with a small and rotund body shape, small head, short tail, rough texture and pebble-matching camouflage. However, unlike any other species of *Tympanocryptis* – which means 'hidden eardrum' in Greek – the new species had a conspicuous tympanum covering the ear. This discrepancy was acknowledged by Storr (1981) in naming the new species *aurita;* Latin for 'ear'. Storr (1981) also noted that the new species had more femoral pores than is typical for *Tympanocryptis.*

In 1984, a fourth *C. aurita* was collected approximately 300–400 km northeast of the two previous sites, near Kalkarindji/Wave Hill (NT) (**Figure 1**). The Kalkarindji specimen was the first *C. aurita* to be photographed in life and this photograph has made numerous appearances in field guides and books about Australian reptiles. A re-examination of *C. aurita* specimens and characters by Witten (1984) highlighted that the scale arrangement patterns of this species were more similar to *Ctenophorus* and *Pogona* than to *Tympanocryptis.* Yet, other features were more similar to *Moloch horridus,* including an extremely short tail. Fundamental differences from *Ctenophorus*, *Pogona*, *Tympanocryptis* and *Moloch* were also noted, including a row of fringed scales along the upper labial area that seemed unique among Australian agamids at the time. Such fringes are generally associated with 'shimmy-burrowing' behaviour in lizards from elsewhere (Arnold 1984). Based on this information, Witten (1984) created the monotypic genus *Cryptagama*. Since then, the relationship between *C. aurita* and other species of Australian agamids has been a source of much speculation (Witten 1984; Greer 1989; Aplin and Smith 2001; Hugall et al. 2008): the four specimens collected in 1979 and 1984 were preserved before tissue collection for phylogenetic analyses became routine.

No further observations of *C. aurita* were recorded until 2011, when botanist Ian Dudgeon incidentally photographed an adult in a very remote area in the Wunaamin-Miliwundi Ranges of the central Kimberley (Griffin et al. 1993), approximately 200 km northwest of the 1979 detections (**Figure 1**). The two photographs – one of which is available on page 96 of Wilson (2012) – show diagnostic features of *C. aurita*: a rotund shape, short tail, large and round tuberculate scales on the back, red-brown colour and an obvious tympanum. These photographs suggested a significant range extension to the west for *C. aurita* (**Figure 1**)**.** No specimen or genetic sample was collected at the time and a follow-up search failed to detect *C. aurita* at this remote, helicopter-accessed, site.

In June 2016, SM found and captured a basking *C. aurita* on the Throssell Shale plains of the central Kimberley (Griffin et al. 1993), 50 km northwest of the 2011 detection. This individual was photographed in detail in the field (**Figure 2**) and tail-clipped to provide the first genetic material for *C. aurita*. It was also measured live in the field by SM before it was released as per permit requirements. Four more individuals were captured, tissue-sampled, photographed, and released during a thorough search of the site the next day by SM, MB and colleagues.

Subsequent searches by MB in similar areas in 2016 revealed *C. aurita* at a second Throssell Shale site 18 km to the southeast and a third Throssell Shale site another 16 km to the south (**Figure 1**). Tissue-samples and photographs were collected from nine individuals across these three sites. SM, Jules Farquhar and Christopher Jolly returned to the first Throssell Shale site in 2018 to collect six specimens. Tissue-sample and specimen details are available in **Supplementary Data**.

Opportunistic searches at Throssell Shale sites 2 and 3 and at other potential sites in the central Kimberley by MB, JP and colleagues in 2017, 2018 and 2019 did not re-detect *C. aurita*. From 2020–2023 at least 50 individuals were detected by JP and colleagues across the three Throssell Shale sites, a new Throssell Shale site approximately 20 km to the east (which had been searched several times previously) and a fifth and disparate site in the east Wunaamin-Miliwundi Ranges, approximately 5 km south of where *C. aurita* was opportunistically photographed in 2011. These last two sites are on conservation estate at the Mornington Wildlife Sanctuary. From 2020–2023, 11 individuals were tissue-sampled and photographed across the three initial Throssell Shale sites, two at the new Throssell Shale site, and two at the fifth central Kimberley site in the Wunaamin-Miliwundi Ranges (**Supplementary Data 1**).

The 6 specimens, 30 tissue-samples, and ample photographs of *C. aurita* that were collected in the central Kimberley from 2016–2023 have enabled several mysteries about this cryptic species to be resolved, including where it occurs within the evolutionary tree of Australian agamids and a more detailed understanding about its distribution (**Figure 1**), habitat, ecology and morphology. Our study completes the overall phylogeny of Australian dragon lizards at the generic level and provides a clear and comprehensive re-description of *C. aurita*.

Methods

Morphological appraisal

A morphological assessment was completed to ensure individuals from the central Kimberley were conspecific with *C. aurita* as described by Storr (1981) and Witten (1984). We measured a series of morphological features on the holotype from Halls Creek (WAM R66296), the two Kandimalal specimens (WAM R64051, WAM R64052), the six central Kimberley specimens (WAM R177990–992, AMS R186655–657), and a field-measured live individual from the central Kimberley (WAM TR1103: a "tissue only" specimen) (**Supplementary Data**). We also compared the Storr (1981) and Witten (1984) descriptions with the six central Kimberley specimens and all live individuals that were photographed and tissue-sampled across the five central Kimberley sites. Electronic callipers were used for all morphological measures (to the nearest 0.1 mm) and all bilateral counts and measurements were recorded on the left side (where possible).

Molecular genetic samples

Molecular data was obtained for 86 (out of 88) Amphibolurinae species from Australia and four species from New Guinea, plus *Physignathus cocincinus* (Chinese water dragon) as an out-group within the Amphibolurinae. The two Australian species that are not included in our dataset – *Tympanocryptis uniformis* and *Diporiphora convergens* – are described from single specimens and they lack tissue samples.

Phylogenetic and evolutionary analyses

We extracted genomic DNA from tail tissue using either a Proteinase K digestion and chloroform-isoamyl alcohol extraction or a Qiagen Blood & Tissue Kit (Qiagen, Hilden, Germany) as per manufacturer guidelines. We amplified five genes that have been used broadly across the Amphibolurinae: mtDNA region ND2 plus adjacent tRNAs (987bp) amplified using primers Metf.1 and COIr.aga using protocols described in Shoo et al. (2008) and nuclear genes RAG1, BDNF, BACH1 and PRLR as described in Townsend et al. (2008). PCR products were amplified using a Bio-Rad MyCycler Thermal Cycler (Bio-Rad, California, USA). Negative controls were used in each PCR run. Amplification products were visualised on a 1.2 % agarose gel with Sybr SAFE (Invitrogen, California, USA), then purified using ExoSAPIT (Thermo-Fisher, California, USA) and sent to Macrogen (Seoul, South Korea) for sequencing. Sequence chromatograms were edited and aligned to published sequences in Geneious 10.2.3 (Biomatters, Auckland, New Zealand) using MUSCLE (Edgar 2004) with alignments checked by amino acid translation and mtDNA tRNAs secondary structure models (Macey et al. 1997). See **Supplementary Data** for full alignments, including partitions, and GenBank accession numbers.

The appropriate partitioning scheme and substitution models were selected using PartitionFinder2, run on the CIPRES Science Gateway v. 3.3. The optimal partitioning scheme and substitution models are provided in the full alignment datasets. The datasets were analysed separately, with phylogeny and divergence dates estimated simultaneously in MrBayes v. 3.2. All sequences were concatenated for both analyses. Multispecies coalescent methods were not implemented due to low variability of some of the nuclear genes. Two nodes in the tree were calibrated, using fossil calibrations previously used in Australian agamids (Edwards et al. 2015) with hard minima and soft 95 % maxima. The tree root was also constrained to 32 mya based on previous dating analyses on these gene regions across acrodont lizards (Melville et al. 2011). Initial stepping-stone analyses favoured the uncorrelated igr relaxed clock over other options and was used in subsequent full analyses. Analyses were run for 50 million generations, with convergence confirmed in Tracer. A burn-in of 25 % was used and a majority-rule consensus tree was computed.

Species redescription

We collated information from over 60 detections of *C. aurita* in the central Kimberley and combined it with information from the original four detections as outlined by Storr (1981) and Witten (1984) to provide an updated species description that includes detailed information about the ecology of this elusive species.

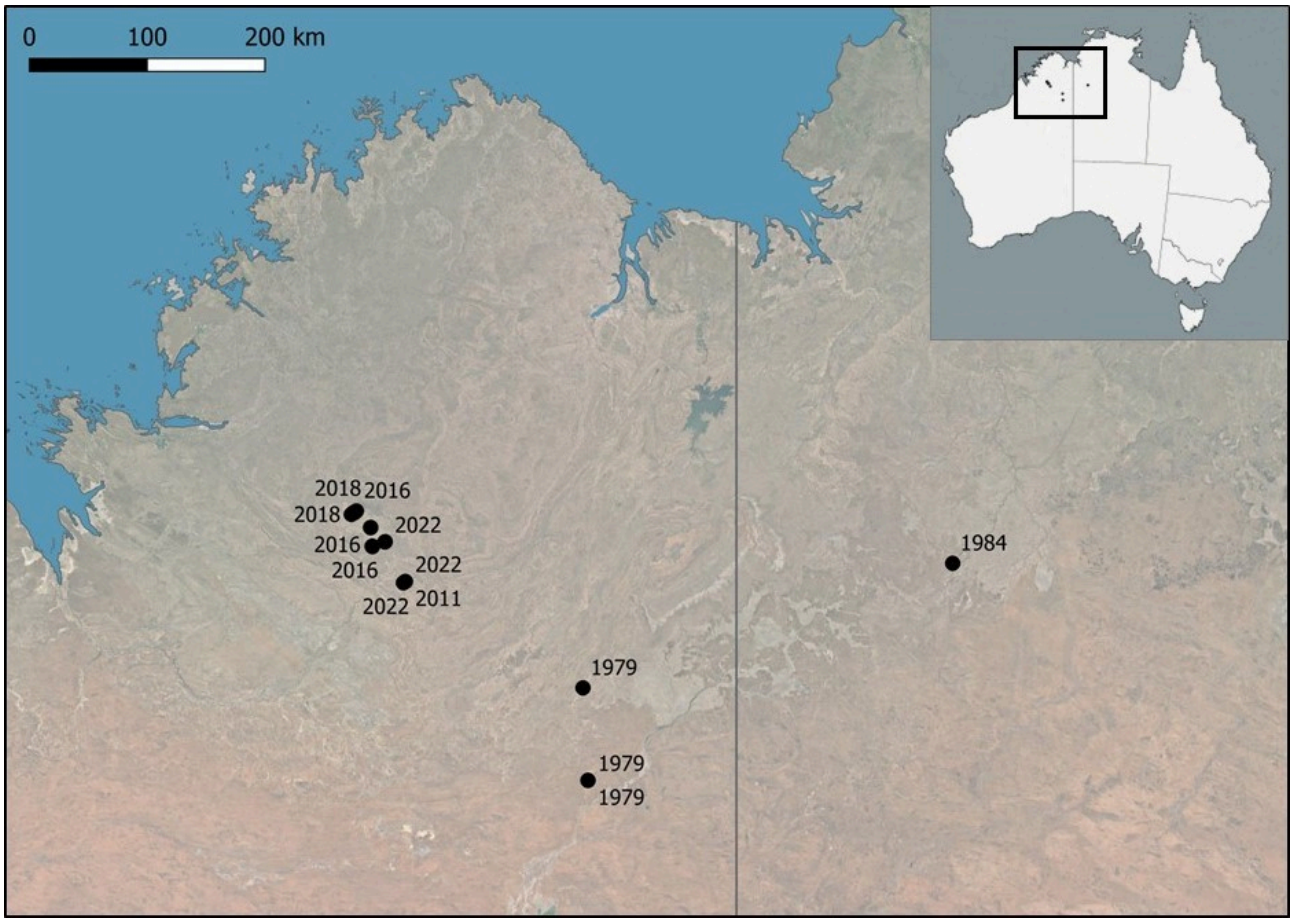

Figure 1. Locations and dates of *Cryptagama aurita* detections in north-western Australia.

Figure 2. The first tissue-sampled *Cryptagama aurita*, detected in 2016 at a Throssell Shale site in the central Kimberley. Photos: Melissa Bruton.

Results

Morphological appraisal

Storr (1981) provides diagnostic features for differentiating *C. aurita* (described as *Tympanocryptis aurita*) from other *Tympanocryptis* species. The key diagnostic features include: an exposed tympanum, a shorter tail that ends abruptly when compared to *"T. cephala"* (subsequently redescribed as *T. pseudopsephos* Doughty, Shoo, Kealley & Melville 2015), and 'Dorsal tubercles not arranged in clusters, distributed over whole of back (rather than leaving vertebral zone free) and extending to tip (rather than only base) of tail' (Storr 1981).

Storr (1981) also describes the following characters:

• Head scales 'feebly rugose or unicarinate (almost smooth)' (page 601).

Figure 3. Variation in colour and pattern of *Cryptagama aurita* in the central Kimberley, from multiple Throssell Shale sites (top left, bottom left, bottom right) and a Wunaamin-Miliwundi Sandstone site (top right). Photos: Stephen Mahony (top left, bottom left) and Joe Porter/Australian Wildlife Conservancy (top right, bottom right).

• Scales on other dorsal surfaces are very small with slightly larger keeled scales not forming regular patterns, specifically 'not absent from vertebral zone as in *T. cephala* and *intima*' (page 601).

• 15–18 subdigital lamellae under the fourth toe.

• 11 femoral pores and 6 pre-cloacal pores on the holotype, less or absent on the two juveniles.

The holotype – the only adult specimen examined by Storr (1981) – was 46 mm SVL and the larger of the two juvenile paratypes was 29 mm SVL (but see Table 1 for re-measured traits). Witten's (1984) reassessment of the type series agreed in general with characters recorded by Storr (1981), however, the pore counts recorded by Witten (1984) were 'about 11' (page 400) for the holotype; 'at least 5' (page 400) for the larger paratype; and there is no mention of the pore count for the smaller paratype.

Witten (1984) also observed:

• 'Supralabial scales forming denticulate fringe along upper lip' (page 400) – noted as a unique and significant character in Australian agamids.

• Pores penetrate the middle of the scale.

• Mid-body scales rows are 140–164.

• Infralabial scales are 16–17.

• The pes formula recorded as 2.3.4.5.4. This is typical for agamids (pers. comm. to Witten by H. Cogger, based on x-rays), whereas *Tympanocryptis* spp. have lost a phalange in the fifth toe, i.e. 2.3.4.5.3 (page 37 of Greer 1989).

Witten (1984) determined that the holotype is a mature female with ovarian follicles and evidence of past reproduction, not a male as recorded by Storr (1981).

Confirmation of species identity for central Kimberley specimens

Morphometric measurements of the three specimens collected in 1979 and 1984, six specimens collected in 2018, and the field-measured and released individual (WAM TR1103) are available in **Supplementary Data**. The nine museum specimens were measured by PD and the released individual was measured in the field by SM. There is minor variation in fine-scale values between the museum-measured and the field-measured specimen, which may be attributable to observer variation. Nevertheless, the morphology of all the central Kimberley specimens is broadly consistent among individuals. This includes a body size of 36.5–40.5 mm SVL, which is less than the SVL of the holotype (45 mm). All adult specimens had a short tail (28.5–32.0 mm). WAM TR1103 appears to be a subadult.

Morphometric data (**Supplementary Data**) and photographs in life (e.g. Figures 2, 3, 5 & 8) confirm all specimens and released individuals in the NT, east Kimberley and the central Kimberley align with descriptions by Storr (1981) and Witten (1984).

Figure 4. Maximum likelihood phylogeny of published mtDNA sequences of Australian agamid species, with additional study samples sequenced for *Ctenophorus aurita, C. nuchalis, C. reticulatus,* and *C. yinnietharra* as part of the current study. MtDNA region incorporates an ~1200bp fragment of the *ND2* (NADH dehydrogenase subunit two) protein coding gene. ML bootstrap values are indicated on branches, with values of 99 % indicated with ** and values of 100 % with *. *Physignathus cocincinus* (Chinese water dragon) was used as the outgroup for analysis. Museum registration numbers for samples sequenced in the current study are provided following species name, with additional specimen details in **Supplementary Data**.

The colour and patterning of individuals photographed in the central Kimberley (Figure 3) resemble that of the holotype in Storr (1981: Figure 2 on page 601) including dark markings along the upper flank and side of the

neck and scattered blotches on the dorsum. The colours and hues of the central Kimberley individuals resemble the live photograph of the Kalkarindji specimen (NTM R12804; Wilson & Swan 2012).

The central Kimberley individuals have variable cross-bands on the side of the tail, with bands tending not to completely encircle the upper part of the tail. The pale interspaces on the tail are larger, or at most equal in area to, the dark bands. The bands tend to taper dorsally.

Morphological, colour and pattern elements are congruent between the central Kimberley individuals and the holotype. However, colour elements on the venter of central Kimberley individuals were not apparent in the holotype. These are described in the redescription below.

Molecular genetic analysis

A phylogenetic analysis across the entire Amphibolurinae group of Agamid lizards provides strong support for phylogenetic placement of *C. aurita* within the genus *Ctenophorus* (**Figure 4**). Based on this phylogenetic placement, we recommend that *C. aurita* be henceforth referred to as *Ctenophorus aurita*. The closest genetic relatives to *Ctenophorus aurita* are the arid-adapted *C. nuchalis* and *C. reticulatus* (**Figure 4**).

Distribution and ecology

Ctenophorus aurita occurs patchily across an area of at least 55,000 km^2 in the monsoon tropics of northwest Australia (**Figure 1**). All detections to-date have occurred in particularly dry areas of this biome where trees are sparse and spinifiex dominates over a broken rocky substrate. *Ctenophorus aurita* frequently shelters under surface rocks in the central Kimberley. Further details about this species' ecology are available in the detailed species redescription below.

Discussion

A review of meristics confirms the central Kimberley individuals are synonymous with *Cryptagama aurita* as originally described. However, genetic analyses place this formerly monotypic species well within the genus *Ctenophorus* Fitzinger, 1843, as a distinctive and early-diverging lineage (**Figure 4**). This placement of a pebble-mimic dragon within *Ctenophorus* requires an expansion of the defining characters for this genus, including removing the requirement for *Ctenophorus* to possess an enlarged row of scales below the eye as outlined in Storr et al. (1983) and Melville & Wilson (2019). This new phylogenetic knowledge has implications for understanding the diversification and evolution of body form in Australian lizards, particularly the *Ctenophorus* genus.

Morphologically and ecologically, *C. aurita* resembles pebble-mimic dragons (*Tympanocryptis* spp.) that occupy rocky and stony areas of arid Australia (Storr 1981; Shoo et al. 2008; Doughty et al. 2015). Pebble-mimic dragons have round heads and bodies, red-orange colour with little or no pattern, and short legs that tuck close to their sides to render them virtually invisible as they nestle among small gibber stones (Melville & Wilson 2019). This also describes the colour, body shape, behaviour and ecology of *C. aurita* (**Figures 2, 3, 5, 6 & 8**). However, our genetic analysis demonstrates that *C. aurita* sits well within the *Ctenophorus* genus. As such, *C. aurita* and the pebble-mimic dragons of the *Tympanocryptis* genus are an example of morphological convergent evolution within the Australian agamid radiation. Morphological convergence in reptiles is known to occur from occupying a similar ecological niche (e.g. Luke et al. 1986; Hibbitts & Fitzgerald 2005). Consequently, a detailed analysis of the morpho-evolutionary and eco-evolutionary patterns of these two genera is warranted.

Biogeography

The Kimberley region is a geologically and ecologically unique region within the Australian Monsoon Tropics (Pepper & Keogh 2014). It is recognised as a biodiversity hotspot in Australia (Slatyer et al. 2007; Powney et al. 2010), where taxa have deep phylogenetic histories and high levels of endemism to a degree that is not found anywhere else on the continent, particularly for reptiles and amphibians (Oliver et al. 2012; Pepper & Keogh 2014). These divergences often correlate with current and ancient geographical formations such as drainage lines, basins and mountain ranges (e.g. Pepper et al. 2011a; Oliver et al. 2012, 2016).

Ctenophorus aurita occurs on either side of (and on) the rugged Wunaamin-Miliwundi Ranges, and on either side of the extensive Martuwarra/Fitzroy River catchment, suggesting these significant local geographical features may not be barriers to dispersal. The continuity of recorded, inferred and potential habitat across the distribution of *C. aurita* (**Figure 7**) suggests this species is unlikely to be fragmented into subpopulations. However, a genetic assessment that includes individuals from the east of this species' distribution will enable the degree of genetic connectivity to be analysed. It is highly likely that additional sites where *C. aurita* occurs will be discovered within, and probably beyond, its recorded range.

Conservation implications

Population abundance and trend information is not currently available for any site where *C. aurita* occurs. However, the cluster of observations in the central Kimberley from 2016–2023 has provided insight into this species' ecology and distribution.

It is unlikely that *C. aurita* is at risk of extinction because it occurs in common ecosystem types (i.e. rocky areas that are dominated by *Triodia* spp.) across a broad geographic range (> 50,000 km^2) encompassing very remote areas. The cryptic habits of *C. aurita* and its occurrence

in areas where few people live and traverse mean it easily eludes detection. It is unlikely that this species is genuinely rare. Further searches and genetic sampling are required to determine if there is subpopulation structuring. Standardised population monitoring is required to identify and understand population trends and their drivers.

A particular resource, such as a shelter site, thermal niche, or a specific food resource, may be driving temporal and/or spatial patchiness in the distribution of *C. aurita* (Manly et al. 2002; Kearney & Porter 2004; Bruton et al. 2014). Limited survey effort indicates that this species may be most detectable following a wet season with above average rainfall. Detectability appears to be highest in the morning and the warmest part of the day, when lizards are actively foraging.

Taxonomy

Ctenophorus aurita comb. nov. (Storr, 1981)

Fig. 3, 5-8

Tympanocryptis aurita (Storr 1981)

Amphibolurus auritus (Cogger 1983)

Cryptagama aurita (Witten 1984)

Phthanodon aurita (Wells & Wellington 1983)

Cryptagama aurita (Wilson & Knowles 1988)

Cryptagama aurita (Cogger 2000)

Cryptagama aurita (Wilson 2012)

Cryptagama aurita (Cogger 2014)

Cryptagama aurita (Doughty et al. 2017)

Cryptagama aurita (Melville & Wilson 2019)

Cryptagama aurita (Wilson & Swan 2021)

Cryptagama aurita (Jolly et al. 2023)

Common name: Hidden dragon.

Holotype: WAM R66296, female, 27 km SSE of Halls Creek, Western Australia (18°27'S, 127°45'E). Collected by M.C. Ellis on 4 September 1979 (Storr 1981).

Paratypes: WAM R64051–2, juveniles, 0.4 km W of Wolf Creek Meteorite Crater, Western Australia (19°107'S, 127°48'E). Collected by A.A. Burbidge on 22 April 1979 (Storr 1981).

Additional material: WAM R177990–92 and AMS R186655–57 (specimens); WAM TR1103–07, WAM TR1119–22, WAM TR2221, WAM TR2254, WAM TR2262–TR2274 (tail tissue only). See **Supplementary Data** for details.

***Diagnosis*.** A small-bodied (to 46 mm SVL), short-tailed (TL<SVL), and robust dragon with a round head (**Figure 3**). It has a broadly rounded canthus rostralis, a clearly visible tympanum, a distinctive supralabial fringe of 16–18 vertically elongate scales that protrude past the mouth, heterogenous scales on its dorsal surfaces (fine scales with scattered enlarged tubercles), and the dorsolateral edge tends to have a row of enlarged scales. It is differentiated from all other species of *Ctenophorus* by lacking a conspicuously enlarged series of scales from below the eye to the ear (**Figure 5b,d**). Occurs in areas of broken rock and rubble with sparse trees and a dominant cover of spinifex within drier areas of the monsoon tropics in northwest Australia.

General morphology. A small (SVL ~40 mm) and rotund *Ctenophorus* with an extremely blunt head (**Figure 5b**) and a wide neck that is only weakly defined when viewed from above (**Figure 5a**). The gular fold is prominent (**Figure 5f,h**). There is often a distinctive, continuous or broken, lateral fold/ridge from above the shoulder that runs along the dorsolateral zone, following the outline of the body, before abruptly terminating above the hind limb (**Figure 3**). Limbs are short and slender and the tail is short and blunt-tipped (**Figure 3**). Finger length 4>3>2>5>1 and toe length 4>3=5>2>1. Claws are long and recurved.

Dorsal and lateral colour. Light yellow-brown infused with rich red hues (particularly near the midline) and yellow (particularly on enlarged tubercles) (**Figure 3**). The crown and nape usually have some darker blotches (**Figure 5a**). Upper labials have a slight indication of darker mottling (**Figure 3, Figure 5b,d**). The zone below the dorsolateral ridge in some individuals is light to darkly pigmented in dark olive to black, which extends to the lateral surface of the tail, where it tends to break up into distinct blotches or bars (**Figure 3**). There are scattered dark spots on the upper surfaces of the limbs (**Figure 3**).

Ventral colour. Pale off-white that contrasts with the dorsal colour in the lateral regions. Gular region is pale off-white to lightly stippled with black, especially near the posterior edge. Males display breeding colours on their venter during the late dry season (September, **Figure 5h**), whereas no ventral markings are evident in the cooler mid-dry season (June, **Figure 5f**). In individuals with breeding colouration, a short and narrow faint

Figure 5. Key morphological characters on live *Ctenophorus aurita* from the central Kimberley: a) average size relative to an adult human hand; b & d) clearly visible tympanum, no conspicuously enlarged series of scales from below the eye to the ear, a fringe of scales along the upper lip, and a broadly rounded canthus rostralis; c & e) variation in dorsal scales including relative size and colour of enlarged tubercles; d) keeled scales on top of the head and pointed tubercles on the neck; f & h) variation in ventral colour and markings; and g) pre-anal and femoral pores. Photos: Stephen Mahony (a,c,d,e,f) and Melissa Bruton (b,g,h).

Figure 6. Habitat of *Ctenophorus aurita* in the central Kimberley: Throssell Shale (top left and right, bottom right) and Wunaamin-Miliwundi Sandstone (bottom left). Photos: Joe Porter/Australian Wildlife Conservancy (top left, bottom left, bottom right) and Melissa Bruton (top right).

grey to black triangular chest patch may be present that extends posteriorly from the gular fold to approximately the level of the axilla. The gular fold area, central venter, anterior thighs, and tail are light yellow with the outer edges of these yellow areas being a darker shade of orange. The outer venter occasionally has irregular dark mottling near the lateral edge (**Figure 5h**).

Pores. Total 10–16. Pre-cloacal pores 4–6, with no pores near the midline and 2 or 3 grouped together on either side of the midline. Femoral pores are widely spaced in the middle to anterior of the thigh, extending across the thigh almost to the knee. All pore perforations are small and positioned in the middle of the scale (**Figure 5g**).

Dorsal scales. Scattered large tubercles with raised keels on the dorsal and lateral surfaces, encircled by slightly enlarged and raised scales (**Figure 5c,e**). However, large tubercles in the vertebral zone are not surrounded by a ring of slightly enlarged scales. Other dorsal scales are relatively flat and irregularly shaped with moderate keels that align to form longitudinal ridges. Some scales are enlarged and have more prominent keels, especially on the lower arm. Rows of keels continue from limbs onto digits. Scales on the lateral surfaces are smaller than on the dorsum, they are raised, and they occur in regular diagonal rows. Legs have enlarged keeled scales that are more prominent and numerous on the upper thigh. Keels on the tail scales form raised ridges, as for limbs and digits, with occasional scattered enlarged tubercles on lateral and dorsal surfaces.

Ventral scales. Ventral scales are diamond-shaped and slightly overlapping. They have a low, weak keel and a posterior spine that does not protrude past the posterior edge of the scale. Gular scales are small and juxtaposed with feeble keels. Scales on the gular fold are smooth and reduced in size relative to ventral scales. Lower surfaces of arms: as for dorsal surfaces but with lower keels. Palmar and plantar scales have sharp keels. Subdigital scales have two rows of keels forming longitudinal mucronate ridges.

Head and nuchal scales. Scales on top of the head are rugose with low, irregular keels. Nuchal area has slightly larger rugose scales around the pineal gland and scale. Scales posterior to the crown/on the neck have scattered conical tubercles. Brow has two rows of scales with aligned longitudinal keels. Eyelid with ~5 rows of scales above the aperture and 6–7 scales below. Projecting scales form a fringe where the upper and lower

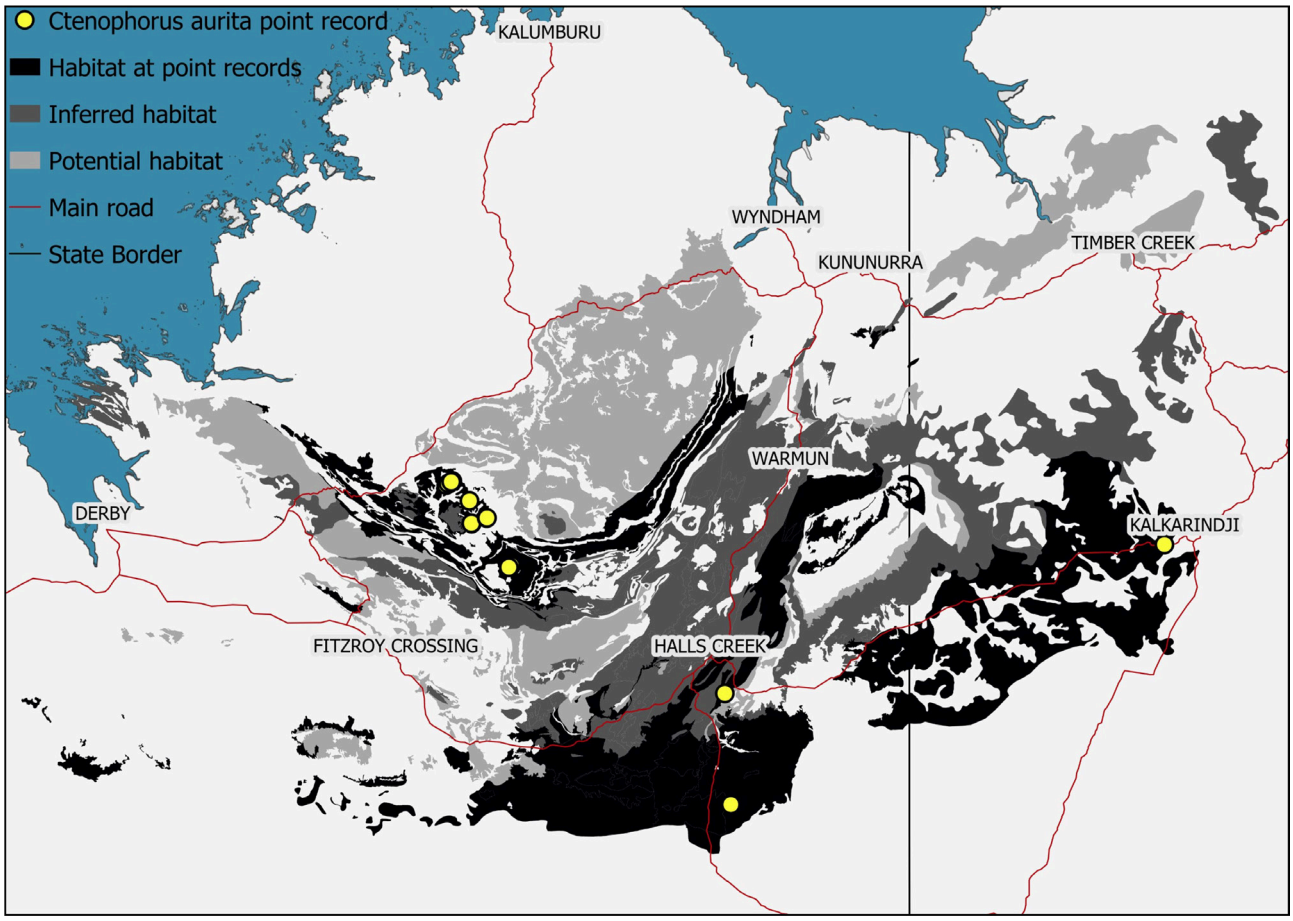

Figure 7. Distribution of *Ctenophorus aurita* based on all records from 1979–2023 (yellow dots), extent of recorded habitat based on mapped and observed ecosystems at detection sites (black), extent of additional areas that are likely to support habitat based on other ecosystem types in the area that have the same habitat attributes as detections sites (dark grey), and areas with potential habitat based on additional mapped ecosystem types with a rocky substrate and a ground cover that is dominated by spinifex (pale grey). Vegetation mapping (Fox et al. 2001) is clipped to tropical savanna bioregions; additional habitat may occur further south.

Figure 8. A *Ctenophorus aurita* displaying pebble-mimicking behaviour on a large stone (left) and two individuals detected under the same rock on successive days (right). Photos: Stephen Mahony (left) and Melissa Bruton (right).

eyelids meet. There are scattered enlarged tubercles between the eye and the tympanum and one or two moderately enlarged tubercles with horizontal keels between the eye and the corner of the mouth. The nostril is slightly below the canthus rostralis: it perforates an enlarged scale near the dorsal edge and opens dorsally. The rostral scale is small and triangular with dorsal edges that are usually concave to slightly convex. The snout is extremely blunt, nearly vertical. Posterior supralabial scales have prominent vertically-oriented keels. Infralabial scale row has horizontal keels on the ventral part of each scale, with the dorsal half smooth where the supralabial denticulate row is in contact when the mouth is closed. Scales in the parinfralabial row are rectangular with horizontal keels in the centre of each scale: the next 3–4 rows of scales are slightly enlarged

with feeble keels. The mental scale is triangular with the ventral edge tapering to a blunt point and extending 1.5–2.0 times beyond the first infralabial scales.

Known distribution. Recorded sparsely from the Kalkarindji area of the Northern Territory to the Hann River area of the Kimberley in Western Australia; specifically at Kalkarindji, Kandimalal, near Hall's Creek, and in the vicinity of Mornington Wildlife Sanctuary in the central Kimberley. Although it is currently unclear how far north, east, or west this cryptic species may occur, the northern boundaries of the Great Sandy Desert to the south and Tanami Desert to the southeast correlate with species boundaries for several other reptiles (see Pepper et al. 2011a,b; Oliver et al. 2014; Maddock et al. 2015). The recorded extent of occurrence (EOO) is 55,600 km^2 based on a minimum convex polygon boundary around all point records from 1979–2023.

Habitat. Consistently detected in mapped (DMIRS 2019) and observed areas of exposed bedrock with loose surface rock and a sparse to dense cover of *Triodia* spp. (spinifex) (**Figure 6**) (Storr 1981). Observed sheltering in shallow scrapes under thick surface rock – and occasionally cow manure – and within sparse to thick clumps of spinifex. Often detected at the top of ridges and rises, where exposed bedrock plates fracture into smaller rocks and tiles that provide an abundance of shelter sites. Mapped (DMIRS 2022) and observed geology and surface structure varies among regions and sites:

1. Kandimalal: two detections from an area with rocks and rubble that has weathered from a complex intermixture of Miocene laterite, Devonian sandstone and meteorite shale balls (Shoemaker et al. 2005). Described by Storr (1981) as a 'lateritic plain'.

2. Halls Creek area: Mapped as the Olympio formation of metasedimentary sandstone, siltstone, mudstone and shale. Described by Storr (1981) as a 'stony hillside'.

3. Central Kimberley Throssell Shale formation: Micaceous siltstone and shale. Most sites have a patchy to continuous cover of loose flat gravel and pebbles over skeletal soil with scattered flat or rounded boulders and cobbles. Also detected in areas with expansive broken sheets of large, flat siltstone and shale tiles (**Figure 6**).

4. Central Kimberley Wunaamin-Miliwundi Sandstone formation: Quartz sandstone pavement with a scattering of cobbles and boulders **(Figure 6).**

Spinifex cover at recorded sites varies from low, sparse, and open patches to medium-sized hummocks and swathes (**Figure 6**)**.** Dominant spinifex species include *Triodia aeria, T. bitextura, T. epactia, T. pungens, T. intermedia* and/or *T. wiseana. Sarga* spp. (native sorghums) may occur where soil has developed and accumulated.

Most recorded sites in the central Kimberley have a sparse to very sparse tree or low shrub layer (**Figure 6**), which may be dominated by *Eucalyptus brevifolia*, *Corymbia collina*, *Lysiphylum cunninghamii*, *Grevillia pyramidalis*, *Acacia* spp., *Grevillea* spp. and/or *Hakea arborescens*. *Eucalyptus brevifolia* is the dominant canopy species at the Wunaamin-Miliwundi Sandstone site and it is mapped as the dominant canopy species at the Halls Creek, Kandimalal and Kalkarindji sites (Fox et al. 2001).

Area of occupancy. Three estimates of the potential area of occupancy of *C. aurita* have been mapped and derived (**Figure 7**) based on habitat attributes where this species has been recorded. The extent of the five mapped ecosystem types where *C. aurita* has been detected (dominated by *Triodia* spp. and *E. brevifolia,* **Supplementary Data**) covers an area of approximately 62,000 km^2 (black shading in **Figure 7**). However, there are nine additional mapped ecosystem types in the general area that are also dominated by *Triodia* spp. and *E. brevifolia* (**Supplementary Data**; dark grey in **Figure 7**) adding another 51,000 km^2 of inferred potential habitat. A further five mapped ecosystem types are dominated by *Triodia* spp. and they occur in rocky areas, with or without *E. brevifolia* as a dominant or sub-dominant species (**Supplementary Data**; pale grey in **Figure 7**). As such, *C. aurita* has the potential to occur across an area of 168,000 km^2 or more in the Kimberley and Victoria-Daly regions of northwest Australia.

Behaviour. Frequently detected sheltering under rocks during cooler parts of the day. Active when temperatures are warm; basking on small rocks, cow manure, termite mounds, and at the base of spinifex hummocks. May shelter primarily within spinifex during the hottest part of the day, when ground temperatures can exceed 50°C.

Uses pebble mimicry as a camouflage defence when disturbed (**Figure 8**). Several individuals were observed running a short distance before crouching and pulling their limbs into their body to expertly mimic a pebble. This behaviour can occur even when there is a suitable rock or spinifex clump nearby that offers shelter. Some individuals have been observed darting from the base of a spinifex clump to shelter under a rock.

Density. May occur at variable densities across its distribution. Ten individuals were detected within a 1 ha area during 0.5 person-hours of searching at one site, whereas at another site one individual was observed in a 500 ha search area during ten person-hours of searching. Two individuals were detected sheltering under the same large rock on successive days at a Throssell Shale site (**Figure 8**). A comprehensive search on the second day by four ecologists revealed two further individuals under different rocks within 150 m of the original capture point, and a fifth individual 1.2 km away. Three individuals were found under different rocks during 3 hrs of comprehensive searching at a different Throssell Shale site in September 2016, an approximately 200 ha area

of small, flat pebbles with scattered round surface cobbles and patches of *Triodia aeria*.

Detectability. Cryptic and elusive. Can be difficult to detect. Despite many field trips by experienced herpetologists (including JM & SM), *C. aurita* has not been seen again at its original collection sites (Kandimalal, Halls Creek, and Kalkarindji). Numerous searches by experienced herpetologists (MB, JP et al.) at the same time of year as initial detections have failed to re-detect this species in subsequent years at multiple sites in the central Kimberley. Eight individuals were observed during targeted active searches at a site in the central Kimberley where multiple comprehensive targeted searches had failed to detect this species in previous years.

Disclosures

Nil

Acknowledgments

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This project may never have commenced without the sharp eyes of SM identifying a tiny *C. aurita* on the side of a track while zooming past. It would have stagnated without MB and JP persistently searching for this species in their spare time, and without the genetic wizardry of JS in the lab. It could not have occurred without the ongoing support and contributions of PD and JM with their depth of knowledge about agamid taxonomy, phylogenetics and morphology.

Supplementary Data

10.6084/m9.figshare.29093924

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