Three new species of north-eastern Australian earless dragons (Agamidae: *Tympanocryptis*)

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Abstract

Earless dragons (*Tympanocryptis* spp.) are found in most open dry environments across the Australian continent, with the 23 currently described species inhabiting a variety of ecological niches, from stony desert to tropical woodland or cracking clay savannahs. Recent species delimitation research using genetics (mtDNA, nDNA, SNPs) and geometric morphometric analyses of CT scans identified three genetic lineages of earless dragons that are yet to be described in Queensland, supporting the need for a taxonomic revision. Focussing on this geographic region, we use supporting evidence from a mitochondrial DNA (ND2) phylogeny, along with external morphological assessment, to undertake a taxonomic revision of Queensland earless dragons. Based on these data, we describe three new species of *Tympanocryptis* from the cracking clay grasslands of the Darling Riverine Basin, the Queensland Central Highlands, and the stony open eucalypt woodlands on the Einasleigh Uplands. The revision of these north-eastern Australian earless dragon species provides further taxonomic clarity within the *Tympanocryptis* genus.

Introduction

Earless dragons (genus *Tympanocryptis*) are small, terrestrial agamid lizards endemic to Australia (Melville and Wilson 2019), with 23 species currently described. The genus is found in a range of dry open habitats throughout the continent, including the stony regions of Western Australia, the arid interior, the Nullabor Plain, and tropical and temperate grasslands and woodlands (Shoo et al. 2008, Stevens et al. 2010, Melville et al. 2014, Doughty et al. 2015; Melville et al. 2019a; Melville et al. 2019b).

Earless dragons have diversified, with subsequent speciation, to region-specific arid conditions throughout Australia since the late Miocene, with broad scale radiations across the continent and subsequent geographically

localised divergence of lineages in specific habitats or ecological niches (Shoo et al. 2008). Habitat corridors were a significant factor in the speciation of many arid interior and desert-based taxa during the late Miocene and Pliocene (Chapple and Keogh 2004, Byrne 2008, Mossop et al. 2015, Jobson et al. 2017), including several of the Western Australian *Tympanocryptis* species (Pianka 1972, Shoo et al. 2008, Doughty et al. 2015). Similarly, climatic oscillations during the Plio-Pleistocene drove expansions of the inland arid grasslands and contractions of the coastal humid rainforests in north-eastern Australia (Stocker and Unwin 1989, Kershaw 1994, Travouillon et al. 2009). Dated fossil evidence of *Tympanocryptis* spp. has been found as far east as the Mount Etna caves near Rockhampton (Hocknull 2005), suggesting that arid habitat corridors or grassland expansions had reached near-coastal areas prior to the late Pleistocene.

Several studies have focussed on species delimitation in earless dragons (Smith et al. 1999, Shoo et al. 2008, Melville et al. 2014, Doughty et al. 2015, Melville et al., 2019a; Melville et al. 2019b; Chaplin et al. 2019). However, a revision of the taxonomy of north-eastern Australian *Tympanocryptis* species is still required. There are currently six earless dragon species described in Queensland; *T. argillosa* recorded from Bulloo Downs in far sw Qld, *T. intima* distributed throughout the inland arid stony desert areas, *T. tetraporophora* in stony shrubland and clay grassland areas, and *T. wilsoni*, *T. condaminensis* and *T. pentalineata* on cracking clay grasslands near Roma, the Darling Downs and Normanton, respectively. Recent species delimitation work (Chaplin et al. 2019), integrating data from mtDNA, nDNA, genomic (SNPs) and geometric morphometric analyses of CT scans across the region, provided strong evidence that there are three undescribed lineages occurring in the Darling Riverine Basin, Queensland Central Highlands and Einasleigh Uplands, respectively (Fig. 1). This work found significant genomic and osteological differentiation between the three lineages (Chaplin et al. 2019), supporting the need for futher taxonomic revision within *Tympanocryptis.*

We undertook a taxonomic assessment of the Queensland earless dragons, with the description of three new species. We provide a mitochondrial DNA (ND2) phylogeny to support findings from genomic species deliniation (Chaplin et al. 2019). In addition to published osteological evidence from CT scans (Chaplin et al. 2019), we also provide a external morphological assessment of these new lineages, with a detailed focus on north-eastern Australia.

Methods

Sampling

Taxonomic revisions were undertaken using the *Australian Society of Herpetologists Official List of Australian Species*, updated on 30 June 2022, as the baseline taxonomy (available from http://www.australiansocietyofherpetologists.org/ash-official-list-of-australian-species). The three putative *Tympanocryptis* species (A, B and C) were sampled throughout their known ranges (Fig. 1), incorporating specimens included in previous phylogenomic work (Chaplin et al. 2019). To determine the phylogenetic relationships within the genus we also incorporated samples from all other *Tympanocryptis* lineages, through additional samples from Museums Victoria, Queensland Museum and Western Australian Museum, or GenBank data from previously sequenced samples. *Amphibolurus muricatus*, *Rankinia diemensis and Pogona vitticeps* were used as outgroups. Locality data, museum registration numbers and GenBank accession numbers of all samples are listed in Supplementary Table S1.

Laboratory Protocols

Genomic DNA was extracted from either tail tissue or liver samples using the Qiagen Blood & Tissue Kit (Qiagen, Hilden, Germany) as per manufacturer guidelines. The mitochondrial gene ND2 (987bp) was amplified using the primers (Metf.1 and COIr.aga) and protocols described in Shoo et al. (2008) in 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 ExoSAP-IT (Thermo-Fisher, California, USA) as per manufacturer guidelines, and sent to Macrogen (Seoul, South Korea) for sequencing. Sequence chromatograms were edited and aligned in Geneious 6.1.8 (Biomatters, Auckland, New Zealand).

Phylogenetic Analysis

Pairwise uncorrected genetic distances for the ND2 alignment were calculated in Mega7 (Kumar et al. 2016), with the codon frame set as the 3rd nucleotide position. Where more than one sample was present for a species, the clade was collapsed into a group prior to analysis. A Bayesian phylogeny of ND2 was produced using MrBayes (Huelsenbeck and Ronquist 2001) on the CIPRES Science Gateway (Miller et al. 2010), with two runs of four independent MCMC chains (each 50,000,000 generations long, sampled every 1,000 generations), under a GTR+I+G model with flat priors and no partitioning scheme (determined by the corrected Akaike Information Criterion (AICc) on PartitionFinder2 (Lanfear et al. 2017) on the CIPRES Science Gateway). Tracer v1.6 (Rambaut et al. 2014) was used to check for stationarity and convergence of the chain outputs. The trees were subject to a 25% burn-in in MrBayes, summarised and posterior probabilities obtained.

External Morphology

Seventeen meristic and metric characters previously used in *Tympanocryptis* taxonomy (Melville et al., 2014) and thought to be potentially diagnostic were recorded
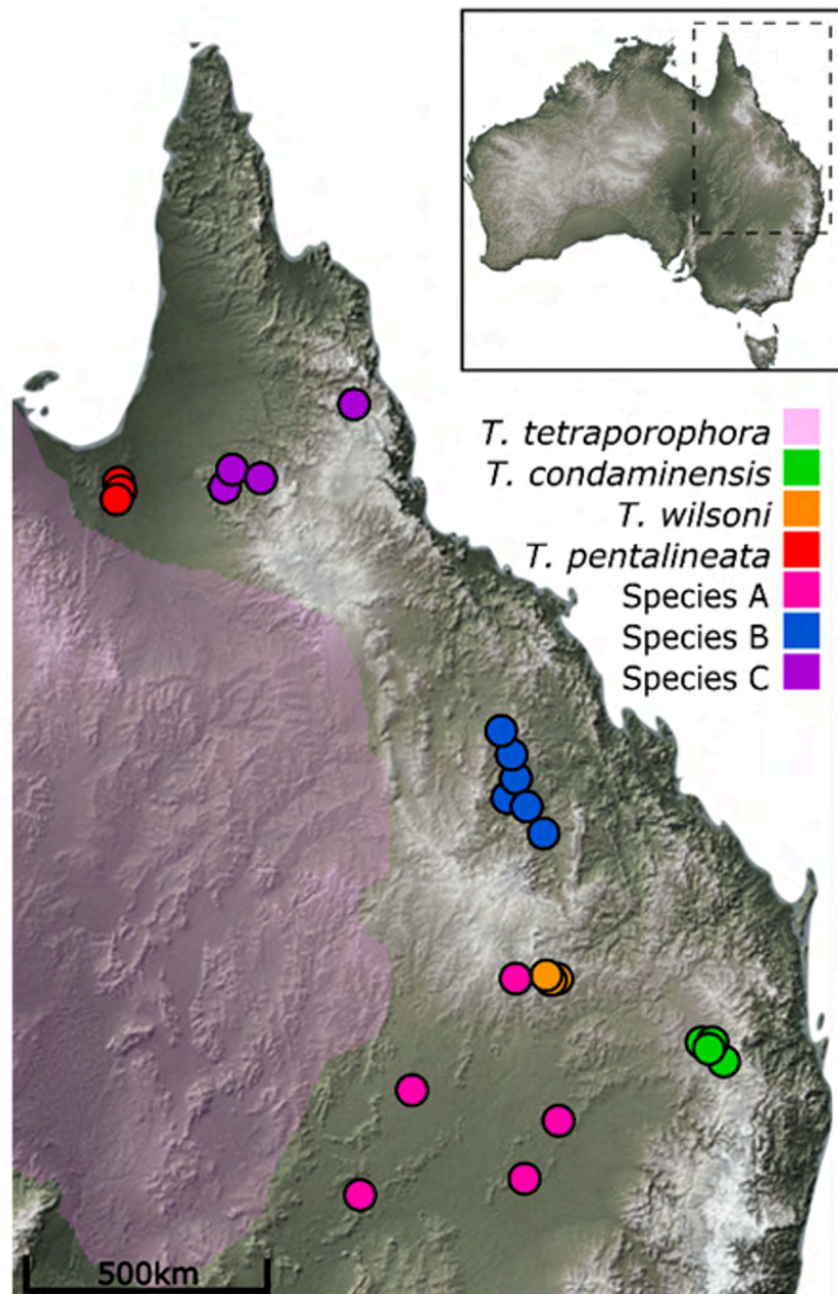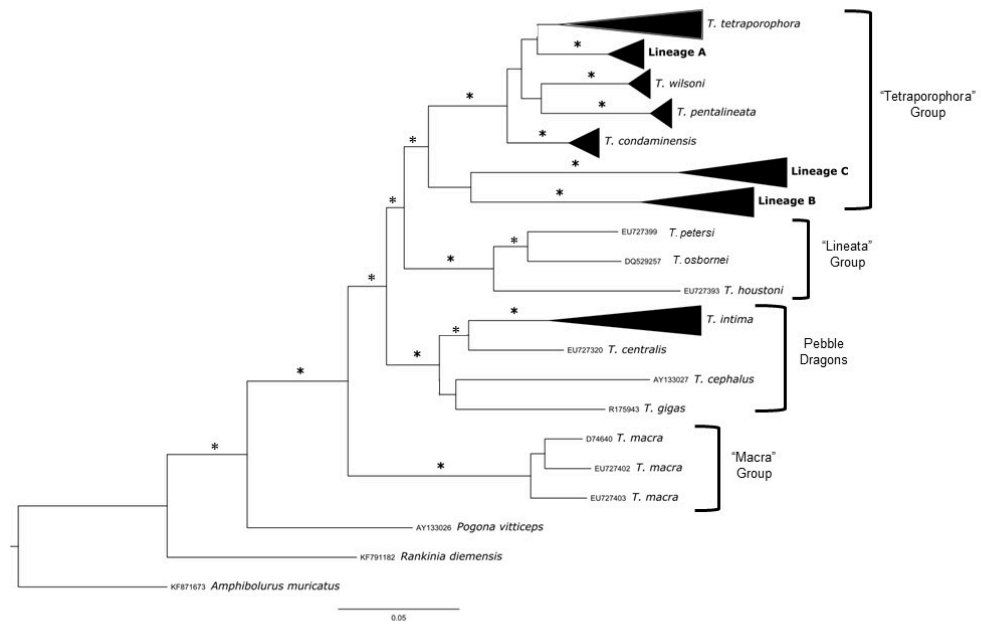
Figure 1. Distributions of north-eastern Australian *Tympanocryptis* species, including specimens included in current study for three putative species (**A**, **B** and **C**). Reproduced from Chaplin et al. (2019).

Results

Phylogenetic Relationships

Previously published phylogenomic data, based on 8783 SNPs across 231 individuals (Chaplin et al. 2019), provided strong evidence of the evolutionary independence of the putative species (A, B and C). Analyses of these data found highly significant ($p<0.001$) pairwise FST results with very high levels of genomic fixation. There was also clear clustering of each lineage using fastSTRUCTURE and distinct grouping in a PCoA, indicating the evolutionary independence of the three lineages (Chaplin et al. 2019). However, this published work did not provide

for the three putative species. Electronic callipers were used for all morphological measures, to the nearest 0.1mm, and all bilateral counts and measurements were recorded on the left side (where possible) and analyses were run in SYSTAT v.13.2. A linear regression was performed on snout-vent length against all other measurements to standardise for size, and the residuals used in further analyses. A Discriminant functional analysis (DFA) was conducted to determine which morphological variables best discriminate between the three putative species.

Figure 2. A Bayesian phylogenetic tree of *Tympanocryptis* lineages and three putative species (A, B and C), using mtDNA (ND2 gene, 987bp). Scale bar indicates the number of nucleotide substitutions per site. Posterior probabilities of clades with support ≥95% are indicated with an asterisk.

the overall phylogenetic placement of these putative species within *Tympanocryptis.*

Our phylogenetic analysis of all *Tympanocryptis* lineages and the three putative species (A, B and C) indicate all taxa are highly supported as monophyletic (Fig. 2), with uncorrected sequence divergence between taxa ranging from 3.4% to 15.5% (Supplementary Table 2). Genetic clades corresponded with previously published phylogenetic relationships (Fig. 2): the "Macra" group (*T. macra*); the Pebble dragons (*T. centralis, T. intima, T. cephalus, T. fortescuensis, T. diabolicus, T. gigas* and *T. pseudopsephos*); and the "Lineata" group (*T. petersi, T. houstoni, T. osbornei*). A fourth lineage (the "Tetraporophora" group), which occurs in central and north-eastern Australia, is that covered in the current study.

Our analyses recovered two clades within the "Tetraporophora" group: one associated with the inland Great Artesian Basin (*T. tetraporophora*, Species A, *T. condaminensis*, *T. wilsoni* and *T. pentalineata*) and a second with the coastal Great Dividing Range (Species B and C). Mean uncorrected pairwise sequence divergence between the Great Artesian Basin (GAB) and Great Dividing Range (GDR) clades was 10.6%, with deep divergences between putative species within each clade. The GDR clade is moderately supported as monophyletic (Bayesian posterior probability of 0.95; Fig. 2), with 13.5% sequence divergence between taxa B and C (Supplementary Table S2). Conversely, the phylogenetic relationships between lineages within the GAB clade are not fully resolved (low Bayesian posterior probabilities, Fig.

2), although each putative species is strongly supported as monophyletic (Bayesian posterior probability of 1.00).

The GAB species group has relatively low sequence divergence between lineages compared with the GDR clade. *T. condaminensis* is the most basal taxon of this group with the lowest pairwise divergences of approximately 4.0% , while *T. pentalineata* has the highest levels of divergence, including 7.0% from the most closely related sister lineage to this species: *T. wilsoni* (Supplementary Table 2, Fig. 2). Each of these species has similar intra-specific lineage divergence, observed in the length of the collapsed species clades, except for *T. tetraporophora*, which exhibits substantial intra-specific clade divergence (Fig. 2).

External Morphology

Although internal skeletal differences in cranial skull shape using CT scans were documented in Chaplin et al. (2019), no assessment of external morphology was provided. Our assessment of external morphology in the putative species (A, B and C) revealed clear differences, particularly in dorsal scalation. There are differences in number and shape of enlarged spinous scales and also whether or not scales are imbricate (further detailed in taxonomic section of this paper). In addition, ventral scales on the torso differ between the putative species with Species C having strongly keeled scales, while the other two have weakly keeled or smooth scales. There is also differentiation based on femoral pores, with Species A having two femoral pores (one on each side), which are absent in the other two species. Finally, body
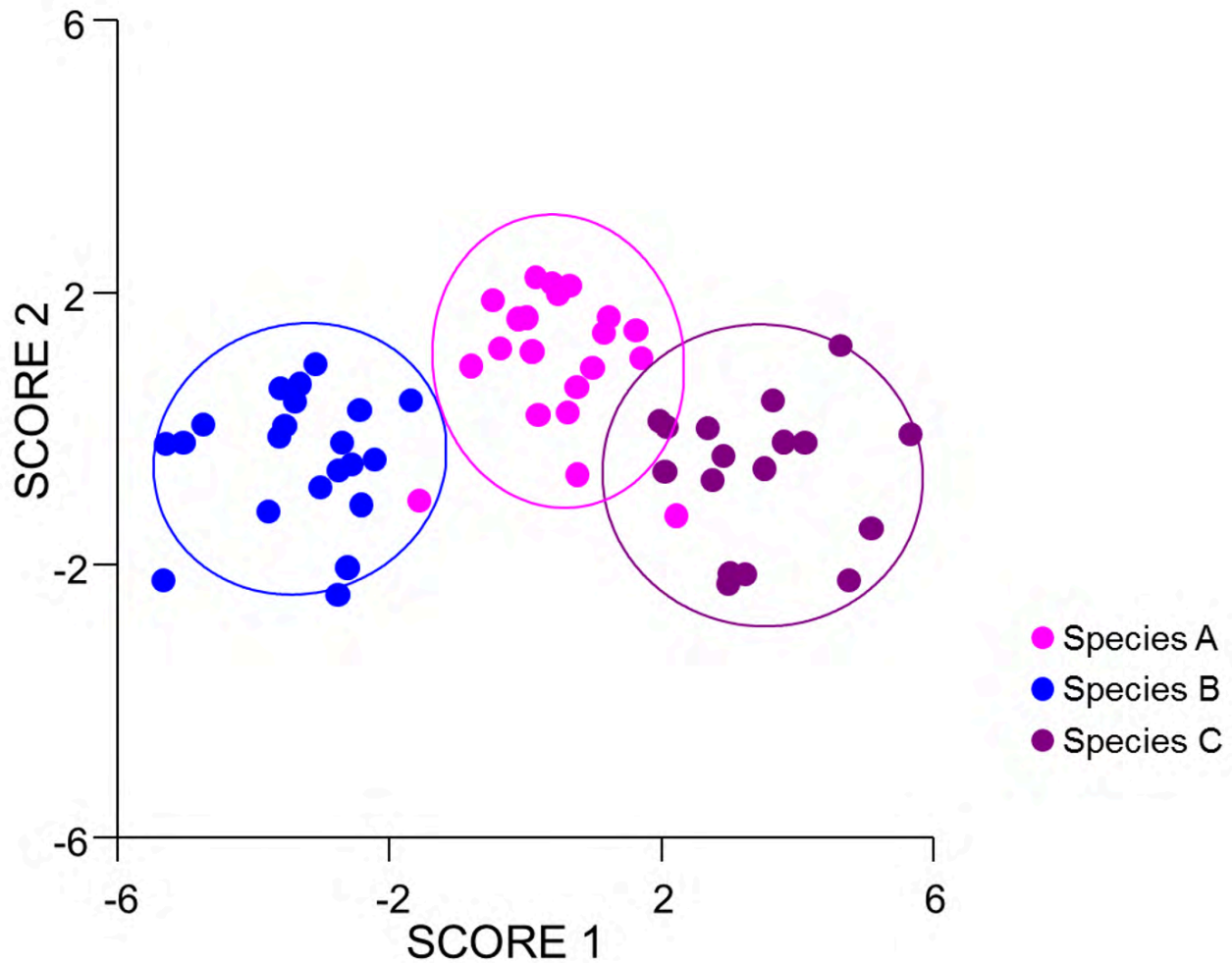
Figure 3. A Discriminant Function Analysis (DFA) of the three putative species (A, B and C), using seventeen external morphological characters. Data included in analyses provided in Supplementary Table S3.

patterning differed between putative species, with differences in the presence/absence and nature of the dorsolateral, vertebral and lateral stripes and also the width of the dark crossbands on the body (detailed fully in the taxonomic section).

We also undertook multivariate analyses of 17 external morphological characters measured as part of this study (Table 1; Supplementary Table S3) to discriminate between putative species. A Discriminant Function Analysis (DFA) of the three putative species (A, B and C) significantly distinguished groups based on external morphology (Wilks' λ8, 2, 56=0.071, F16,98=16.860, p<0.001). The DFA correctly classified 97% of animals (2/ 59 specimens) into the assumed *a priori* species classes, with only two Species A animals being incorrectly classified, one as Species B and one as Species C (Fig. 3). Canonical factor 1 (93.1% of variance), when corrected for within group variance, was associated with head width, neck width and hindlimb length, where Species C had wide heads, narrow necks and short hindlimbs,

while Species B had narrow heads, wide necks and long hindlimbs. On Canonical factor 1, Species A was intermediate between Species B and C. Canonical factor 2 (6.9% of variance), which did not separate species significantly, was associated with tail length and neck width, where high scores had long tails and narrow necks.

Discussion

Strong phylogenetic (mtDNA, nDNA; Chaplin et al. 2019), phylogenomic (Chaplin et al. 2019) and morphological evidence supports that a taxonomic revision of north-eastern Australian *Tympanocryptis* is warranted. In particular, three evolutionary lineages from the cracking clay grasslands of the Darling Riverine Basin (Species A), the Queensland Central Highlands (Species B), and the stony open eucalypt woodlands on the Einasleigh Uplands (Species C) are supported as undescribed putative species (Fig. 1). Divergence times between these earless dragon species of north-eastern Australia are probably similar to other *Tympanocryptis* (Melville et al. 2007, Hugall et al. 2008, Shoo et al. 2008, Doughty et

Table 1. Mean ± standard error (with minimum and maximums in parentheses) values (in mm) of seventeen meristic and metric characters assessed and measured for all specimens of three new species of earless dragons (A, B and C). N = number of specimens, PP = number of pre-anal pores, FP = number of femoral pores, SDL = number of sub-digital lamellae on the fourth toe of the hindlimb, SVL = snout-vent length, ILL= inter-limb length from axilla to groin, HL= head length, HW = head width at the widest point, SW = snout width at the nostrils, HD = head depth, NW = neck width, FLL1 = length of proximal forelimb section, FLL2 = length of mid forelimb section, FLL3 = length of distal forelimb section including claws, HLL1 = length of proximal hindlimb section, HLL2 = length of mid hindlimb section, HLL3 = length of distal hindlimb section including claws.

	Species A	Species B	Species C
N	21	21	17
	(11♂, 10♀)	(12♂, 9♀)	(4♂, 6♀, 7 juvenile)
PP	2±1.33	1.33±0.21	1.29±0.24
	(0.21-0)	(0-2)	(0-2)
FP	0±1.24	0±0	0±0
	(0.22-0)	(0-0)	(0-0)
SDL	21±19.71	28.67±0.43	19.12±0.27
	(0.21-18)	(23-31)	(18-21)
SVL	63±56.29	50.9±1.15	47.18±2.68
	(0.94-51)	(38-59)	(30-63)
TL	79±85.68	70.1±1.72	55.18±4.09
	(1.41-76)	(54-83)	(31-79)
ILL	30.96±25.03	21.41±0.64	19.91±1.55
	(0.67-20.37)	(15.94-28.39)	(11.23-30.96)
HL	23.16±20.48	19.03±0.3	18.05±0.86
	(0.26-18.51)	(14.98-21.04)	(12.06-23.16)
HW	13.7±12.91	11.99±0.24	11.56±0.45
	(0.16-11.91)	(9.82-14.5)	(8.4-13.7)
SW	7.09±5.61	5.39±0.16	5.3±0.18
	(0.08-5.07)	(4.53-8.02)	(4.01-7.09)
HD	9.79±8.56	8.29±0.21	7.83±0.36
	(0.15-6.92)	(5.39-9.99)	(5.67-9.79)
NW	5.82±3.9	4.41±0.19	3.39±0.28
	(0.13-3.06)	(3.04-6.19)	(1.96-5.82)
FLL1	9.27±8.48	8.49±0.18	6.71±0.31
	(0.19-6.76)	(6.95-10.15)	(4.7-9.27)
FLL2	9.51±9.05	8.73±0.18	6.99±0.39
	(0.14-7.71)	(7.26-10.34)	(4.35-9.51)
FLL3	9.09±9.87	9.39±0.2	6.89±0.31
	(0.24-8.05)	(7.47-11.32)	(4.67-9.09)
HLL1	12.83±11.91	11.82±0.3	9.15±0.45
	(0.15-9.95)	(9.35-13.93)	(6.29-12.83)
HLL2	13.4±14.71	14.95±0.28	10.49±0.53
	(0.19-13.14)	(11.86-17.33)	(7.32-13.4)
HLL3	14.03±16.57	18.03±0.32	11.79±0.49
	(0.28-14.47)	(14.93-20.46)	(8.64-14.03)

al. 2015). A rough estimate of 2% divergence per million years (Brown et al. 1982, Wilson et al. 1985), indicates deep divergences between these lineages, dating back to the Plio-Pleistocene (Fig. 2), which corresponds to previous estimates within the genus (Shoo et al. 2008, Melville et al. 2014, Doughty et al. 2015). During the Plio-Pleistocene, climatic fluctuations in north-eastern Australia would have shaped diversification and speciation of *Tympanocrpytis* within this region (Price 2012). The aridification and expansion of grasslands from inland to coastal areas resulted in the restriction of rainforest-specialist taxa to refugia, and vice-versa as the environmental oscillations continued (Martin 1982, Joseph et al. 1995, James and Moritz 2000). Evidence from the fossil records suggest the extinction of many species occurred during this period of instability, although the diversification and/or distributional shifts of more suitably adapted species (especially arid and semi-arid taxa) replaced these losses in the community (Hocknull et al. 2007). These shifts in community composition and species turnover have been well-documented throughout north-eastern Australia, including through dated fossil studies of faunal assemblages (Hutchinson and Mackness 2002, Hocknull 2005, Price et al. 2011). Fossil evidence of *Tympanocryptis* spp. near Rockhampton on the east coast indicate that previous earless dragon species or populations were widely distributed (Hocknull 2005), and the ranges of the extant *Tympanocryptis* species in north-eastern Australia are likely to be a relic of these Plio-Pleistocene climate oscillations.

The two GDR species form one of the most highly diverged clades within *Tympanocryptis*, with particularly long branches in the mitochondrial phylogeny indicating a deep divergence. These two species are the only north-eastern Australian species to be found on the eastern side of significant upland areas of the GDR (Fig. 1). While *T. condaminensis* is found on the Toowoomba plateau of the GDR at higher elevations (up to 500m above sea level) than either Species B or C, the Darling Downs plains slope steadily westwards to the lowlands of the Darling Riverine Plains and Mulga Lands, encompassing the distributions of *T. wilsoni*, Species A and *T. tetraporophora*, with no abrupt elevational variations throughout these areas. The lowlands on the western side of the GDR also extend north through the Mitchell Grass Downs to the Gulf Plains, including the distribution of *T. pentalineata.* Thus, it is probable that divergence within and between the GAB and GDR lineages is highly correlated with geology and topography of the region. Although there have been countless studies of geographic barriers of GDR taxa along latitudinal gradients (James and Moritz 2000, Chapple et al. 2011, Pepper et al. 2014), there is surprisingly little literature published on longitudinal phylogeographic patterns of GDR taxa with sister lineages in the western plains or GAB regions.

There is deep divergence and geographic isolation within the GDR clade. Species B exists on the Central Highlands of Queensland, with rugged escarpments and notable areas of high elevation (including the Drummond Range to the west, Carnarvon Range to the south, and Expedition Range to the east) encircling the species' distribution. In contrast, Species C is distributed across the Einasleigh Uplands region of northern Queensland. The Einasleigh Uplands is a rugged plateau with several escarpments and varied elevation, extending from the Atherton Tablelands in the east to the Gulf Plains in the west (White 1965, Whitehead 2010). The deep molecular divergence and disjunct distributions of Species B and C are consistent with biogeographic breaks in north-eastern Australia, such as the Burdekin Gap and St Lawrence Gap, known to be associated with phylogeographic structure of a range of other herpetofauna (James and Moritz 2000, Chapple et al. 2011, Edwards and Melville 2011, Smissen et al. 2013). Although the paleoenvironmental fluctuations between arid and rainforest conditions in this region are likely to have contributed to the geographic isolation and molecular divergence of the two GDR species, it is possible that the deep branch lengths of these taxa are indicative of intermediate population extinctions, with only remnant lineages still extant, consistent with similar documented Plio-Pleistocene community composition shifts and species turnover (Hocknull 2005).

Taxonomy

Tympanocryptis darlingensis Chaplin, Wilson, Sumner & Melville, sp. nov.

Figs 4 & 5.

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Holotype. QM J96308 (formerly NMV D77151), *male*, Balonne Plains, south of St George, Queensland, Australia (-28.2638, 148.6748).

Paratypes. (9 specimens) NMV D77117, *male*, Stock route off Bollon Rd, Mitchell, Queensland, Australia (-26.4996, 147.9373); QM J96309, *female*, Stock route off Bollon Rd, Mitchell, Queensland, Australia (-26.4996, 147.9374); NMV D77147, *male*, Hortonvale, north of Cunnamulla, Queensland, Australia (-27.9525, 145.7368); QM J96311, *male*, Hortonvale, north of Cunnamulla, Queensland, Australia (-27.9482, 145.7405); QM J96310, *female*, Hortonvale, north of Cunnamulla, Queensland, Australia (-27.9463, 145.7376); NMV D77143, *female*, Hortonvale, north of Cunnamulla, Queensland, Australia (-27.9471, 145.7375); QM J96312, *female*, Balonne Plains, south of St George, Queensland, Australia (-28.2654, 148.6860); NMV D77153, *female*, Balonne Plains, south of St George, Queensland, Australia (-28.2654, 148.6838); NMV D77156, *male*, Myall Plains, Nindigully, Queensland, Australia (-28.3770, 148.6474).
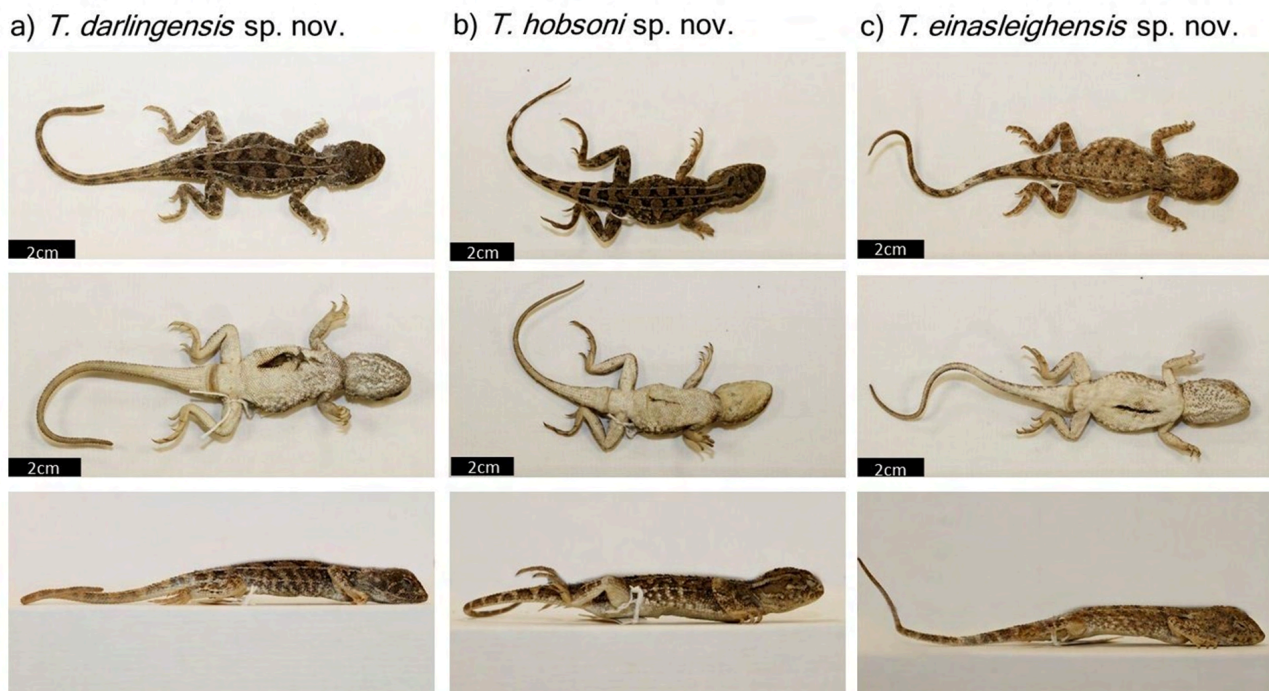
Figure 4. Dorsal, ventral and lateral views of the holotype specimens for three new species of earless dragons; a) *Tympanocryptis darlingensis* sp. nov., b) *T. hobsoni* sp. nov. and c) *T. einasleighensis* sp. nov.

Diagnosis. *Tympanocryptis darlingensis* (Species A) differs from all other species of the genus by enlarged, scattered dorsal scales that are strongly imbricate and strongly keeled; keel terminating in spine; posterior edge of scale very narrowly raised. Small dorsal scales, weakly imbricate and weakly keeled. Narrow to wide dorsolateral stripes that are often discontinuous and only visible on dark cross bands. Dorsolateral stripes approximately same width as vertebral stripe, which is often discontinuous or poorly defined. Usually a well-defined lateral stripe from axial to groin. Dorsal patterning consists of 5 dark crossbands usually wider than pale crossbands. Dorsal surface of head patterned often with pale supra-ocular bar. If present, mottling on ventral surface of head consists of coarsely mottled dark pattern, tending to create diffuse linear white patches in gular region and adjacent to jaw. Two femoral pores (one on each side).

Description of holotype. SVL 54 mm. A medium-sized *Tympanocryptis*, with a slender body and neck, moderately long limbs and tapered snout. Dorsal scales imbricate and heterogeneous, with scattered enlarged scales. These enlarged scales are strongly imbricate, strongly keeled with keel terminating in spine and posterior edge of scale very narrowly raised. Small dorsal scales weakly imbricate, weakly keeled without terminating spine. Ventral scales smooth to weakly keeled. Prominent light grey dorsolateral stripes running from the neck to approximately half way down tail, gradually fading into background colour, approximately same width as vertebral stripe. Continuous vertebral stripe running from neck to pelvis. Five dark brown-black dorsal crossbands

between neck and base of tail, slightly narrow than intervening pale crossbands. Approximately 17 dark bands on tail, slightly wider than intervening pale bands. Flanks with scattered cream flecks on dark background with a narrow pale lateral stripe. Dorsal head patterning present with narrow pale supra-orbital bar. Ventral patterning present, with coarse grey mottling on the head tending for form linear white patches adjacent to jaw, faint grey mottling on upper chest and lateral areas of torso. Pre-anal pores: 2, femoral pores: 2; gular fold present.

Meristic and metric characters of type specimens are provided in Supplementary Table S3.

Variation. Table 1 (as Species A) & Fig. 4. Dorsolateral stripes variable, from narrow to wide and grey or cream, often discontinuous where only visible on dark cross bands, approximately same width as vertebral stripe, which is often discontinuous or poorly defined. Length of dorsolateral stripes variable, terminating on first third of tail or sometimes continuing halfway down tail, while vertebral stripe terminates at pelvis. Usually a well-defined lateral stripe from axial to groin; although sometimes very narrow. Dorsal patterning consists of 5 dark crossbands usually wider than pale crossbands, often disjunct across dorsal stripe. Flanks from side of neck to base of tail has mottling often with dark dorsal crossbands terminating at pale lateral stripe. Dorsal head patterning present, usually with pale supra-ocular bar but sometimes very faint. Ventral surface usually has strong contrasting mottling on head and gular region and often the lateral portions of torso. Mottling
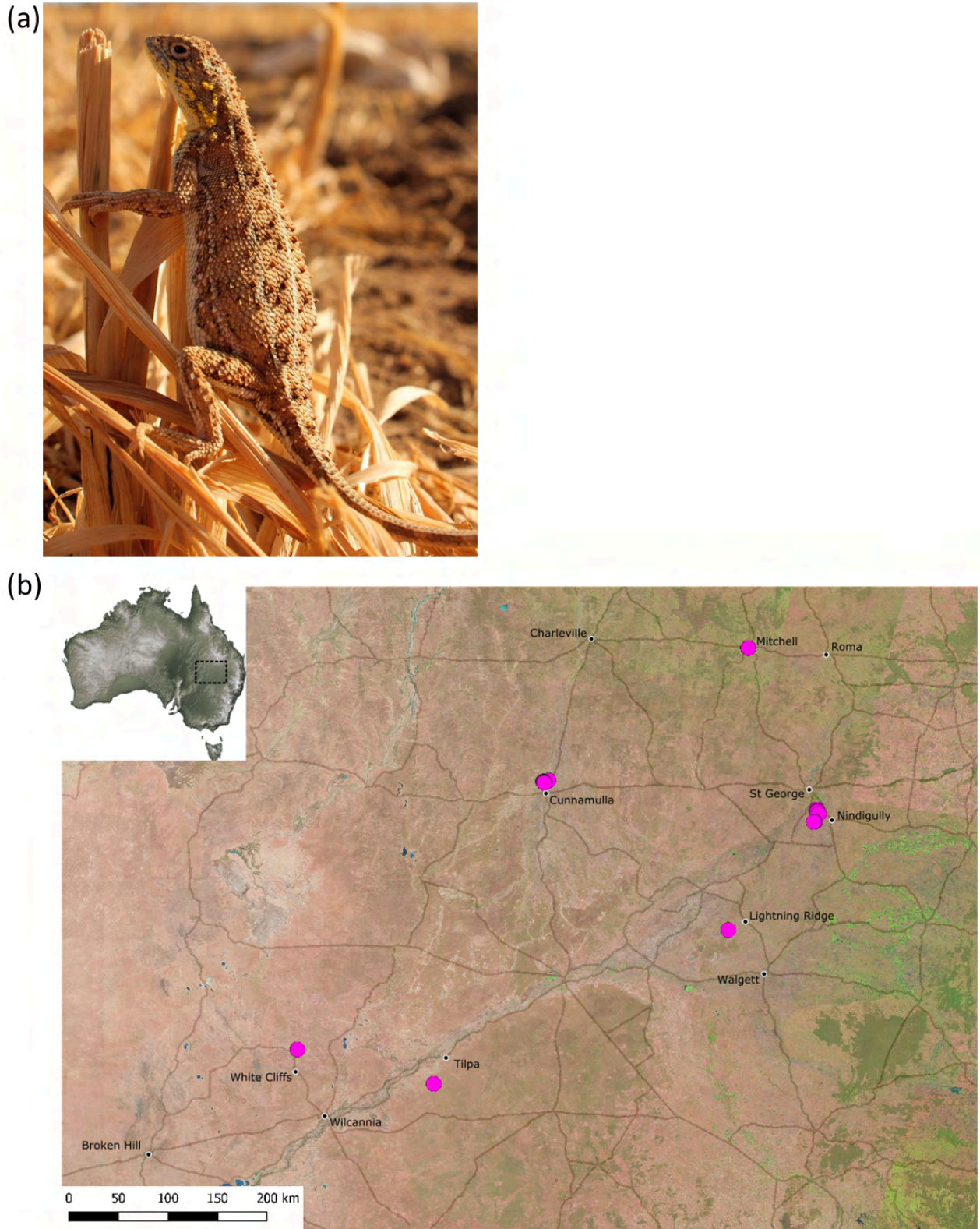
Figure 5. (a) *Tympanocryptis darlingensis* sp. nov.; **(b)** geographic distribution of *Tympanocryptis darlingensis* sp. nov. on the Darling Riverine Plains and Mulga Lands.

on ventral surface of head is coarse and tends to form linear patches of white, towards gular region and adjacent to jaw. Some individuals have strong contrasting mottling extending onto the upper chest. Species has two femoral pores (one on each side), however, they are often difficult to find in females and sub-adults.

Comparison to other species. *T. darlingensis* sp. nov., *T. wilsoni* and *T.tetraporophora* are morphologically very similar. Distribution and colour patterns are the key

characters to distinguish *T. darlingensis* sp. nov. from the other two species. *T. darlingensis* sp. nov. is allopatric to *T. wilsoni,* which occurs east of Amby, QLD. The distribution of *T. darlingensis* sp. nov. is approximately ~30km to the west, on the western side of the Maranoa River in Mitchell. These two species are very similar in appearance but can be somewhat distinguished based on colour and patterning: *T. darlingensis* has a a well-defined lateral stripe from axial to groin, whereas *T. wilsoni* usually has little or no indication of a pale lateral stripe but heavy brown-black speckling along flanks. *T. darlingensis* sp. nov. is probably sympatric with *T. tetraporophora*, however samples of *T. tetraporophora* from the Darling Basin region may have been misidentified and may actually be *T. darlingensis* sp. nov. Body colour of *T. darlingensis* sp. nov. is generally slightly greyer or browner than the rust-red colour of *T. tetraporophora* from sympatric regions.

Habitat. Native grasslands or cropping fields (including wheat, sorghum and chickpea) on grey, brown or red-brown vertosols in Queensland. It is assumed to occupy similar habitat in New South Wales.

Distribution. The distribution of *T. darlingensis* sp. nov. is not yet fully understood but known to occur in the Mulga Lands and Darling Riverine Basin bioregions. Known locations from samples confirmed by molecular data include near Mitchell, Cunnamulla, St George and Nindigully in Queensland, and Lightning Ridge, Tilpa and White Cliffs in New South Wales (Fig. 5).

Common name. Darling earless dragon.

Etymology. Named for the Darling Riverine Plains and Darling Basin this species inhabits.

Tympanocryptis hobsoni Chaplin, Wilson, Sumner & Melville, sp. nov.

Figs 4 & 6.

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**Holotype.** QM J96313, *male*, Retro, Capella North, Queensland, Australia (-22.8606, 147.8763).

Paratypes. (8 specimens) QM J96314, *male*, Retro, Capella North, Queensland, Australia (-22.8604, 147.8761); QM J96315, *male*, Homelea Downs, north of Clermont, Queensland, Australia (-22.6918, 147.6768); NMV D77134, *male*, Homelea Downs, north of Clermont, Queensland, Australia (-22.6936, 147.6762); NMV D77135, *female*, Homelea Downs, north of Clermont, Queensland, Australia (-22.6948, 147.6776); QM J96317, *male*, Glendariwell, Gemfields, Queensland, Australia (-23.6034, 147.8247); NMV D77164, *female,* Glendariwell, Gemfields, Queensland, Australia (-23.6154, 147.8293); NMV D77136, *male,* Orana Downs, Orion, Queensland, Australia (-24.2579, 148.3510); QM J96316, *female,* Orana Downs, Orion, Queensland, Australia (-24.2597, 148.3468).

Diagnosis. *Tympanocryptis hobsoni* (Species B) differs from all other species of the genus by numerous enlarged dorsal scales, not imbricate but strongly keeled with keel terminating in prominent spine; posterior edge of enlarged scales not raised. Small dorsal scales not imbricate and weakly keeled. Wide, continuous dorsolateral stripes, approximately twice as wide as, and more prominent than, vertebral stripe. Usually a narrow lateral stripe from axial to groin. Dorsal patterning consists of 5-6 dark crossbands approximately the same width or slightly narrower than pale background, often disjunct across dorsal stripe. Dorsal surface of head strongly patterned with multiple alternating pale and dark transverse bars from supra-ocular region to snout. If present, mottling on ventral surface of head is coarse but not tending to form linear white patches. Femoral pores absent.

Description of holotype. SVL 51 mm. A medium-sized *Tympanocryptis*, with long limbs, a slender body, and somewhat dorsoventrally flattened skull with a blunt snout. Dorsal scales heterogeneous, with scattered enlarged scales; not imbricate. These enlarged scales are not imbricate, strongly keeled with keel terminating in spine and posterior edge of scales not raised. Small dorsal scales not imbricate, weakly keeled without terminating spine. Ventral scales are unkeeled on the head and neck, and weakly keeled on the torso. Narrow light grey dorsolateral stripes running from behind the eye to approximately a third of the way down the tail, gradually fading into background colour. Dorsolateral stripes approximately twice as wide as the vertebral stripe on the neck, narrowing to the same width as vertebral stripe on the back and tail. Continuous vertebral stripe running from neck to pelvis. Six dark brown-black dorsal crossbands between neck and base of tail, slightly narrower than pale background, disjunct across dorsal stripe. Approximately 12 dark bands on tail, approximately the same width as the intervening pale bands. Flanks with scattered cream flecks on dark background with a narrow pale lateral stripe. Dorsal surface of head strongly patterned with three dark transverse bars from supra-ocular region to snout; dark bars narrower than background colour; prominent white stripe from under eye to tympanum region. Ventral patterning absent. Pre-anal pores 2, femoral pores absent; gular fold present.

Meristic and metric characters of type specimens are provided in Supplementary Table S3.

Variation. Table 1 (as Species B) & Fig. 4. Dorsolateral stripes variable, from narrow to wide and grey or cream; dorsolateral stripes often twice as wide and more prominent than vertebral stripe; dorsolateral stripes usually wider on neck becoming more narrow on back, often continuing anteriorly along neck onto head and culminating in 'C'-shaped arc (bounded dorsally by black) to the dorso-posterior portion of the orbit. Length of dorsolateral stripes variable, terminating on first third
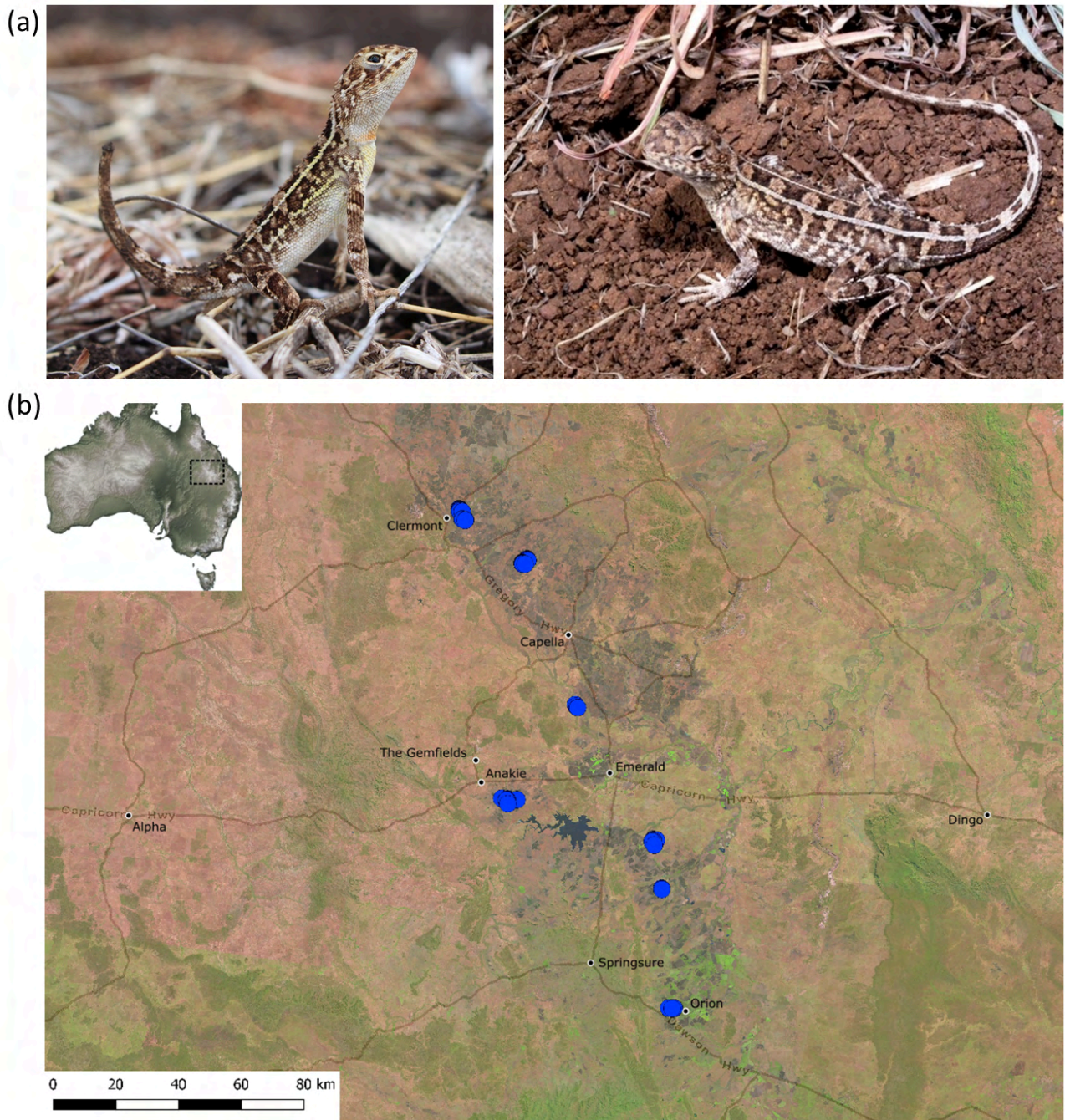
Figure 6. (a) *Tympanocryptis hobsoni* sp. nov. in life; **(b)** Geographic distribution of *Tympanocryptis hobsoni* sp. nov. on the Queensland Central Highlands.

of tail or sometimes continuing halfway down tail, while vertebral stripe terminates at pelvis. Lateral stripe usually narrow from axial to groin; although sometimes indistinct. Dorsal patterning consists of 5-6 dark crossbands usually similar width to pale crossbands but sometimes slightly narrower, usually disjunct across dorsal stripe. Dorsal head patterning usually strong although somewhat variable with some individuals having a diffuse dark transverse bars from supra-ocular region to snout and somewhat indistinct pale stripe from under eye to tympanum region. Ventral surface usually has mottling on head and gular region and in

a few individuals the lateral portions of torso; some individuals lack ventral patterning. Males have longer tails and pre-anal pores can be difficult to distinguish in females.

Comparison to other species. The distribution of *T. hobsoni* sp. nov. is isolated from other *Tympanocryptis* taxa, with *T. tetraporophora* being the closest species (approximately 200 km to the west of the known range of *T. hobsoni* sp. nov.). However, *T. hobsoni* sp. nov. can easily be distinguished by the lack of femoral pores, compared with 2 femoral pores in *T. tetraporophora*. Additionally, *T. hobsoni* sp. nov. has an unusually long

second toe on the hindlimbs (Table 1), compared with other *Tympanocryptis* species.

Habitat. Native grasslands or cropping fields (including wheat, sorghum and chickpea) on black vertosols.

Distribution. Currently known to exist in populations on cropping lands to the north, west and south of Emerald, adjacent to the Dawson, Gregory, Capricorn and Peak Downs Highways on the Queensland Central Highlands, bordered by Orion in the south, Clermont in the north and Anakie in the west (Fig. 6).

Common name. Emerald earless dragon.

Etymology. Named in recognition of the outstanding contributions of Rod Hobson to the conservation of *Tympanocryptis* species and Queensland herpetology, and his direct input into the collection and ecological understanding of this new species on the Central Highlands.

Tympanocryptis einasleighensis Chaplin, Wilson, Sumner & Melville, sp. nov.

Figs 4 & 7.

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Holotype. QM J96318, *male*, Richmond Rd, north of Esmeralda, Queensland, Australia (-18.5672, 145.5626).

Paratypes. AUSTRALIA: Queensland: (7 specimens) NMV D77187, male, Richmond Rd, north of Esmeralda (-18.5649, 142.5646); QM J96320, male, Richmond Rd, north of Esmeralda (-18.5645, 142.5651); QM J96322, male, Richmond Rd, north of Esmeralda (-18.5616, 142.5682); NMV D74081, female, Richmond Rd, north of Esmeralda (-18.5619, 142.5678); QM J96319, female, Richmond Rd, north of Esmeralda (-18.5675, 142.5625); QM J96321, female, Richmond Rd, north of Esmeralda (-18.5645, 142.5651); NMV D77265, female, Thornborough Rd, south of Thornborough (-16.9991, 145.0312).

Diagnosis. *Tympanocryptis einasleighensis* (Species C) differs from all other species of the genus by scattered enlarged dorsal scales, weakly imbricate but strongly keeled with central keel terminating in a weak spine; posterior edge of enlarged scales very narrowly raised. Small dorsal scales weakly to strongly keeled without terminating spine, weakly imbricate. Vertebral, dorsolateral and lateral stripes usually absent. If dorsal patterning present, consists of 5-6 dark narrow crossbands, poorly defined and much narrower than intervening pale background colour. Dorsal surface of head weakly patterned or unpatterned, sometimes with faint pale supra-ocular bar. If present, mottling on ventral surface of head is very fine speckling and not forming linear white patches. Femoral pores absent.

Description of holotype. SVL 54 mm. A medium-sized *Tympanocryptis*, with a stocky shape; short limbs, a round body, long head and blunt snout. Dorsal scales heterogeneous, with scattered enlarged scales; weakly imbricate. Enlarged scales are weakly imbricate, strongly keeled with keel terminating in weak spine; posterior edge of scale very narrowly raised. Small dorsal scales weakly imbricate, weakly to strongly keeled without terminating spine. Ventral scales weakly keeled. Indistinct, broken dorsolateral stripes running from the shoulders to pelvis. Vertebral stripe absent. Indistinct, diffuse crossbands between neck and base of tail, narrower than background colour. Approximately 12 dark bands on tail, narrower than intervening pale bands. Flanks with scattered cream flecks on darker background; lacking distinct lateral stripe. Dorsal head patterning weak and indistinct; lacks pale supra-orbital bar. Ventral patterning present; fine grey speckling under chin, extending posteriorly onto throat; lacks speckling on torso. Pre-anal pores 2, femoral pores absent; gular fold present.

Meristic and metric characters of type specimens are provided in Supplementary Table S3.

Variation. Table 1 (as Species C) & Fig. 4. Vertebral, dorsolateral and lateral stripes usually absent. Broken, indistinct dorsolateral stripes in some individuals from the neck up to 1/3 of the way down the tail. If dorsal patterning present, consists of 5-6 dark narrow crossbands, poorly defined a much narrower than intervening pale background colour. Dorsal surface of head weakly or not patterned, sometimes with faint pale supra-ocular bar. Dorsal colour variable, ranging from red to light brown; spines on dorsal keeled scales varies from a light red-brown to a very dark brown-black. Males generally have stronger dorsal patterning than females. Flanks usually dark, sometimes with contrasting pale flecking or mottling. Ventral surface variable, from plain to mottling on head and gular region and in a few individuals the lateral portions of torso.

Comparison to other species. This distribution of *T. einasleighensis* sp. nov. appears not to overlap with any other *Tympanocryptis* species. It occupies the Einasleigh Uplands region of northern Queensland, with the closest sister taxa found over 180km away, to the south and west of Normanton (*T. pentalineata, T. tetraporophora* and *T. intima*). It can be distinguished from these species by the lack of five distinct longitudinal stripes (observed in *T. pentalineata*), lack of femoral pores (a key characteristic of *T. tetraporophora*) and scattered mucronate dorsal scales (normally in longitudinal rows in *T. intima*).

Habitat. Open eucalypt woodland on stony red rudosols or podosols, in rugged or undulating terrain.

Distribution. Currently known from several locations on the Einasleigh Uplands; along Richmond Rd and Inorunie Rd east of Croydon, Elizabeth Creek near Talaroo, the north-western area of Undara National Park and near Thornborough (Fig. 7).

Common name. Einasleigh earless dragon.
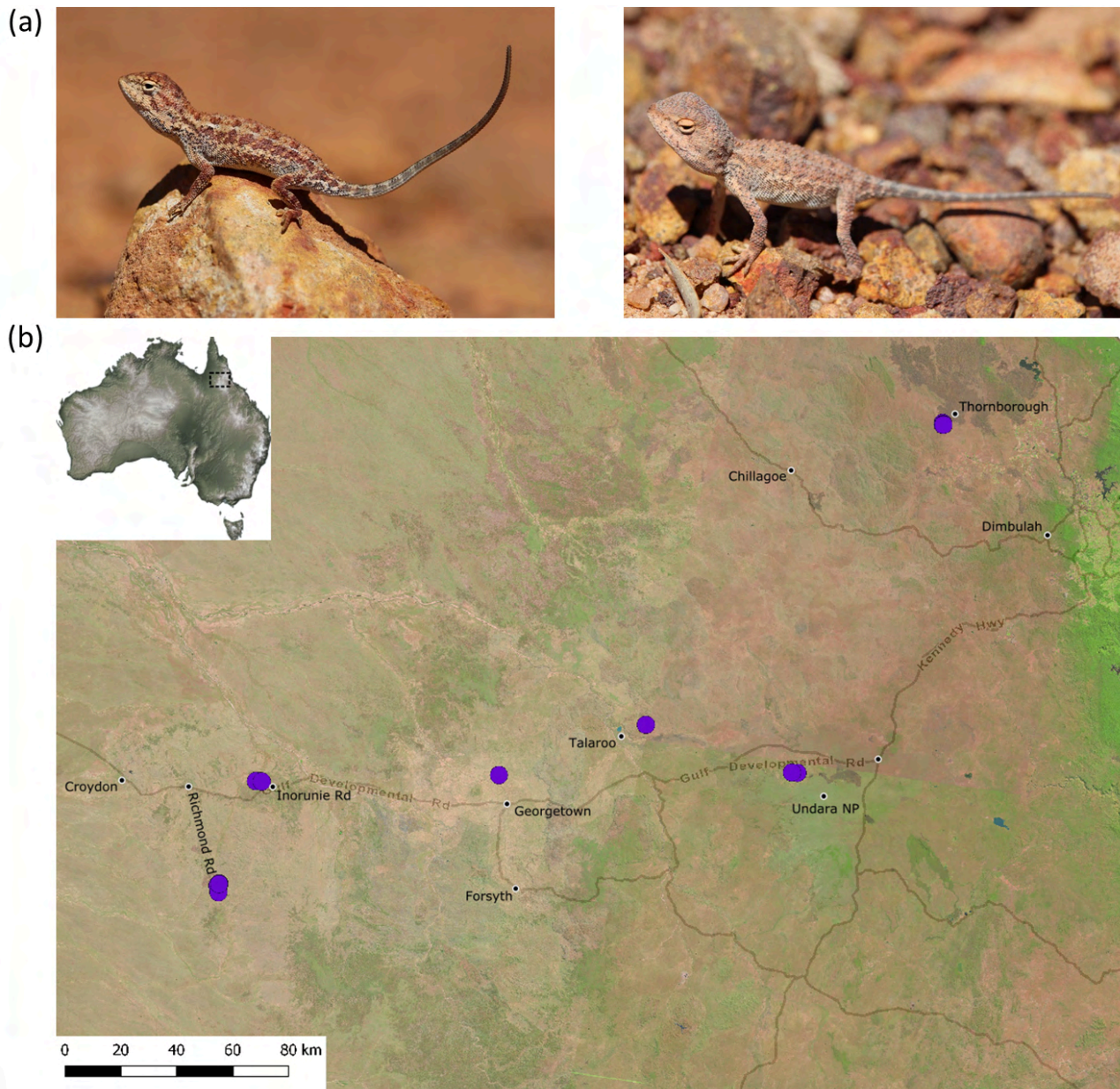
Figure 7. (a) *Tympanocryptis einasleighensis* sp. nov. in life; **(b)** Geographic distribution of *Tympanocryptis einasleighensis* sp. nov. on the Einasleigh Uplands.

Etymology. Named for the bioregion this species occupies.

Acknowledgments

Supplementary Data

Supplementary Tables. https://doi.org/10.26180/19799458

Supplementary Table S1. Museum registration and locality data for specimens used in this study.

Supplementary Table S2. Pairwise uncorrected genetic distances.

Supplementary Table S3. Seventeen meristic and metric characters of type specimens.

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