

1447-2554 (On-line)

<http://museumvictoria.com.au/about/books-and-journals/journals/memoirs-of-museum-victoria/>

DOI <https://doi.org/10.24199/j.mmv.2019.77.01>

## Taxonomic revision of dragon lizards in the genus *Diporiphora* (Reptilia: Agamidae) from the Australian monsoonal tropics

(<http://zoobank.org/urn:lsid:zoobank.org:pub:08B3925A-6720-44E4-BF1C-EED106581DD4>)

JANE MELVILLE<sup>1\*</sup>, KATIE SMITH DATE<sup>1</sup>, PAUL HORNER<sup>2</sup> AND PAUL DOUGHTY<sup>3</sup>

<sup>1</sup> Department of Sciences, GPO Box 666, Museum Victoria, Melbourne, Victoria, 3001, Australia.

<sup>2</sup> Museum and Art Gallery of the Northern Territory, GPO Box 4646, Darwin, Northern Territory, 0801, Australia (current address: Cannonvale, Queensland, 4802, Australia).

<sup>3</sup> Department of Terrestrial Zoology, Western Australian Museum, 49 Kew St, Welshpool, Western Australia, 6016, Australia.

\* Corresponding author: [jmelv@museum.vic.gov.au](mailto:jmelv@museum.vic.gov.au)

### Abstract

Melville, J., Smith Date, K.L., Horner, P., and Doughty, P. 2019. Taxonomic revision of dragon lizards in the genus *Diporiphora* (Reptilia: Agamidae) from the Australian monsoonal tropics. *Memoirs of Museum Victoria* 78: 23–55.

The Australian dragon lizard genus *Diporiphora* currently comprises 21 species based on genetic and morphological evidence, with 11 of these species occurring in the monsoonal tropics of northern Australia. *Diporiphora* are climbing lizards that are found on either trees, grasses or rocks, with usually only subtle morphological differences to distinguish between species. Since the last taxonomic treatment of this genus in northern Australia over 40 years ago, species delimitation using genetic techniques has clarified the number of lineages and increased collections from recent surveys have significantly broadened the distributions of these taxa. However, no formal taxonomic assessments have been undertaken to redefine species, including the many lineages that represent undescribed species. Currently, there are seven species of *Diporiphora* with vast distributions across northern Australia and a broad and variable set of morphological characteristics that make species identification challenging, even for experienced field workers. Here, we provide a comprehensive taxonomic treatment of *Diporiphora* species across northern Australia based on previously published genetic data and morphological examination of voucher specimens. Our analyses demonstrate that these broadly distributed taxa actually comprise multiple, often allopatric, species, with especially high diversity in the Kimberley region of Western Australia.

We redescribe nine previously described species and describe five new species of *Diporiphora* based on historical types, newly collected material and older museum vouchers. In the *D. australis* species group, we resurrect *D. jugularis* Macleay from synonymy. In the *D. bennettii* species group, we synonymise *D. arnhemica* Storr with *D. albilabris* Storr, and raise to full species the latter and *D. sobria* Storr. In addition, we describe as new a wide-ranging saxicoline species previously attributed to *D. bennettii* Gray. In the *D. bilineata* species group, we resurrect *D. margaretae* Storr from synonymy with *D. magna* Storr and describe three new species. Lastly, we describe a species from the northwest Kimberley that is more closely related to an arid zone radiation.

The revision of the northern *Diporiphora* dragons here stabilises the taxonomy, redefines many species distributions and reveals many new species. Further work on *Diporiphora* includes further surveys to better understand distributions and habitat preferences and continue to refine their evolutionary history and biogeography in northern Australia.

### Keywords

Agamid lizards; Australia; Cape York Peninsula; *Diporiphora carpentariensis* sp. nov.; *Diporiphora gracilis* sp. nov.; *Diporiphora granulifera* sp. nov.; *Diporiphora pallida* sp. nov.; *Diporiphora perplexa* sp. nov.; Kimberley; monsoonal tropics; taxonomy; Top End.

### Introduction

The Australian monsoonal tropics (AMT) constitute a significant element of the Australian landmass, spanning the northern quarter of the continent from the far west coast of the Kimberley region in Western Australia (WA), across the Top End of the Northern Territory (NT) and around the Gulf of Carpentaria to the Cape York Peninsula in Queensland. Tropical savannah woodlands and grasslands are the region's

dominant vegetation types and are characterised by a dense grass understorey and an over-storey of widely scattered trees (Bowman et al., 2010). These woodlands are home to a major component of Australian biodiversity, with sandstone escarpments possibly having similar levels of diversity to the rainforests (Bowman et al., 2010). Despite the importance and size of this region in terms of phylogenetic diversity, there are many vertebrate groups for which there remain significant

taxonomic problems, particularly in terms of under-representing the true species diversity (e.g. Doughty 2011; Laver et al., 2018; Moritz et al., 2018; Pepper et al., 2011).

One group with such taxonomic problems is the dragon lizard genus *Diporiphora* (family Agamidae, sub-family Amphibolurinae), which is a diverse group of slender small-bodied dragons, including some of the most common and widespread diurnal lizards across the tropical savannah woodlands. This genus presents particular difficulties in species-level identification, with many of the morphological characters used in keys and diagnoses being as variable within species as between species. The last significant taxonomic treatment of *Diporiphora* in this region of northern Australia was published more than 40 years ago, describing eight species and subspecies (Storr, 1974). More recently, genetic work has shown that the current taxonomy significantly under-represents

the true species diversity (Couper et al., 2012; Edwards and Melville, 2011; Smith et al., 2011).

We undertook a comprehensive taxonomic review of *Diporiphora* species across northern Australia, with particular focus on the taxa that have been identified as species complexes in previously published and unpublished genetic work (fig. 1). Although Storr's (1974) work provides a good framework towards resolving the taxonomy of northern *Diporiphora*, many issues remain. As was typical of Storr's work, his revision was based on collections at the Western Australian Museum (WAM); he did not address Queensland, despite *Diporiphora* occurring across the Gulf of Carpentaria region including the Cape York Peninsula.

Storr (1974) recognised considerable diversity within several species and described multiple subspecies to accommodate this variation: *D. albilaris* (*D. a. albilaris*, *D. a. sobria*), *D. bennettii* (*D. b. bennettii*, *D. b. arnhemica*) and *D.*

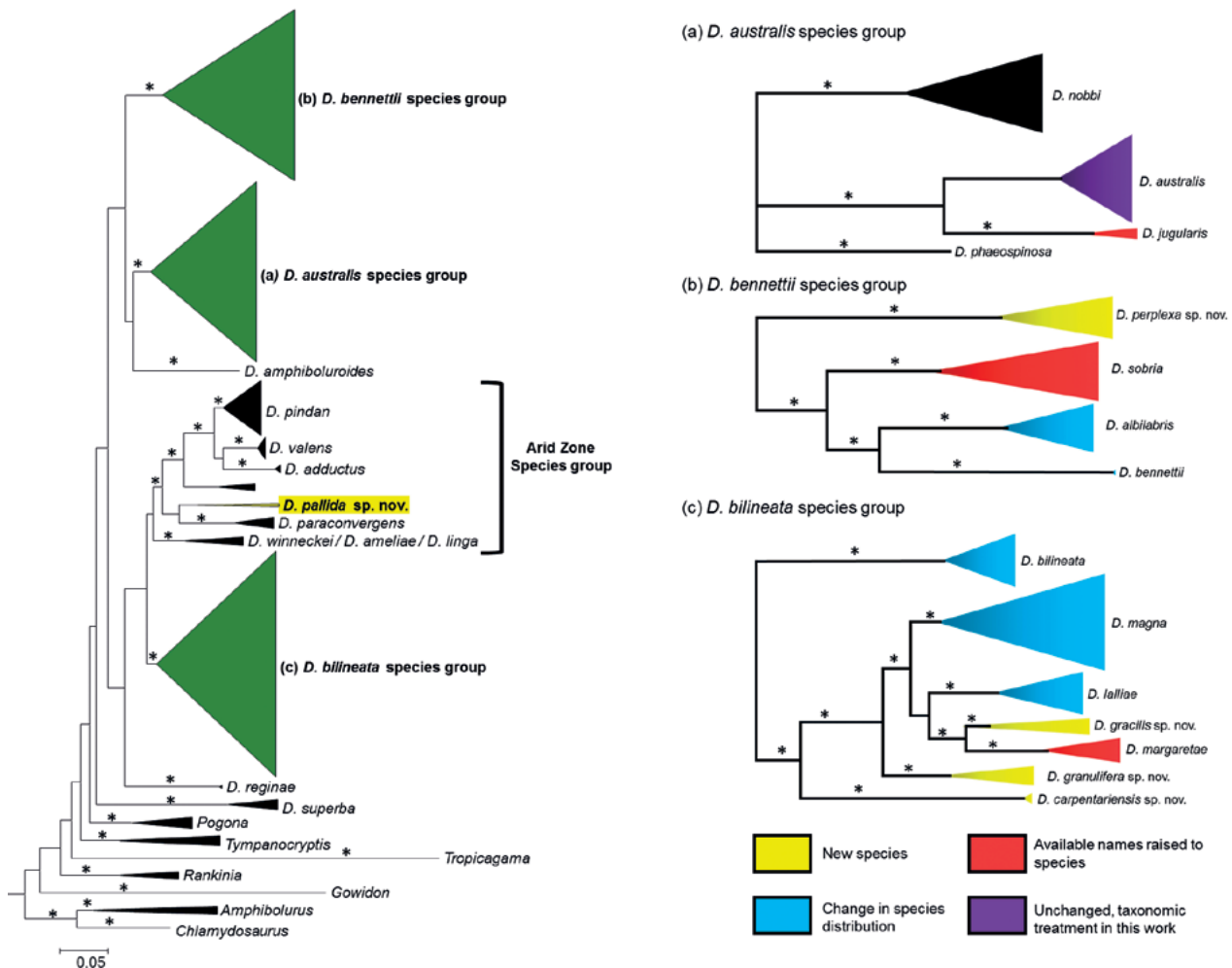


Figure 1. Bayesian 50% majority-rules phylogenetic tree for *Diporiphora* based on mtDNA on ~1200 bp mitochondrial DNA (ND2). Asterisks on branches represent >99% posterior probability support. Clades highlighted in green are expanded, with phylogenetic relationships within each of the species groups reviewed in the current paper: a, *D. australis*; b, *D. bennettii*; c, *D. bilineata*. Species reviewed in the current paper are coloured to represent the taxonomic revision that is undertaken.

Table 1. Meristic characters scored and morphological characters measured in this study

<b>Meristic characters</b>	
Pre-cloacal pores	Number of pre-cloacal pores in total
Femoral pores	Number of femoral pores in total
Canine teeth	Number of canine teeth on each side of upper jaw
Guar fold	Absent/weak/present
Post-auricular fold	Absent/weak/present/strong
Scapular fold	Absent/weak/ present/strong
Dorsal scales	Homogenous/weakly heterogeneous/strongly heterogeneous
Throat stripes	Absent/weak/strong
Position of lateral dark spot	On side of neck/axilla (arm pit)
Paravertebral and dorsolateral scales	Enlarged or homogenous with surrounding scales
Vertebral scales	Enlarged or homogenous with surrounding scales
4th toe lamellae (4TL)	Number of enlarged subdigital lamellae under fourth toe, counted from toe junction to base of claw
Infralabials (ILB)	Number of infralabial scales, ending with the last small scale in contact with the posterior margin of the last upper labial
Supralabials (SLB)	Number of supralabial scales
<b>Measurements</b>	
SVL	Snout-vent length
Tail (TL)	Tail length from cloaca to tip (unbroken tails only)
Head length (HL)	Head length, measured obliquely from tip of snout to anterior margin of tympanum
Head width (HW)	Head width, measured at the widest point
Interlimb length (IL)	Length from the axilla to the groin
Forelimb (FLL)	Length, measured from the elbow bend to the tip of the 4th finger including claw
Hindlimb (HLL)	Length, measured from the knee bend to the tip of the 4th toe including claw

*bilineata* (*D. b. bilineata*, *D. b. margaretae*). At the time of Storr's revision, subspecies were fashionable to employ to deal with the variation observed and to hedge against taxonomic uncertainty, especially with the relatively small number of specimens he had to work with. Since Storr's revision, the concept of these species has changed according to various authors and field guides but without any formal taxonomic treatment. For example, the subspecies *D. b. arnhemica* is usually recognised as a full species (e.g. Cogger et al., 2014; Wilson and Swan, 2017). Additionally, the distributions of these subspecies have significantly expanded since Storr's (1974) original descriptions. For example, *D. b. arnhemica* was originally limited to the type location, *D. a. sobria* was limited to two locations in the central NT and *D. a. albilabris* was limited to four locations in the northwest Kimberley. Subsequently, the distributions of these taxa have expanded to encompass vast areas of northern Australia (e.g. Cogger, 2014; Wilson and Swan, 2017).

Taxonomic problems, such as those outlined above, extend across all northern *Diporiphora* species. Storr (1974) described

*D. b. margaretae* as a new subspecies of *D. bilineata*, with distributions of the two subspecies (*D. b. bilineata* and *D. b. margaretae*) defined as being disjunct in the NT and northern Kimberley, respectively, with the intervening savannah woodlands occupied by *D. magna* (also described in the same work). Finally, *D. lalliae* was described as a generalist species with a broad east–west distribution across the southern portions of the AMT (Storr, 1974). Since the description of these species and subspecies, many of the distributions of these lineages have expanded to be widespread and broadly sympatric across the AMT and even into the arid zone (*D. lalliae*) without further taxonomic treatment. Storr apparently changed his mind about the legitimacy of *D. b. margaretae*, omitting it from Storr et al. (1983) without comment 10 years later. This change has been largely followed since (e.g. Cogger, 2014; Wilson and Swan, 2017) despite being listed as a full species by Cogger et al. (1983). Thus, the currently used taxonomy of northern Australian *Diporiphora* does not reflect Storr's original work and a full taxonomic assessment of these lizards is long overdue.

Table 2. Diagnostic characters to distinguish between lineages

	(a) <i>D. australis</i> species group	(b) <i>D. bennettii</i> species group	(c) <i>D. bilineata</i> species group	(d) Arid zone species group
1. No. of canine teeth on each side of upper jaw	One	Two	One	One
2. Axilla granular scales	Absent	Absent	Present Exception: absent in <i>D. lalliae</i>	Absent
3. Lateral dark spot	On side of neck	Axial if present	Axial	Absent
4. Femoral pores	Absent	Present ( <i>D. albilabris</i> , <i>D. sobria</i> ) or absent	Absent	Absent

Here, we provide the first comprehensive taxonomic treatment of *Diporiphora* species across northern Australia since Storr's work, using an understanding of relationships based on genetic data and an examination of newly collected and historical collections, including type specimens.

## Methods

### *Specimens examined and external morphology*

Specimens were examined from the collections of the Western Australian Museum (WAM), Queensland Museum, Brisbane (QM), Museum Victoria (NMV), Museum and Art Gallery of the Northern Territory (MAGNT), Darwin, Australia Museum, Sydney (AMS), the Natural History Museum, London (NHMUK, registration prefix – BMNH), the Naturhistorisches Museum, Vienna (NHMW) and the Swedish Museum of Natural History (NHRM). New type material is deposited in the WAM and QM.

A set of 13 meristic and seven morphometric characters (Table 1) were recorded for all primary types. Measurements were made with electronic callipers to the nearest 0.1 mm, except for snout-vent length (SVL) and tail length (broken tails were not measured), which were measured with a ruler to the nearest 0.5 mm. Individuals were sexed by observations of everted hemipenes in males or heavily gravid females, or by direct examination of the gonads. Aside from the type series, an additional  $\geq 10$  well-preserved adult specimens (where available) from each taxon were examined (listed in Appendix 1). On the dorsum, we refer to the vertebral scale row at the midline, with the paravertebral scale row adjacent and with the 2nd paravertebral scale row (often enlarged and hence referred to in the text) to the outside of the paravertebral row. We detail both meristic and morphological characters to diagnose species and to identify the species groups from each other. In the *Comparisons with other species* sections, we compare the focal species with other species that have overlapping distributions.

We provide a taxonomic revision of each of the species groups outlined in fig. 1. This encompasses most of the *Diporiphora* that occur across the AMT and a species description for a taxon that falls outside these species groups but occurs within the AMT:

- (a) *D. australis* species group
- (b) *D. bennettii* species group
- (c) *D. bilineata* species group
- (d) arid zone species group.

Five *Diporiphora* species that occur in the northern tropical savannahs are not reviewed in the current study. *Diporiphora superba* Storr is extremely elongate and green or yellow, and is easily distinguished from all other Australian dragon lizards (Storr et al., 1983; Wilson and Swan, 2017). The type of *D. convergens* Storr was examined as part of this study but an account is not included because this specimen has the keels of the dorsal scales converging towards the midline, which is unique in AMT *Diporiphora*. This species is only known from the type specimen, which was collected from Crystal Creek in the northern tip of the Kimberley (Storr, 1974) and has not been collected again. Taxonomic treatments of *D. nobbi* (Witten), *D. phaeospinosa* Edwards and Melville or *D. pindan* Storr are also not provided because they have been recently treated elsewhere (Doughty et al., 2012a; Edwards and Melville, 2011).

## Phylogenetic analyses

The phylogenetic tree (fig. 1), based on a region of ~1200 bp mtDNA (including the protein coding gene ND2 and five tRNAs) across 283 *Diporiphora* samples, provides strong support for all lineages covered in this taxonomic review. The ND2 coding region and flanking tRNA regions were found to follow the GTR+I+G model of substitution with no partitioning schemes using the corrected Akaike information criterion on PartitionFinder2 on the CIPRES Science Gateway (Lanfear et al., 2016). Bayesian analysis was performed using MrBayes (Huelsenbeck and Ronquist, 2001) on the CIPRES Science Gateway, with two runs of four independent Markov chain Monte Carlo analyses (each 50,000,000 generations long and sampled every 1,000 generations) under a GTR+I+G model with flat priors. Tracer v1.6 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.

***Diporiphora* Gray, 1842**

*Type species.* *Diporiphora bilineata* Gray, 1842, by monotypy.

A diverse genus, distributed across all states and territories, except Tasmania, predominately in semi-arid, arid and AMT biomes. Small- to medium-sized lizards that are mostly terrestrial or semi-arboreal. Moderately long snout with relatively long legs and tail. All species have exposed tympanum, and most species have pre-cloacal pores with femoral pores occasionally present. Generally lacking prominent crests, large spinose scales or dermal appendages, although present in some species (e.g. *D. amphiboluroides*). Colour patterning variable within species, particularly between breeding males and females or juveniles. In general, most species have pale dorsolateral stripes, dark transverse dorsal bars, a black circular blotch on shoulders or neck, and a pink to mauve flush on hips and tail base (particularly in adult males).

**(a) *D. australis* species group (fig. 1a)**

*Content:*

*Diporiphora australis* (Steindachner, 1867)  
*Diporiphora jugularis* (Macleay, 1877)  
*Diporiphora nobbi* (Witten, 1972)  
*Diporiphora phaeospinosa* Edwards and Melville, 2011

*Diagnostic characters for group (Table 2):*

- one canine tooth on each side of upper jaw (see fig. 2 for illustration of this character)
- scales in axillary region not granular
- lateral dark spot on side of neck.

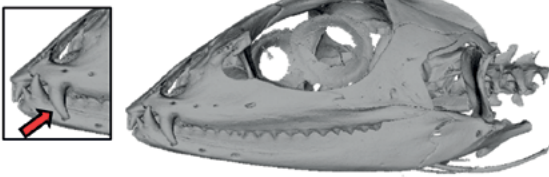
**(a) *D. bennettii* species group****(b) *D. bilineata* and *D. australis* species groups**

Figure 2. Images from micro X-ray computed tomography scans showing the differences in pleurodont (canine) tooth number in the upper jaw: a, arrangement in *D. bennettii* species group; b, other species groups included in the current study.

**Remarks**

This species group is restricted to the eastern portion of the AMT (fig. 3), occurring along the east coast, adjacent inland areas and throughout the Cape York Peninsula. Relative to other species groups in the AMT, they tend to be large bodied (68–75 mm SVL) with generalist habits. We do not include *D. nobbi* and *D. phaeospinosa* below because Edwards and Melville (2011) recently reviewed these species. Our analyses of all *Diporiphora* species (fig. 1a) recovered the same relationships among species within this group as the mtDNA phylogeny in Edwards and Melville (2011), with *D. australis* and *D. jugularis* being highly supported as sister species, but the relationships between this lineage and *D. phaeospinosa* and *D. nobbi* are not well resolved. We provide an account of *D. australis* and *D. jugularis*, raising the latter species from a junior synonym of *D. bilineata* (Cogger et al., 1983) based on genetic results in Edwards and Melville (2011) and examination of types and specimens herein.

***Diporiphora australis* (Steindachner, 1867)**

*Common name.* Tommy roundhead.

Figure 4, Tables 3, 4

*Calotella australis* Steindachner, F. 1867. Reptilien. pp. 1–98 in, *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Willerstorff-Urbair. Zoologie* 1(3). State Printer: Vienna. [1869 on title page] [29, pl. 1 fig. 9]. Type data: lectotype – NHMW 19821.1 Australia (“Cape York, QLD” on type label), taxonomic designation, this work.

*Grammatophora macrolepis* Günther, A. 1867. Additions to the knowledge of Australian reptiles and fishes. *Annals and Magazine of Natural History* 20: 45–68 [51]. Type data: holotype – BMNH 1946.8.12.74, Australia (by implication).

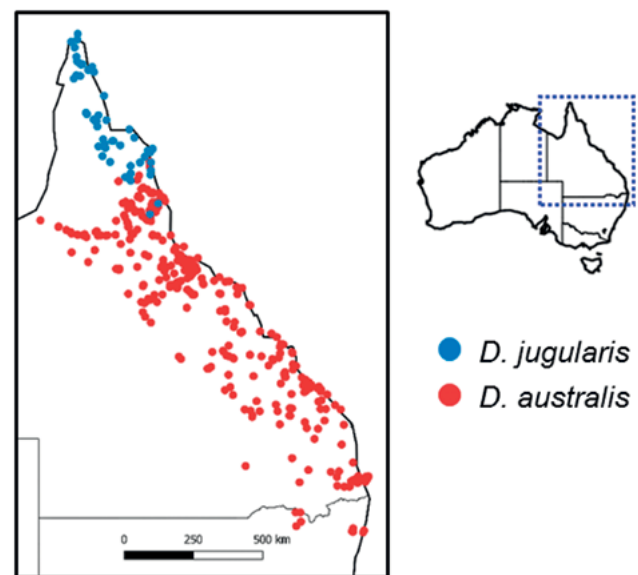


Figure 3. Distributions of *D. australis* and *D. jugularis* based on specimens examined and collection records.

Table 3. Measurements and sex of types. All measurements are in millimetres (mm) and key to abbreviations can be found in Table 1. Museum abbreviations are as follows: Western Australian Museum (WAM); Australian Museum, Sydney (AMS); Queensland Museum (QM); Natural History Museum, United Kingdom (BMNH); Naturhistorisches Museum, Vienna, Austria (NHMW)

Species	Accession No.	Sex	SVL	TL	HL	HW	IL	HLL	FLL	4TL	SLB	ILB
<i>D. australis</i>	NHMW 19821:1	female	69	146	18	12	33	49	27	23	11	12
<i>D. jugularis</i>	AMS R40672	juvenile	38	96	12	7	16	35	22	23	11	12
<i>D. jugularis</i>	AMS R40673	juvenile	35	82	12	8	16	34	22	23	11	12
<i>D. jugularis</i>	AMS R40674	juvenile	30	65	11	8	16	30	19	22	10	11
<i>D. bennettii</i>	BMNH 1946.8.12.77	female	50	68	15	13	24	36	23	17	11	10
<i>D. albilabris</i>	WAM R43517	female	44	94	14	9	20	40	24	18	10	10
<i>D. sobria</i>	WAM R23180	subadult	34	68	12	8	14	25	19	18	11	12
<i>D. perplexa sp. nov.</i>	WAM R177290	male	63	140	22	11	24	52	31	21	11	11
<i>D. bilineata</i>	BMNH 1946.8.12.75	male	58	56*	18	13	24	46	26	23	11	10
<i>D. bilineata</i>	BMNH 1946.8.12.76	male	57	131	17	12	24	42	24	22	10	11
<i>D. lalliae</i>	WAM R23020	male	62	152	18	11	34	44	27	23	9	9
<i>D. magna</i>	WAM R42786	female	47	141	15	9	20	42	25	23	11	11
<i>D. margaretae</i>	WAM R27648	female (gravid)	55	128	16	9	24	41	27	19	11	13
<i>D. gracilis sp. nov.</i>	WAM R177291	male	57	165	18	10	20	49	27	23	11	9
<i>D. granulifera sp. nov.</i>	QM J96362	male	65	176	21	12	29	46	31	23	11	12
<i>D. carpentariensis sp. nov.</i>	QM J88197	male	62	185	20	12	28	55	33	22	11	11
<i>D. pallida sp. nov.</i>	WAM R177292	male	46	95	15	10	24	40	24	16	10	11

\* = tail broken

*Diporiphora nuchalis* De Vis, C.W. 1884. On new species of Australian lizards. *Proceedings of the Royal Society of Queensland* 1: 97–100 [98]. Type data: syntype(s) – whereabouts unknown, central and south-coast district, Queensland.

*Diporiphora ornata* De Vis, C.W. 1884. On new species of Australian lizards. *Proceedings of the Royal Society of Queensland* 1: 97–100 [99]. Type data: holotype – whereabouts unknown, locality unknown.

*Physignathus nigricollis* Lönnberg, E., and Andersson, L.G. 1915. Results of Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia 1910–1913. VII. Reptiles collected in northern Queensland. *Kongliga Svenska Vetenskaps-Academiens Nya Handlingar, Stockholm* 52: 1–9 [4] [incorrect spelling as *Physignatus nigricollis*]. Type data: holotype – NHRM 3209, Cooktown, Queensland.

**Diagnosis.** Body size moderately large (to 70 mm SVL) with long tail (2.3–2.7 × SVL). Gular, post-auricular and scapular folds present. Lacks spinose scales on thighs or neck. Pre-cloacal pores 4; femoral pores 0.

**Description of lectotype.** Female; 69 mm SVL; 146 mm tail length. Medium-sized dragon, moderately robust with moderately long limbs and tail. Single canines on each side of upper jaw. Gular and post-auricular folds present and scapular fold weak. Dorsal scales homogenous but prominent keels form longitudinal ridges along dorsum along midline with dorsolateral ridges on each side; these raised vertebral and dorsolateral scale rows extend anteriorly onto nape to head and posteriorly onto base of tail, not extending down tail. Scales on

flanks heterogeneous with scattered slightly enlarged scales. Scales on neck, limbs and tail not spinose. Scales in axilla small but not granular. Ventral scales strongly keeled. Pre-cloacal pores 4; femoral pores 0.

Dorsum strongly patterned. Vertebral and dorsolateral lines very faint, almost undiscernible with colouring a slightly paler replication of dorsum patterning, running from back of head to pelvis. Five wide dark transverse bands across dorsum between head and pelvis. Dark bands are a similar width to the pale background. Head relatively plain with little patterning, labials similar colour to rest of head and lacking pale line between eye and ear. Lacks dark spot on posterior of tympanum. Flanks a similar colour to dorsum. Lacks lateral stripe between axilla and groin. Dark patch on sides of neck at anterior edge of shoulder. Arms weakly banded with dark bands slightly narrower than light. Legs and tail strongly banded with dark bands narrower than light. Ventral surface cream with no patterning.

**Variation.** 46–70 mm SVL; 105–174 mm tail length. Tail long, ranging from 2.3–2.7 × SVL. Strong scapular fold present, post-auricular fold usually absent although present but weak in a few individuals. Dorsal scales homogenous but prominent keels form longitudinal ridges. There are often five longitudinal ridges: one along the vertebral midline, one each on the 2nd paravertebral scale rows and one on each of the dorsolateral stripes. Some individuals only have these longitudinal ridges running along the

Table 4. Diagnostic characters distinguishing species within species groups

	Tail length (× SVL)	Dorsolateral stripes	Gular fold	Post-auricular fold	Scapular fold	Dark spot on tympanum edge	Extent of axial dark granular scales	Dorsal scales between dorsolateral stripes	Pre-cloacal pores (total)	Femoral pores (total)
<b>(a) <i>D. australis</i> species group</b>										
<i>D. australis</i>	Long (2.3–2.7)	Present	Present	Weak/absent	Present	Absent	Absent	Homogeneous	4	0
<i>D. jugularis</i>	Long (1.8–2.7)	Usually	Absent	Absent	Absent	Absent	Absent	Homogeneous	4	0
<b>(b) <i>D. bennettii</i> species group</b>										
<i>D. albilabris</i>	Long (1.8–2.5)	Present	Present	Strong	Absent	Absent	Absent	Strongly heterogeneous	4	2
<i>D. bennettii</i>	Short (<2.0)	Absent	Present	Strong	Weak	Absent/weak	Absent	Homogeneous	2	0
<i>D. perplexa</i> sp. nov.	Long (1.9–2.5)	Present	Weak	Strong	Weak	Strong	Absent	Homogeneous	2–4	0
<i>D. sobria</i>	Long (2.3–2.6)	Present	Present	Weak/present	Weak/present	Absent/weak	Absent	Homogeneous in Western Australia (some Northern Territory populations heterogeneous)	4	2
<b>(c) <i>D. bilineata</i> species group</b>										
<i>D. bilineata</i>	Long (2.2–2.7)	Present	Absent	Absent	Present	Absent	Over arm onto shoulder and posteriorly along flanks, with pale flecks	Moderately heterogeneous with outer row of dorsolateral stripe having weakly raised trailing edge	2	0
<i>D. gracilis</i> sp. nov.	Very long (2.7–3.0)	Sometimes	Absent	Weak/absent	Weak	Absent	Over arm to scapular fold	Homogeneous lacking raised scales in dorsolateral stripes	4	0
<i>D. lalliae</i>	Very long (2.7–3.4)	Usually	Present	Strong	Strong	Absent	Absent	Homogeneous lacking raised scales in dorsolateral stripes	4	0
<i>D. magna</i>	Very long (2.6–3.0)	Present	Absent	Strong	Strong	Absent	Over arm but not to sides of neck	Homogeneous lacking raised scales in dorsolateral stripes	4	0
<i>D. margaretae</i>	Long (2.5–2.7)	Present	Absent	Weak/present	Weak/present	Absent	On top of arm and posteriorly along flanks, with pale flecks	Homogeneous but with outer row of dorsolateral stripe having raised trailing edge	4	0
<i>D. granulifera</i> sp. nov.	Very long (2.7–3.0)	Present	Absent	Weak–strong	Strong	Absent	Over arm and along the full length of the scapular fold; anterior to scapular fold small, slightly granular scales	Homogeneous but with outer row of dorsolateral stripe having raised trailing edge	4–6 (usually 4)	0

	Tail length (× SVL)	Dorsolateral stripes	Gular fold	Post-auricular fold	Scapular fold	Dark spot on tympanum edge	Extent of axial dark granular scales	Dorsal scales between dorsolateral stripes	Pre-cloacal pores (total)	Femoral pores (total)
<i>D. carpentariensis</i> sp. nov.	Very long (2.1–3.0)	Present	Absent	Weak–strong	Strong	Absent	Over arm and along the full length of the scapular fold	Homogeneous lacking raised scales in dorsolateral stripes	4–5 (usually 4)	0
<b>(d) Arid zone species group</b>										
<i>D. pallida</i> sp. nov.	Short (2.0)	Absent	Present	Absent	Present	Absent	Absent	Homogeneous	2	0

second scales out from the midline, giving a smoother appearance to the dorsum. Some individuals have weakly heterogeneous dorsal scales with the 2nd paravertebral scale rows slightly enlarged. In individuals with weak post-auricular fold, a row of 4–6 enlarged but not spinose scales may be present.

Dorsal pattern variable from strong, complex patterning to unpatterned. Dorsolateral stripes always present, wide cream to grey vertebral stripe present in all but weakly patterned individuals. In strongly patterned individuals, usually six dark transverse bands across dorsum between head and pelvis but ranges from 4–7. Transverse bands similar in size or slightly narrower than pale background. Flanks in these individuals have similar patterning to dorsum and commonly have wide pale lateral stripe between axilla and groin. In weakly patterned individuals, transverse bands are either absent or are narrow dark bands contacting the dorsolateral stripes and extending towards, but not contacting, the vertebral stripe. In these plain animals, the bands on the tail also contact the dorsolateral stripes but do not meet at the midline. Flanks in these individuals lack patterning, including a lateral stripe between axilla and groin. Dark patch on sides of neck often present but variable from being absent to running along scapular fold and extending anteriorly onto the sides of neck from the dorsal extent of the fold, with the dark pigmentation contacting the pale dorsolateral stripe. This dark spot on the neck never extends posteriorly from the scapular fold towards the axial region or onto the ventral surface. Ventral surface usually unpatterned and cream in colour, but a few individuals, usually females, have pale grey colouring on gular region.

**Distribution and ecology.** Widespread along the north-eastern coast of Australia, as far south as the Coffs Harbour area in northern New South Wales, extending north along the coast into the south-eastern portions of Cape York Peninsula as far north as the Cooktown area (fig. 3). It extends inland approximately 600 km from the coast, across the base of Cape York Peninsula to the Normanton area. It extends south along the Great Dividing Range, into northern New South Wales.

A common and abundant species that is an ecological generalist, occurring in most dry forests and woodlands within its distribution (fig. 5c and e). Individuals use low vegetation, fallen timber and termite mounds as perches. This species is a common sight in some of the northern cities and appears to

have adapted well to bushy suburban areas (Kutt et al., 2011). Although *D. australis* is one of the most common species encountered in suburban areas of eastern Queensland, relatively little is known about its biology.

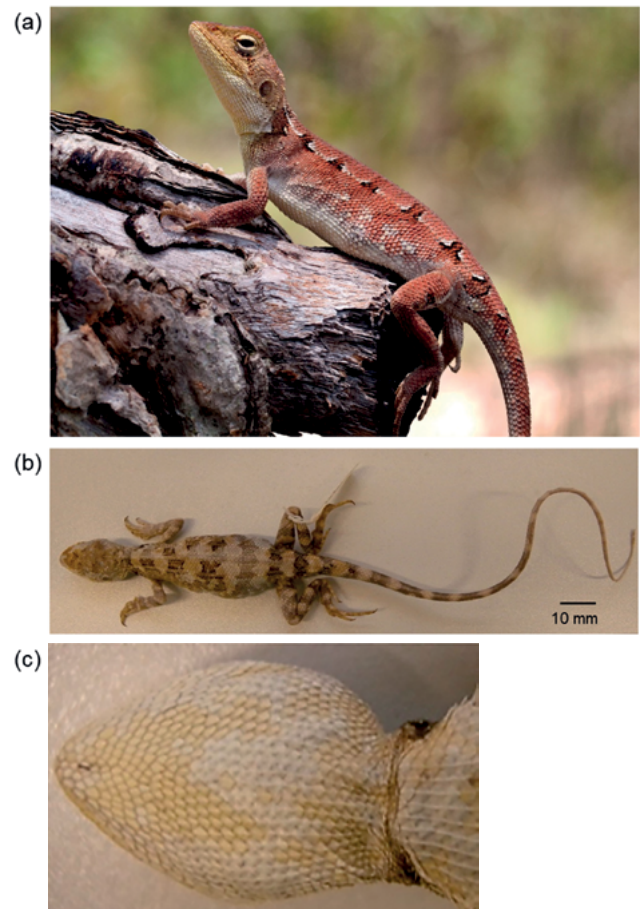


Figure 4. *Diporiphora australis*: a, adult, Karawatha, south-eastern Queensland (photo: S. Wilson); b, lectotype NHMW 19821.1, Australia (“Cape York, QLD” on type label); c, ventral view of head showing gular fold.



*Comparison with other species.* Overlaps extensively with the distribution of *D. nobbi* and overlaps broadly with *D. jugularis* at the northern edge of its range (fig. 3) and with *D. carpentariensis* sp. nov. in the north-western extent of its range. It differs from *D. nobbi* in having smaller body size and lacking spinose scales on the thighs or neck. It can be distinguished

morphologically from *D. jugularis* and *D. carpentariensis* sp. nov. by possessing a gular fold.

*Remarks.* As part of this study we examined all available types, including those of synonymised species, held in Australian and European collections. In addition, we examined a specimen

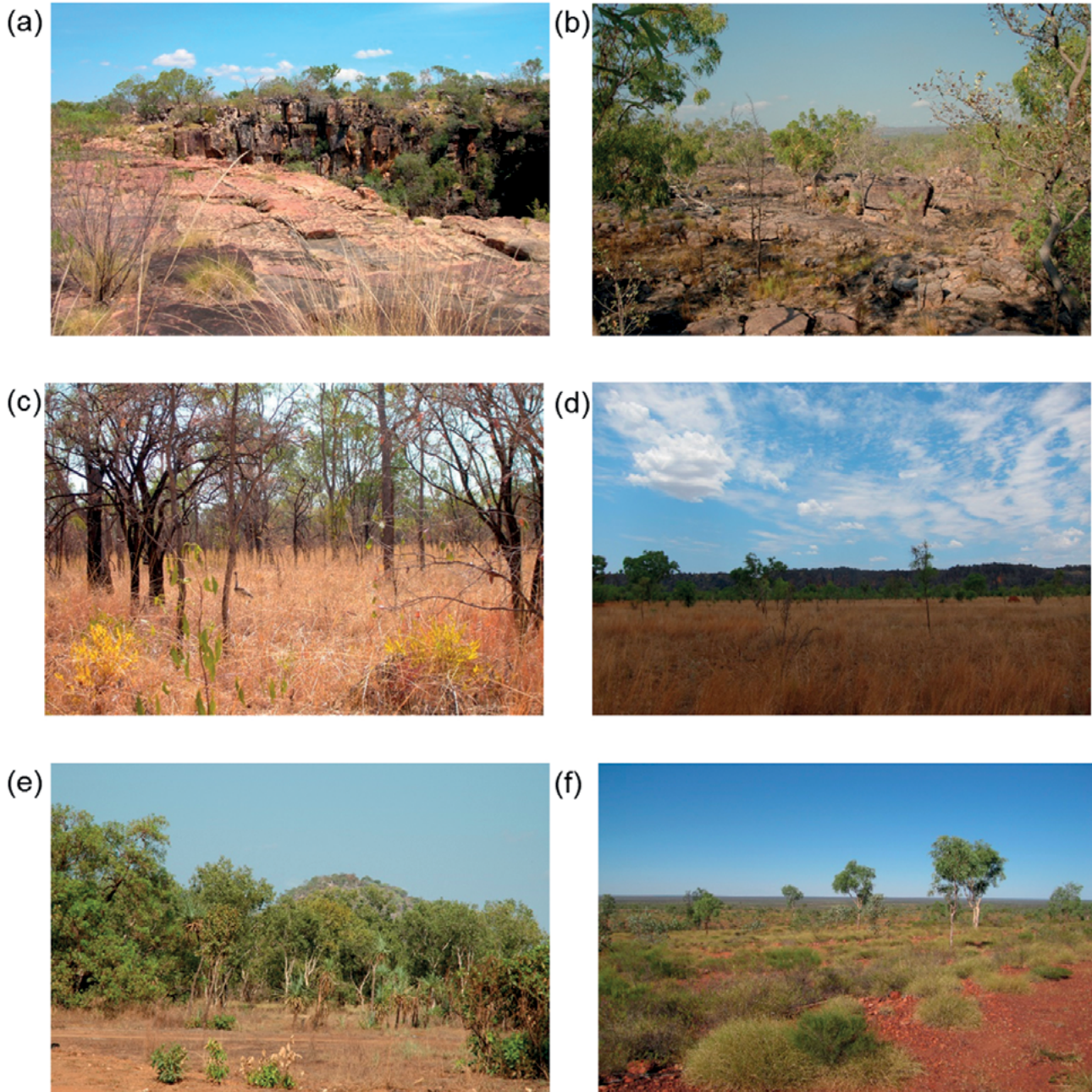


Figure 5. Examples of the range of habitats in which the *Diporiphora* species of the Australian monsoon tropics occur: a, sandstone escarpment, Mitchell Plateau, Kimberley region, Western Australia; b, rocky outcrops in savannah woodlands, western Arnhem Land, Northern Territory; c, savannah woodlands, Kimberley region, Western Australia; d, savannah grasslands on cracking clay soils, floodplain of the Lennard River, Kimberley Region, Western Australia; e, savannah woodlands, western Arnhem Land, Northern Territory; f, arid spinifex grasses with scattered trees on stony ground, Tennant Creek, Northern Territory (photos: J. Melville).

held in the NHMUK that is housed in the type collection based on an account by Günther (1867). This account named *Grammatophora calotella* as a replacement name for a species described earlier in the same year by Steindachner, who described *Calotella australis*, basing his name on specimens in the Vienna collection. Günther renamed *Calotella australis* as the species *Grammatophora calotella* and referred to the two specimens in the NHMUK from Cape York. However, examination of the *Grammatophora calotella* specimen revealed that it lacks a gular fold, indicating that it is *D. jugularis* from Cape York, and not *C. australis*. In the same paper, Günther described *Grammatophora macrolepis* as a new species, which examination confirms is *D. australis*.

Cogger et al. (1983) suggested that the two specimens with the single registration number of NHMW 19821 were likely to be the syntypes and that these bore the locality “Cape York”, suggesting that they were collected by Daemel. As such, they would have been collected by Daemel at the same time as the *Grammatophora calotella* specimens in the NHMUK (BMNH 66.12.28.22–23). However, it is probable that the location of these specimens is incorrect and they were not from Cape York but were from Rockhampton. Comparison of the lectotype NHMW19821:1 to the image provided in the original description (fig. 6) suggests that this specimen was the one described by Steindachner but with incorrect locality data. There are several species with types collected by Daemel where there is a mix-up between specimens collected in Cape York and Rockhampton (G. Shea, personal communication).

The type of *Physignathus nigricollis* Lönnberg and Andersson was also examined as part of this study and was confirmed to be a specimen of *D. australis*.

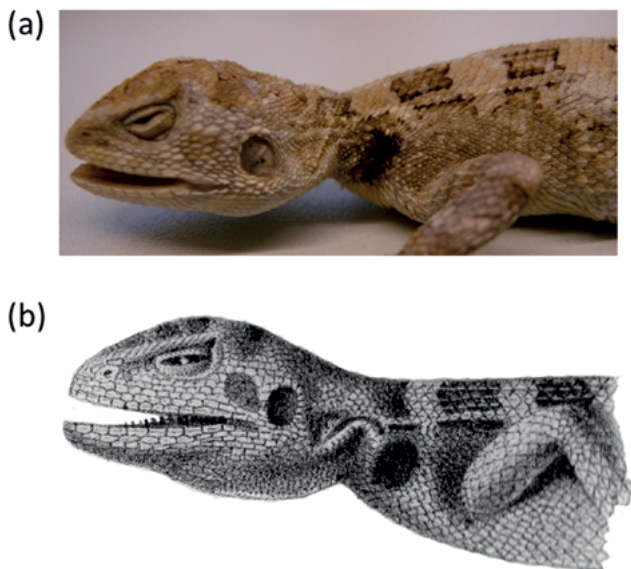


Figure 6. Lateral images of the *Diporiphora australis* syntype NHMW 19821:1: a, Naturhistorisches Museum, Vienna (photo: J. Melville); b, taken from the original species description (Steindachner, 1867).

### *Diporiphora jugularis* (Macleay, 1877)

*Common name.* Black-throated two-pored dragon.

Figure 7, Tables 3, 4

*Grammatophora jugularis* Macleay, W. 1877. The lizards of the Chevert Expedition. Second paper. *Proceedings of the Linnean Society of New South Wales* 2: 97–104 [1878 on title page] [104]. Type data: syntype(s) – AMS R40672–4, Cape Grenville, Cape York Peninsula, Queensland.

*Diporiphora brevicauda* De Vis, C.W. 1884. On new species of Australian lizards. *Proceedings of the Royal Society of Queensland* 1: 97–100 [99]. Type data: holotype – whereabouts unknown, Cape York Peninsula, Queensland.

*Diporiphora pentalineata* De Vis, C.W. 1884. On new species of Australian lizards. *Proceedings of the Royal Society of Queensland* 1: 97–100 [99]. Type data: holotype – whereabouts unknown, Cape York Peninsula, Queensland.

*Diagnosis.* Body size moderately large (to 68 mm SVL) with long tail (1.8–2.7 × SVL). Gular and scapular folds absent; post-auricular fold absent or weak. Scales in axilla not granular. Lacks spinose scales on thighs or neck. Pre-cloacal pores 4; femoral pores 0.

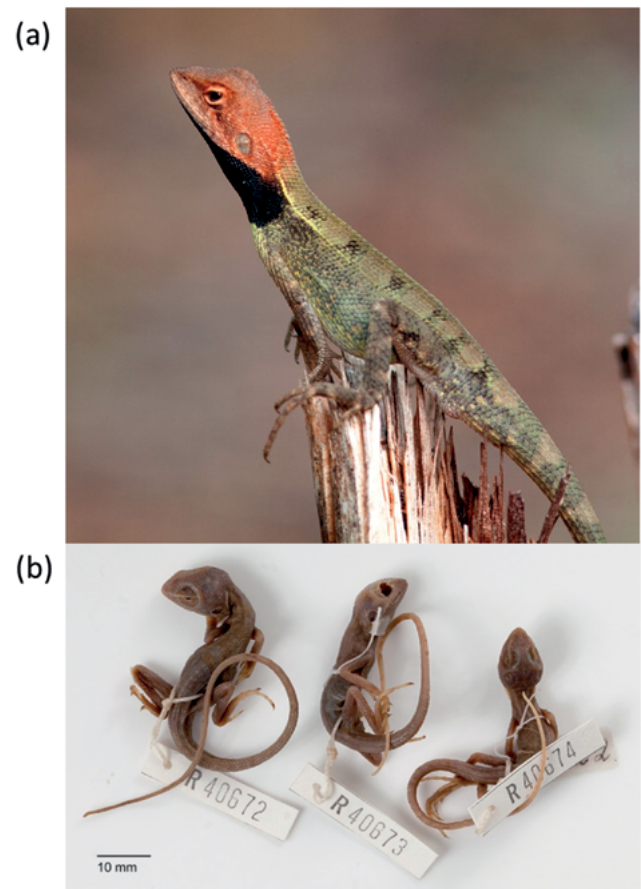


Figure 7. *Diporiphora jugularis*: a, adult male with breeding colouration, Iron Range, Queensland (photo: S. Wilson); b, syntype(s) AMS R40672–4, juveniles, Cape Grenville, Cape York Peninsula, Queensland.

*Description of syntypes.* Juveniles; 30–38 mm SVL; 65–96 mm tail lengths. Small dragons, moderately robust with moderately long limbs and tail. Single canines on each side of upper jaw. Gular, scapular and post-auricular folds absent. Dorsal scales homogenous but raised keels form four prominent longitudinal ridges along dorsum, with a ridge on either side of midline running along the 2nd paravertebral scale row, and a dorsolateral ridge on along each side. These raised vertebral and dorsolateral scale rows extend anteriorly to neck, terminating at head and extending posteriorly onto base of tail. Scales on flanks strongly heterogeneous with scattered scales that are distinctly larger than rest, with keels angling away from dorsum towards ventral surface from midbody. Scales on neck, limbs and tail not spinose. Scales in axilla small but not granular. Ventral scales strongly keeled, keels forming longitudinal ridges running length of body. No pre-cloacal pores visible in these juvenile specimens (usually 4); femoral pores 0.

Dorsum not patterned, which may be due to preservation. Lack vertebral and dorsolateral lines. Dark transverse bands across dorsum absent. Heads plain without patterning, labials same colour to rest of head and lacking pale line between eye and ear. Lacking dark spot on posterior of tympanum. Flanks same colour as dorsum. No lateral stripe between axilla and groin. Faint dark pigmented patch on either side of neck at anterior edge of shoulder. Arms, legs and tail plain. Ventral surface cream with no patterning.

*Variation.* 54–68 mm SVL; 99–178 mm tail length. Tail long, ranging from 1.8–2.7 × SVL. Gular, scapular and post-auricular folds absent in all individuals examined. Dorsal scales homogenous but prominent keels form longitudinal ridges. There are often five longitudinal ridges: one along the vertebral midline, one on either side midline running along the 2nd paravertebral scale row and one on each of the dorsolateral stripes. However, some individuals only have these longitudinal ridges running along the 2nd paravertebral scale row, giving a smoother appearance to the dorsum. Weakly heterogeneous scales in some individuals, with the scale rows second out from the midline being slightly enlarged. Spinose scales absent, but some individuals have 4–6 enlarged (not spinose) scales where a post-auricular fold would occur. Pre-cloacal pores 4; femoral pores 0.

Dorsal patterning variable from plain to strongly patterned. Adult males often have little patterning, but with strongly keeled dorsolateral ridge of scales with a pale cream colour forming prominent dorsolateral stripes. Flanks on these individuals are dark brown with the scattered enlarged pale brown or cream scales giving a speckled or flecked appearance, lacking lateral stripe. Patterned individuals, typically adult females and juveniles, have approximately 4–7 broken dark transverse bands across dorsum on a pale background. Dark bands are of similar width or slightly broader than pale background. These bands are broken by a pale grey or light brown vertebral stripe. The dark transverse bands continue laterally beyond the pale cream dorsolateral stripes, becoming diffuse and terminating at a poorly defined lateral stripe. Wide dark band on sides of neck mostly present, extending from the

dorsolateral stripe to the gular ventral surface and anteriorly from where a post-auricular fold would be to the anterior of the shoulder. The dark band is prominent in males and smaller or occasionally absent in females. This dark gular band does not extend onto chest but forms a well-defined posterior edge across the gular region. In adult males, the dark gular band extends anteriorly to the labials, while in individuals with smaller gular bands, the apex of the small central triangle extends anteriorly. Individuals without the dark gular band may have a dark spot on either side of the neck or a narrow grey band across gular. Legs and tail banded in strongly patterned individuals, otherwise little patterning on legs and tail.

*Distribution and ecology.* Restricted to the eastern edge of the Cape York Peninsula, extending as far south as Mount Misery, southwest of Cairns (fig. 3). Widespread along the eastern extent of Cape York Peninsula, extending inland 150 km from the coast. Little is known about the ecology of this species, but presumed to be similar to that of its sister species *D. australis* in the NT. If so, it would be a generalist species that occurs in dry open forests, woodlands and shrublands.

*Comparison with other species.* Overlaps geographically with *D. australis*, *D. nobbi* and *D. carpentariensis* sp. nov. It differs morphologically from both *D. australis* and *D. nobbi* in lacking a gular fold. Also differs from *D. nobbi* in being smaller in body size (65 mm vs. 75 mm SVL), lacking spinose scales on the thighs or neck, having fewer pre-cloacal pores and lacking femoral pores. It differs from *D. carpentariensis* sp. nov. in that it lacks a scapular fold, scales in axilla are not reduced in size and not granular, scales on flanks strongly heterogeneous with scattered scales that are distinctly larger than surrounding scales, and a black gular band or black spots on sides of neck.

*Remarks.* *Diporiphora jugularis* is restricted to the Cape York Peninsula and has been referred to as *D. bilineata* owing to the lack of a gular fold (e.g. Cogger, 2014; Wilson and Swan, 2017). The distribution maps for *D. bilineata* usually show a distribution (e.g. Cogger, 2014; Wilson and Swan, 2017), with most of the range in the NT extending across the Gulf of Carpentaria region of Queensland and onto the Cape York Peninsula. However, genetic work has shown that the Cape York Peninsula population is not closely related to *D. bilineata* and is instead the sister lineage to *D. australis* (Edwards and Melville, 2010), from which it is distinguished by lacking a gular fold (as opposed to a gular fold being present in *D. australis*).

There are a number of names available for *Diporiphora* on the Cape York Peninsula. Examination of specimens held in the type collection at the NHMUK showed that the earliest known treatment of this species was in 1867 by Günther. As detailed above for *D. australis*, *Grammatophora calotella* is a replacement name created by Günther in 1867 for a species described earlier in the same year by Steindachner. The *Grammatophora calotella* treatment was based on BMNH 66.12.28.22–23, but these specimens are the taxon from Cape York Peninsula (i.e. *D. jugularis*). However, because *Grammatophora calotella* Günther, 1867 is a replacement name for *Calotella australis* Steindachner, 1867 and the

account contains no description of that species, these BMNH specimens have no type status. Thus, the first valid description of this species was in 1877: *Grammatophora jugularis* Macleay.

### (b) *D. bennettii* species group (fig. 1)

Content:

*D. albilabris* Storr, 1974  
*D. bennettii* (Gray, 1845)  
*D. perplexa* sp. nov.  
*D. sobria* Storr, 1974

Diagnostic characters for group (Table 2):

- two canine teeth on each side of upper jaw (fig. 2)
- scales in axillary region not granular
- lateral dark spot in axilla, if present.

Remarks

The *D. bennettii* species group is widely distributed across northern Australia from the Kimberley to north-western Queensland (fig. 8). This species group has moderate size overall, with *D. sobria* and *D. perplexa* sp. nov. attaining maximum sizes of <70 mm SVL, and with the two Kimberley endemics reaching only 61 mm SVL (*D. albilabris*) or 55 mm SVL (*D. bennettii*).

A key character in distinguishing the *D. bennettii* species group from the other species groups in northern Australia, and in particular the broadly sympatric *D. bilineata* species group, is the number of canine teeth on each side of the upper jaw (fig. 2). Agamid lizards have two kinds of teeth: acrodont, which are fused to the jaw and constitute most of the teeth running along the extent of the jaw, and pleurodont, which sit in sockets (Richman and Hadrigan, 2011). The canines in *Diporiphora* are pleurodont teeth. In all members of the *D. bennettii* species group, there are two canines on each side of the upper jaw, where the posterior pleurodont tooth is usually slightly larger than the anterior tooth, a possible consequence of the tooth replacement process. In contrast, all of the species in the *D. bilineata* and *D. australis* species groups have a single canine on each side of the upper jaw. This variation in tooth number

is consistent within these species groups. However, in some juvenile and hatchling lizards, the pleurodont teeth may be absent or not fully enlarged, so this character is best used to distinguish adult lizards from each species group.

Owing to the structure of the tree in this group (fig. 2c), major changes to the current taxonomy are required. From the molecular data, we recovered a sister relationship between true *D. bennettii* (i.e. a small-bodied north-west Kimberley form) and *D. albilabris albilabris*. Sister to this pair was a monotypic lineage with specimens assigned to either *D. albilabris sobria* or *D. bennettii arnhemica*, which indicated that the latter two subspecies were a single species. Lastly, an unnamed species that was assigned to *D. bennettii* but lacked the short body and tail of the holotype was sister to these three lineages.

To resolve conflicts with subspecies and stabilise the taxonomy, several changes were necessary. First, *D. albilabris albilabris* was raised to full species because its sister taxon is the distinctive true *D. bennettii*. Next, we raised *D. albilabris sobria* to full species and synonymised *D. bennettii arnhemica* with *D. sobria* owing to page precedence in Storr's (1974) original descriptions (*sobria* – p. 135; *arnhemica* – p. 137). With the description of the widespread taxon usually attributed to *D. bennettii* (i.e. *D. perplexa* sp. nov.), we feel stability has been achieved in this species group from these taxonomic changes. Should further work show structure in the *D. sobria* lineage, then the name *D. arnhemica* would be available if it corresponded to an unnamed lineage. But at this point, there is insufficient evidence from genetic work and morphology to warrant recognition of two taxa within this group.

### *Diporiphora albilabris* Storr, 1974

Common name. White-lipped two-lined dragon.

Figure 9, Tables 3, 4

*Diporiphora albilabris albilabris* Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146 [133]. Type data: holotype – WAM R43517, Mitchell Plateau, WA [14° 48' S, 125° 50' E].

**Diagnosis.** Body size moderate (to 61 mm SVL), tail moderately long (from 1.8–2.5 × SVL). Gular and post-auricular folds present; scapular fold absent. White dorsolateral stripes on raised scale rows. Lacks dark smudge on posterior of tympanum. Scales between dorsolateral stripes are heterogeneous (fig. 10a), with paravertebral row reduced, 2nd paravertebral row enlarged. Pre-cloacal pores 4; femoral pores 2.

**Description of holotype.** Female. 44 mm SVL, 94 mm tail length. Small body size, moderately robust with long limbs and tail. Two canines on either side of upper jaw. Gular and post-auricular folds present, scapular fold absent. Dorsal scales heterogeneous, with dorsolateral row of enlarged, strongly keeled white scales running from back of head to pelvis and forming well-defined white dorsolateral stripes. Paravertebral rows, either side of the vertebral scale row, are reduced in size compared with adjacent scale rows, leading to the scales of the paravertebral and adjacent scale rows being strongly heterogeneous. To the outer edge of the white dorsolateral stripes, scales are relatively small and keeled,

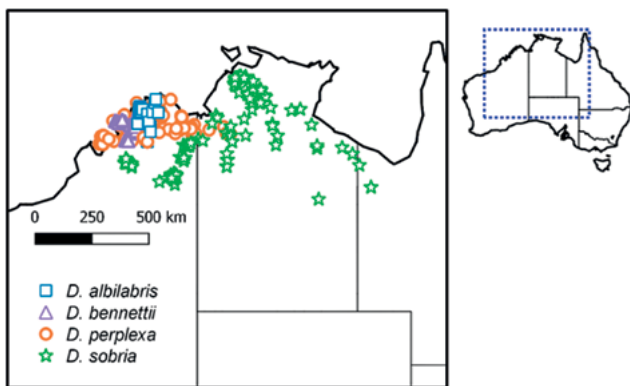


Figure 8. Distributions of *D. albilabris*, *D. bennettii*, *D. sobria* and *D. perplexa* sp. nov. based on specimens examined and collection records.

with keels angling toward ventral surface at midbody. Scales on flanks are heterogeneous with scattered slightly enlarged scales. Scales on limbs and tail not spinose, a row of enlarged pale spines on the post-auricular fold. Scales in axilla not granular. Ventral scales strongly keeled. Pre-cloacal pores 3 (2 right; 1 left); femoral pores 2.

Dorsum pattern complex. Wide (~3 scales) poorly defined grey vertebral stripe and prominent white dorsolateral lines from back of head to base of tail. Five wide dark transverse bands between dorsolateral stripes between head and pelvis. Dark bands extend irregularly from the outer side of the white stripes, fading into the colour patterns on the sides. Dark bands are narrower, approximately half the width, than the pale interspaces with background colour. Head strongly patterned: poorly defined line of pale scales from back of eye, over top of ear towards white dorsolateral stripes, although not contacting stripes; labials pale cream, with a few darker flecks, extending as a broad pale band along jaw to back of head and ending at the enlarged spinose scales on the post-auricular fold. Lacks dark spot on posterior of tympanum. Lateral surfaces distinct from dorsum, with sides dark brown with light brown spots, the spots consisting of

clusters of 2–4 pale scales on the dark brown scales. Lateral stripe between axilla and groin absent. Lateral dark spot absent. Arms weakly banded with dark bands approximately the same width as intervening pale colour. Banding on legs not well defined, dark bands on anterior two-thirds of tail, with dark bands wider than the light bands, fading to unbanded for remainder of tail. Gular region with six grey longitudinal stripes ending at gular fold, ventral surface of torso and tail with cream colouration and unpatterned.

*Variation.* 43–61 mm SVL; 92–125 mm tail length. Tail long, ranging from 1.8–2.5 × SVL. Usually a spine above tympanum, with several spines along post-auricular fold. A short row of spines extends from post-auricular fold to above tympanum, variably expressed with most reaching less than half way to tympanum. Nuchal crest absent to very low in profile. On dorsum, paravertebral row sometimes approaches the size of vertebral row, but is typically reduced in size. The enlarged dorsolateral row decreases in size posteriorly, reaching normal size at the base of the tail.

Dorsal patterning variable and complex with 5–6 dark brown bands from nape to legs between dorsolateral white stripes, intersected by a poorly defined vertebral stripe of grey, approximately 3 scales wide. These dark bands extend irregularly to the outer side of the white stripes, fading into the colour patterns on the sides, which are dark brown with light brown spots. Dorsal patterning tends to be obscured in full breeding colouration, where they have strongly contrasting charcoal black, white and chestnut or orange-red colouring on head and upper body, with ventral surface of head, chest and tail also having an orange-red flush in some individuals. Labial scales pale cream with a few darker flecks, extending as a broad pale band along jaw to back of head ending at the enlarged spinose scales on the post-auricular fold. Ventral surface of head often has grey longitudinal stripes ending at gular fold. Ventral surface of body and tail unpatterned and cream in colour.

*Distribution and ecology.* Restricted to the central and northern Kimberley region (fig. 8). Most records are from the Mitchell Plateau and Prince Regent River National Park, with other records from Kalumburu, Theda and Doongan stations. No specimens known from islands.

A habitat generalist occurring in tropical savannah woodlands and grasslands. Although it occurs in savannah woodlands, it appears to be found in rockier areas within these habitats, including laterite, basalt and sandstone. Observed to perch on rocks or termite mounds.

*Comparison with other species.* The distribution overlaps a number of other *Diporiphora* species in the Kimberley. From *D. sobria* it can be distinguished in lacking a scapular fold and having strongly heterogeneous scales between the pale dorsolateral stripes. It differs from *D. perplexa* sp. nov. in having heterogeneous dorsal scales, 2 (vs. 0) femoral pores and no dark markings on the tympanum. It differs from *D. magna* in having a gular fold, femoral pores, double canine teeth in upper jaw and white labial scales. It differs from *D. margaretae* in having a gular fold and double canine teeth on each side of upper jaw.

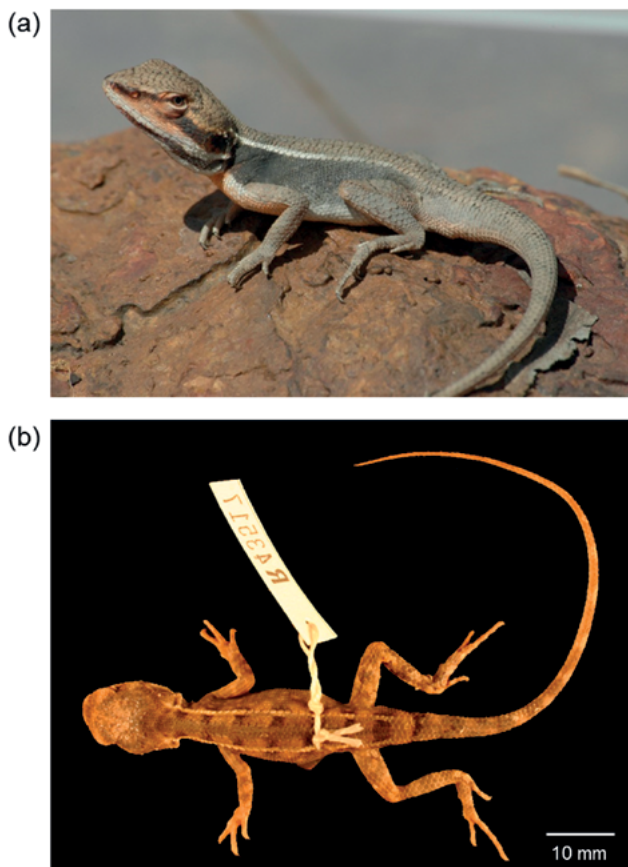


Figure 9. *Diporiphora albilabris*: a, adult male in breeding colouration (registered specimen NMV D73860) from King Edward River crossing, Western Australia (photo: J. Melville); b, dorsal view of holotype WAM R43517, Mitchell Plateau, Western Australia.

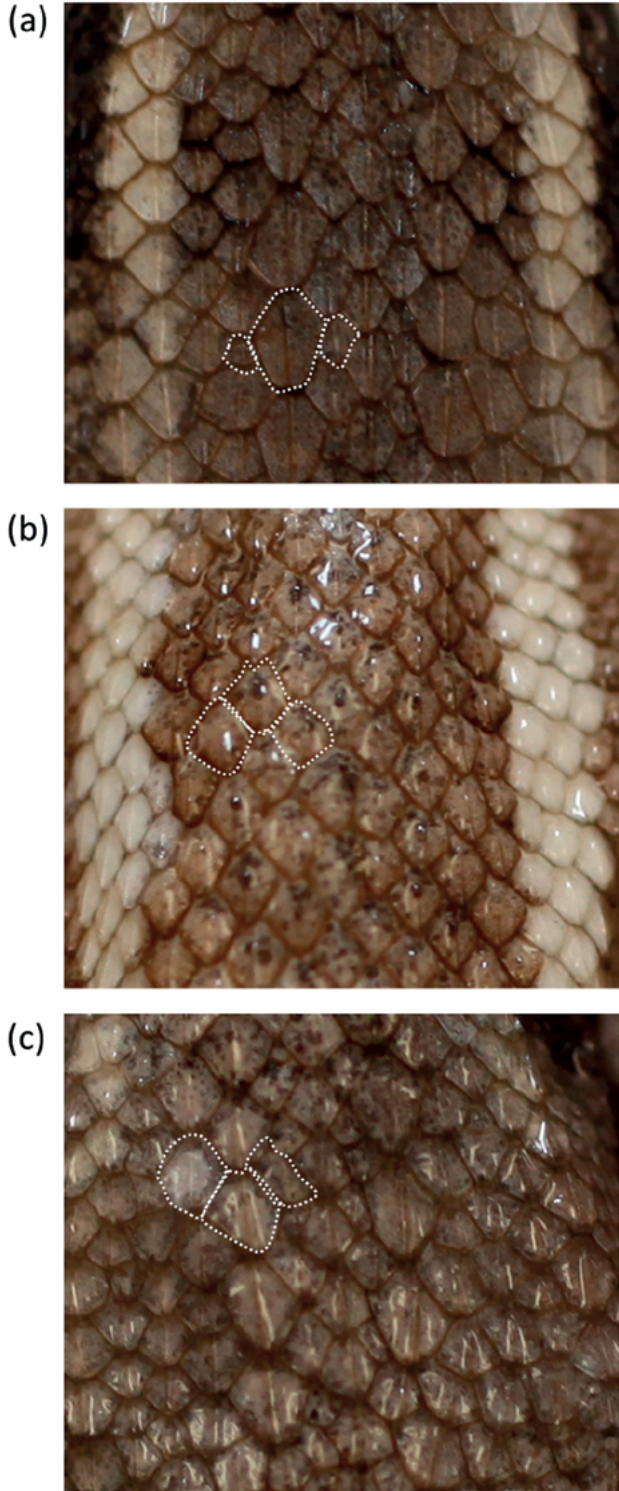


Figure 10. Images of dorsal scales of *D. albilabris* and *D. sobria*, depicting: a, heterogeneous dorsal scales in *D. albilabris*; b, homogeneous dorsal scales in *D. sobria* from Western Australia; c, moderately heterogeneous dorsal scales in *D. sobria* from northern and eastern Northern Territory.

*Remarks.* Originally a nominate subspecies, elevated here to full species (see account above). Although, based on mtDNA, this species is sister to *D. bennettii*, with which it overlaps in distribution, it is quite different in appearance. *Diporiphora albilabris* has a more typical *Diporiphora* appearance of slender body shape and contrasting markings on the dorsum, whereas *D. bennettii* has a more derived morphology of small body size, short tail length and lack of highly contrasting dorsolateral stripes. *Diporiphora albilabris* has a relatively small distribution in the northern central Kimberley, yet it is reasonably abundant where it occurs and not under immediate threat, making its conservation status likely to be of least concern.

***Diporiphora bennettii* (Gray, 1845)**

*Common name.* Kimberley sandstone dragon.

Figure 11, Tables 3, 4

*Gindalia bennettii* Gray, J.E. 1845. *Catalogue of the specimens of lizards in the collection of the British Museum*. British Museum: London. xxviii+289 pp. [247]. Type data: holotype – BMNH 1946.8.12.77, “N.W. Coast of Australia”.

*Diagnosis.* Small body size (to 55 mm SVL) and short tail (<2.0 × SVL), with robust habitus and wide head with short snout. Gular fold present, post-auricular fold strong, scapular fold weak. Dorsals homogeneous, scales in axilla not granular. Lacks

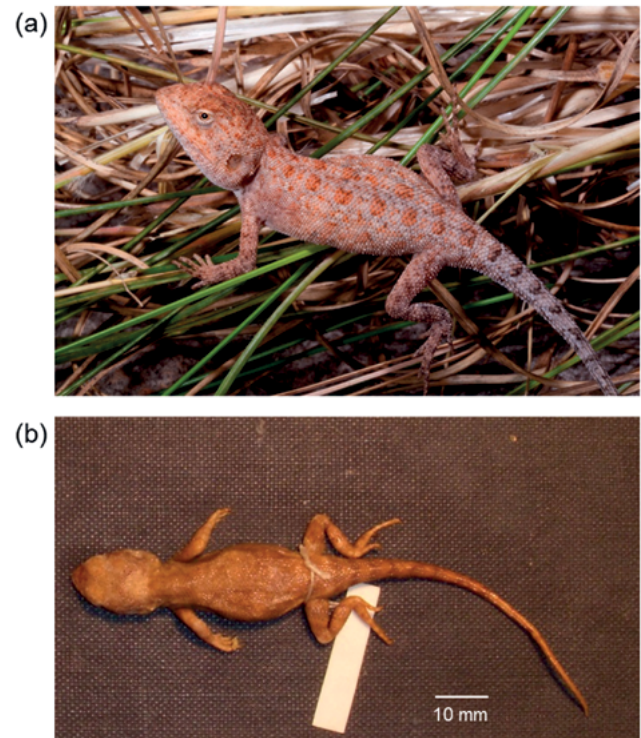


Figure 11. *Diporiphora bennettii*: a, adult from Little Mertens Falls area, Mitchell Plateau, Western Australia. (photo: S. Wilson); b, holotype BMNH 1946.8.12.77, from the “NW coast of Australia”, showing dorsal view.

dorsolateral stripes. Usually lacks dark smudge on tympanum, although some individuals have a faint dark spot on posterior edge of tympanum. Pre-cloacal pores 2; femoral pores 0.

*Description of holotype.* Female; 50 mm SVL; 68 mm tail length. Small body size with wide head and short wide neck. Two canines on either side of upper jaw. Gular fold present. Strong post-auricular fold, weak scapular fold. Post-auricular fold with 1–3 spines. Dorsal scales mostly homogeneous, strongly keeled with keels parallel to midline forming lines running longitudinally down dorsum from shoulders to one third of the way down the tail; enlarged scales associated with vertebral or dorsolateral stripes are absent. Scales on flanks homogeneous, with keels angled towards dorsum. Lacks spinose scales on limbs or tail. Scales in axilla not granular. Weakly keeled scales on ventral gular region and strongly keeled scales on ventral torso. Pre-cloacal pores 2; femoral pores 0.

Dorsum patterning faint and diffuse. Lacks vertebral or dorsolateral stripes. Lacks visible dark transverse bands between head and pelvis. Head virtually unpatterned, without pale labials or pale line between eye and ear. Faint dark spot on posterior of tympanum. Flanks similar to dorsum, with sides of torso being slightly darker than dorsum with a few light brown spots. Lateral stripe between axilla and groin absent. Lateral dark spot absent. Very faint banding on lower hind limbs, dark banding on tail, with light bands much wider than darker bands. Arms lack dark banding. Ventral surface of head, torso and tail unpatterned and cream colouration.

*Variation.* 41–55 mm SVL, 53–83 mm tail length. Tail short, less than  $2.0 \times$  SVL. Gular fold ranges from weak to strong, always with reduced scales along fold, even if skin does not fold over; post-auricular fold strong and scapular weak. Head triangular with usually pronounced adductor muscles, snout short. Typically, one or two enlarged spinose scale above tympanum and on post-auricular fold, with 0–3 adjacent slightly enlarged scales. No conspicuous nuchal crest, but occasionally slightly raised scales present. Dorsal scales homogeneous with no abrupt demarcation of dorsal and lateral scale sizes. Keels of scales on sides angled dorsally and posteriorly. Scales above cloaca on sides of tail at base with raised keels. Tail short, terminating in a blunt tip.

Background colour an admixture of dark brown, tan and pale white scales generating a rather diffuse background pattern with no highly contrasting dorsolateral stripes. Dark brown cross-bands obscure, but in some heavily marked individuals they can form loose networks that enclose pale spots. In some individuals, especially juveniles, there are alternating wide dark brown blotches and thinner pale lines along the dorsum, although these are usually interrupted by variable admixture of different-coloured scales. Lateral surfaces tend to be darker with pale stippling. Tails with thin dark bands with wide pale interspaces. Usually lacks dark spot on tympanum. Ventral surface pale with occasional dark stippling on chin, sometimes extending to ventrum.

*Distribution and ecology.* Restricted to the northern Kimberley (fig. 8), with many records from the Mitchell Plateau and Prince Regent River National Park, extending east to Drysdale River National Park and including a few neighbouring offshore islands: Augustus, Darcy and Unwins.

Collection records (over 40) are nearly all from sandstone rock outcrops and escarpments with spinifex cover.

*Comparison to other species.* This species is similar to *D. perplexa* sp. nov., with extensive distributional overlap and occurring in similar habitats, but differs in having a much smaller body size, a short tail and no dorsolateral stripes. It differs from *D. albilabris* in having a smaller body size, a short tail, no femoral pores, homogeneous dorsal scales and in pattern by lacking any prominent vertebral or dorsolateral stripes. It differs from *D. magna* and *D. margaretae* in having a smaller body size, a short tail, a gular fold and a pair of enlarged canines on each side of upper jaw. It differs from *D. pallida* sp. nov. in having two canine teeth on each side of upper jaw.

*Remarks.* The species was previously believed to include what we describe below as *D. perplexa* sp. nov. *Diporiphora bennettii*, however, is the sister species to *D. albilabris* (fig. 1b; also restricted to the northern Kimberley), with these two being sister species to *D. sobria*, which is now understood to be widely distributed in the southern AMT. *D. perplexa* sp. nov. occurs over a broad area in the Kimberley and extends to the NT, and accordingly, *D. bennettii* is now known to be restricted to the north-west Kimberley. *Diporiphora bennettii* has an unusual morphology for a *Diporiphora*, owing to its small body size, short tail, robust habitus, obscure dorsal patterning and close association with sandstone outcrops in the northern Kimberley. The redefinition of this species and reduction of its range adds to the large number of endemic reptiles and frogs from this region (e.g. Powney et al., 2010; Palmer et al., 2013).

#### *Diporiphora perplexa* sp. nov.

ZooBank LSID: <http://zoobank.org/urn:lsid:zoobank.org:act:4A6A3A8B-5FB1-40D5-843B-258D095238F3>

*Common name.* Kimberley rock dragon.

Figure 12, Tables 3, 4

*Holotype.* WAM R177290 (formerly NMV D73819) (adult male), Gibb River Rodd, 20 km west of Ellenbrae Station, WA (15° 57.31' S, 126° 52.9' E). Collected by J. Melville on 9 September 2005.

*Paratypes.* NMV D73805 (adult female), Home Valley Station, WA (15° 44.39' S, 127° 49.83' E); NMV D73841 (adult female), King Edward River Campground, Mitchell Plateau Road, WA (14° 56' 57.1" S, 126° 12' 10.4" E); NMV D73978 (adult male), Buchanan Highway, south of Jasper Creek, NT (16° 02' 46.8" S, 130° 51' 49.3" E); NMV D73980 (adult female), Bullo Road off Victoria Highway, NT (15° 48' 39.2" S, 129° 40' 13.5" E); WAM 119719 (male), Emma Gorge, Cockburn Range, WA (15° 50' S, 128° 02' E); WAM R162517 (female), 25 km S Wyndham, WA (15.7154° S, 128.2684° E); WAM R171418 (male), Prince Regent River National Park, WA; WAM R175785 (female), Waterfall Yard, 15 km N Mt Elizabeth Homestead, WA (16.2822° S, 126.1059° E).

*Diagnosis.* Body size moderately large (to 68 mm SVL) with long tail ( $1.9$ – $2.5 \times$  SVL). Gular and scapular folds present but weak; post-auricular fold strong. Homogeneous dorsal scales. Pale dorsolateral stripes from back of head to one-third down torso. Black smudge on posterior edge of tympanum, extending on to scales posterior to tympanum. Pre-cloacal pores 2–4; femoral pores 0.



Figure 12. Holotype of *Diporiphora perplexa* sp. nov. (WAMR177290, formerly NMV D73819): a, in life – adult male in breeding colouration from Gibb River Road, west of Ellenbrae Station, Western Australia; b, c, d, preserved specimen in dorsal, ventral and lateral (head) views. Yellow arrow highlights a key diagnostic character: dark pigment “smear” on posterior of tympanum spreading onto neighbouring head scales (photos: J. Melville).

*Description of holotype.* Male; 63 mm SVL; 140 mm tail length. Moderately stout with long tail and limbs. Two canines on either side of upper jaw, with posterior canines extremely enlarged relative to anterior canines. Gular fold present but weak. Strong post-auricular fold, weak scapular fold. Dorsal scales homogeneous, strongly keeled with keels parallel to midline forming lines running longitudinally down dorsum from shoulders to base of the tail; enlarged scales associated with vertebral or dorsolateral stripes not conspicuous. Scales on flanks homogeneous, with keels on posterior flanks angled towards dorsum. Lacks spinose scales on head, limbs and tail. Scales in axilla small but not granular. Ventral scales weakly keeled in gular region and strongly keeled on body. Pre-cloacal pores 2; femoral pores 0.

Dorsum patterning faint. Lacks vertebral stripe and faint dorsolateral stripes from back of head to one-third down torso. Lacks visible dark transverse bands between head and pelvis. Head relatively unpatterned: labials same colour as rest of head; and faint, narrow pale line from posterior of eye to above ear. Prominent black smudge on posterior edge of tympanum, extending onto scales behind ear. Flanks have large dark patches in axillary region extending up onto shoulder, then extending posteriorly and fading to dark speckled appearance on a pale background. Lateral stripe between axilla and groin absent. Large lateral dark patch in axilla, extending up onto shoulder. Arms lack dark banding. Very faint banding on hind limbs and tail, with light bands much wider than darker bands. Ventral surface plain cream to white.

*Variation.* 48–76 mm SVL; 101–183 mm tail length. Tail long, ranging from 1.9–2.5 × SVL. In some individuals keeling on dorsal scales converge towards the midline approximately halfway down torso but run parallel to midline from mid-dorsum to pelvis. Usually a single spinose scale above tympanum, with 1–3 spines on post-auricular fold, occasionally with a short row of spines extending from post-auricular fold to above tympanum. Dorsolateral scale rows raised on neck. In some individuals, a slightly raised nuchal crest (males) and the scales of dorsolateral rows on body appear to be enlarged with slightly thickened keels, but this is barely perceptible (hence, we have not included it as a diagnostic character). Pre-cloacal pores were usually 2, but many had 4; no specimens with femoral pores.

Dorsal colouration variable from strongly patterned (mainly smaller individuals and females) to unpatterned (adult males). Most individuals have pale dorsolateral stripes running from the back of the head to at least a third of the way down the torso. In strongly patterned individuals, these stripes continue onto the tail where they converge approximately halfway down. More patterned individuals have 5–7 dark cross-bands between the pale dorsolateral stripes, continuing onto the tail. These cross-bands are intersected by a narrow pale white, cream or grey vertebral stripe. Also, these individuals will often have a black patch on shoulder, into the axilla, with pale flecks. Individuals with little patterning are usually adult males with breeding colours, which includes a large black patch in axillary region extending up onto shoulder, then posteriorly fading to dark speckled appearance with a bright yellow background,



and a pink flush on tail and rear legs. No distinct patterning on head, upper labials flecked with light brown and cream, with no pale labial stripe. Ventral surfaces plain cream to white. Gular region plain or with diffuse brown speckling (no lines).

**Distribution and ecology.** Widespread in the Kimberley and extreme western Top End of the NT. They occur from the Yampi Peninsula in the south-western Kimberley, extending eastwards to the Kununurra area and to the western NT in the Jasper Gorge area.

This species is almost always associated with rocks. It will also climb onto vegetation, such as cane grass, small shrubs and trees, spinifex and even pandanus and mangroves, but with rocks or creek lines nearby.

**Etymology.** Named from the Latin for confused or cryptic, in reference to Allan Greer's (former curator at the AMS) thoughts on this species when carrying out earlier work on the group in the 1990s. This species remained hidden until a genetic analysis and consultation of the *D. bennettii* type with its small body size, short tail and diffuse pale patterning.

**Comparison with other species.** Similar to *D. bennettii*, occurring in similar rocky habitats, but differs in having a long tail and limbs and dorsolateral stripes. Can be distinguished from *D. albilabris* and *D. sobria* in mostly lacking femoral pores, having no white or pale stripes on the head (on upper labials or between eye and ear), no stripes under chin and homogenous dorsal scales. Differs from *D. magna*, *D. margaretae* and *D. pindan* in having a gular fold, a black spot on tympanum and two canine teeth on each side of upper jaw. *Diporiphora lalliae* differs from *D. perplexa* sp. nov. in lacking both a black spot on tympanum and double canine teeth on each side of upper jaw.

**Remarks.** This species has previously been confused with *D. bennettii* (see account above), and this is the species usually depicted in field guides as *D. bennettii*. However, both genetic work and examination of the original specimens have now distinguished these two species. Interestingly, *D. perplexa* sp. nov. is the only member of the *D. bennettii* species group that is sympatric with the three other species (which are generally allopatric). This distributional pattern suggests that *D. perplexa* sp. nov. may have different habitat preferences and ecology to the other species that allows for sympatry.

Recent unpublished phylogenomic research using single-nucleotide polymorphisms shows that *D. perplexa* sp. nov. is highly divergent and genetically distinguishable from the *D. sobria* (as defined below), even in areas of syntopy (J. Fenker, unpublished data).

### *Diporiphora sobria* Storr, 1974

**Common name.** Northern savannah two-pored dragon.

Figure 13, Tables 3, 4

*Diporiphora albilabris sobria* Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146 [135]. Type data: holotype – WAM R23180, Pine Creek, NT [14° 04' S, 131° 58' E].

*Diporiphora bennettii arnhemica* Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146 [137]. Type data – holotype ANWC R740, near upper Katherine River, NT [14° 13' S, 132° 36' E]. Synonymy decision of current work.

**Diagnosis.** Body size moderately large (to 69 mm SVL) with moderately long tail (2.3–2.6 × SVL). Gular fold present, post-auricular fold strong and scapular fold present but often weak. Dorsolateral stripes present. Lacks dark smudge on posterior edge of tympanum. In WA, the scales between dorsolateral stripes are homogeneous (fig. 10b); in the NT, heterogeneous (fig. 10c). Pre-cloacal pores 4; femoral pores 2.

**Description of holotype.** Subadult, unknown sex; 34 mm SVL; 68 mm tail length. Moderately robust with long limbs and tail. Two canines on either side of upper jaw. Gular fold present, scapular and post-auricular folds present but weak. Dorsal scales homogeneous between faint pale dorsolateral stripes. These homogeneous scales are relatively large and strongly keeled. On the outer sides of the faint dorsolateral stripes are smaller keeled scales. Scales on flanks homogeneous, with keels running parallel to dorsum. Lacks spinose scales on head, limbs or tail. Lacks granular scales in axilla. Ventral scales homogenous and strongly keeled. Pre-cloacal pores 4; femoral pores 2.

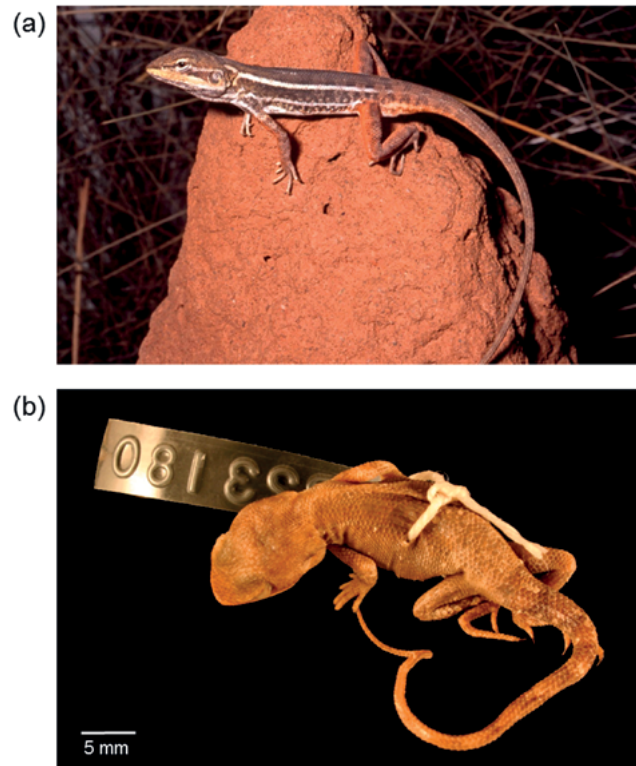


Figure 13. *Diporiphora sobria*: a, adult male with breeding colouration, Halls Creek, Western Australia (photo: S. Wilson); b, holotype WAM R23180 from Pine Creek, Northern Territory.

Dorsal colour uniform brown and grey tones, without apparent patterning. Lacks vertebral stripe but has faint dorsolateral stripes on anterior half of body, fading to background colour midway down torso. Lacks visible dark transverse bands between head and pelvis. Head relatively unpatterned: labials pale; and very faint, narrow pale line from posterior of eye to above ear. Dark smudge on posterior of tympanum absent. Flanks unpatterned and consistent with dorsal colouration. Lateral stripe between axilla and groin absent. Lacks lateral dark patch. Arms lack dark banding. Very faint banding on hind limbs; dark bands on anterior two-thirds of tail, with dark bands being narrower than the light, fading to unbanded for remainder of tail. Ventral surface of head, torso and tail unpatterned and white or cream colouration.

**Variation.** 46–69 mm SVL; 114–162 mm tail length. Tail long, ranging from 2.3–2.6 × SVL. Gular fold always present and often strong, post-auricular fold from weak to strong and scapular fold present but variable. No low nuchal crest. Most individuals have homogeneous dorsal scales between pale dorsolateral stripes, with all individuals examined from WA having homogeneous scales. However, animals examined from the eastern NT, on the Barkly Tablelands and the Gulf of Carpentaria region, and from north-central regions, such as the Mt Wells and Pine Creek area, had somewhat heterogeneous scales between pale dorsolateral stripes. In these animals, paravertebral rows on either side of the vertebral scale row are not reduced in size in comparison to the vertebral scale row, but the 2nd paravertebral scale row is slightly enlarged, with a strong central keel that is aligned to the scales immediately anterior and posterior. These strongly keeled scales that are aligned form a ridge running along the dorsum either side of the midline. Animals with these dorsal scales include NMV D72666–68, D72706, D72707, D72715, D72720, D73995, D74001, D74003, D74022, D74024 and D74262. Scales on the sides are similar to typically sized dorsal scales and are angled up towards midline. Ventral scales homogenous and strongly keeled. Pre-cloacal pores 4 (occasionally up to 5); femoral pores 2 (occasionally 3 or 4).

Dorsal patterning variable from plain to strongly patterned. Strongly patterned individuals, typically adult females and juveniles, have approximately 7–9 irregular dark transverse bands from nape to legs across dorsum on a pale background. Dark bands are of similar width or narrower than pale background. These bands are separated by an indistinct faint grey or light brown vertebral stripe. The dark transverse bands continue laterally beyond the pale cream dorsolateral stripes, becoming diffuse and terminating on sides, with defined lateral stripe absent. Labial scales pale cream, with a few darker flecks, extending as a broad pale band along jaw to back of head ending at the post-auricular fold. In these animals, the lateral surfaces of the neck, axilla and flanks lack a defined dark patch. Some individuals are less strongly patterned, particularly in the NT, and lack the pale dorsolateral stripes or the dorsolateral stripes fade midway down dorsum. Adult males in breeding colouration often have little patterning, having strongly contrasting charcoal black, white and chestnut or orange-red colouring on head, flanks and upper body, with tail also having a pink flush in some individuals. Arms and legs banded. Ventral surface of head,

torso and tail usually unpatterned and white or cream colouration. However, adult males may have up to three pairs of grey stripes in gular region, terminating at gular fold.

**Distribution and ecology.** Widely distributed from the southern Kimberley region (i.e. south of the barrier ranges: King Leopold and Durack), Top End of the NT (but with no records from Arnhem Land) and just extending into western Queensland (fig. 8). Extends south to the Katherine area.

A habitat generalist occurring in tropical savannah woodlands and grasslands, within these habitats it appears to be associated with rockier areas. Similar habitats to *D. albilabris*. Seen to perch on low vegetation, rocks or termite mounds.

**Comparison with other species.** This species has a very wide distribution and overlaps with numerous other *Diporiphora* species. In WA, it can be distinguished from *D. albilabris* in having a scapular fold, fewer spines around tympanum and post-auricular fold and having homogenous scales between the dorsolateral stripes. It differs from *D. perplexa* sp. nov. in having pale rows of dorsolateral scales, usually a strong post-auricular fold, two femoral pores and lacks dark markings on the posterior of the tympanum. Differs from *D. bilineata*, *D. magna* and *D. lalliae* in having femoral pores, two pairs of canines in upper jaw and white labial scales. It also differs from *D. bilineata*, *D. magna* and *D. margaretae* in having a gular fold and two pairs of canine teeth on each side of upper jaw.

**Remarks.** This species incorporates what was *D. arnhemica* and much of the distribution of *D. albilabris albilabris sensu lato*. Despite the original name, this species does not appear to occur in Arnhem Land from our observations, although collections from this region are scarce. This taxon is diverse and exhibits morphological variation in dorsal scalation. Where it occurs near the morphologically similar *D. albilabris* in the Kimberley region, the homogeneous dorsal scalation differs and separates the two species.

### (c) *D. bilineata* species group (fig. 1c)

#### *Content:*

*D. bilineata* Gray, 1842

*D. lalliae* Storr, 1974

*D. magna* Storr, 1974

*D. margaretae* Storr, 1974

*D. gracilis* sp. nov.

*D. granulifera* sp. nov.

*D. carpentariensis* sp. nov.

#### *Diagnostic characters for group (Table 2):*

- one canine tooth on each side of upper jaw
- granular scales in axilla present, with the exception of *D. lalliae*
- lateral dark spot in axilla
- femoral pores absent.

#### *Remarks*

The *D. bilineata* species group is widely distributed across northern Australia (fig. 14), from the Kimberley to the Cape York

Peninsula. Almost all species appear to be generalists, with the possible exception of *D. gracilis* sp. nov. being specialised for grasses. Body size ranges from small (*D. margaretae*, to 55 mm SVL) to large (*D. magna*, to 77 mm SVL). This is a genetically diverse species group (Smith et al., 2011) for which there has been significant difficulty in species delimitation based on morphology. We provide species accounts for *D. bilineata*, *D. lalliae* and *D. magna*, with key morphological characters for species identification and a revision of their distributions. We also raise *D. margaretae* from synonymy of *D. bilineata* (Cogger et al., 1983), based on genetic results and examination of types. We also describe three new species: two from Queensland and one from the southern Kimberley.

### *Diporiphora bilineata* Gray, 1842

*Common name.* Two-lined dragon.

Figure 15, Tables 3, 4

*Diporiphora bilineata* Gray, J.E. 1842. Description of some hitherto unrecorded species of Australian reptiles and batrachians. Pp. 51–57 in: Gray, J.E. (ed.). *The zoological miscellany*. Treuttel, Würz & Co: London. [54]. Type data: syntype(s) – BMNH 1946.8.12.75–76, Port Essington, NT.

*Diagnosis.* Body size moderate (to 58 mm SVL) with long tail (2.2–2.7 × SVL). Gular and post-auricular folds absent, scapular fold present but weak. Granular scales in axilla, extending over arm to neck. Dorsal scales moderately heterogeneous: scales on 2nd paravertebral row and the two rows of pale dorsolateral scales slightly enlarged and raised. Flanks dark in colour with dark colour of granular scales extending posteriorly onto flanks, which have a speckled appearance due to scattered white scales on the dark background. Pre-cloacal pores 2; femoral pores 0.

*Description of syntypes.* Males; 57 and 58 mm SVL, 151 and 56 (broken) mm tail length. Medium-sized *Diporiphora*, moderately gracile with long limbs and long tail. One canine on either side of upper jaw. Gular and post-auricular folds absent, scapular fold present. Dorsal scales heterogeneous; vertebral row of scales, plus the 3–4 rows immediately adjacent on either side, are enlarged and strongly keeled. The vertebral row and the fourth longitudinal scale row from the vertebral are raised. Beyond these enlarged vertebral scales are four rows of small homogenous scales and then a dorsolateral longitudinal row of

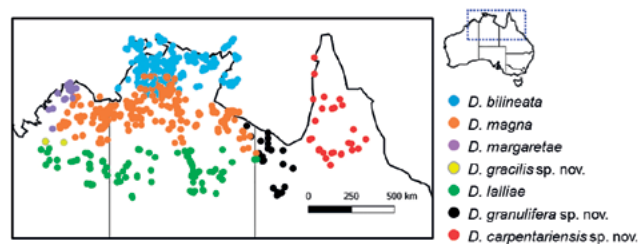


Figure 14. Distributions of *D. magna*, *D. bilineata*, *D. lalliae*, *D. margaretae*, *D. gracilis* sp. nov., *D. granulifera* sp. nov. and *D. carpentariensis* sp. nov. based on specimens examined and collection records.

enlarged scales, with scales on each side strongly keeled. Raised vertebral and dorsolateral scale rows extend up onto neck onto the back of head and posteriorly onto tail. Scales on flanks homogeneous, although changing from small granular scales in

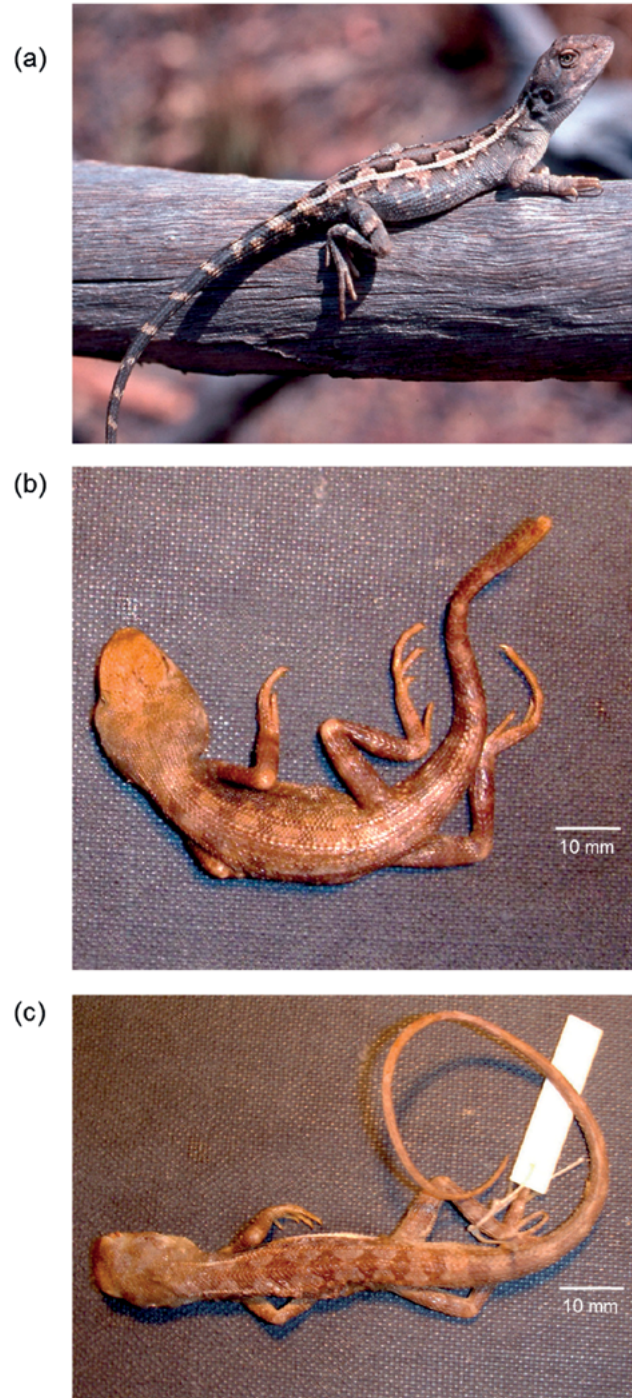


Figure 15. *Diporiphora bilineata*: a, adult in non-breeding colours, Casuarina, Northern Territory (photo: S. Wilson); b, syntypes BMNH 1946.8.12.75–76, Port Essington, Northern Territory.

axilla to small but non-granular scales on the posterior two-thirds of flanks. A few small pale spinose scales at back of head on each side, lacks spinose scales on limbs or tail. Granular scales in axilla, extending over arm onto neck. Ventral scales strongly keeled. Pre-cloacal pores 2; femoral pores 0.

Dorsum strongly patterned. Wide pale, poorly defined vertebral stripe associated with enlarged vertebral scale rows and narrow pale dorsolateral stripes associated with row of enlarged scales, extending from back of head onto base of tail. Six dark transverse bands between head and pelvis, narrower than the pale background. Head relatively plain with little patterning, labials similar colour to rest of head and lacking pale line between eye and ear. Dark smudge on posterior of tympanum absent. Flanks dark in colour with dark colour of granular scales extending posteriorly onto flanks, which have a speckled appearance due scattered white scales on the dark background. Lateral stripe between axilla and groin absent. Dark patch in axilla extending up onto shoulder. Arms and legs lack dark banding. Faint banding on hind limbs; dark bands down length of tail, with dark bands being wider than the light bands. Ventral surface cream with no patterning.

**Variation.** 46–58 mm SVL; 113–156 mm tail length. Tail long, ranging from 2.2–2.7 × SVL. Gular fold always absent and scapular fold present in all animals examined. In a few specimens a small post-auricular fold present. Outer raised trailing edge of scales on outer row of dorsolateral stripes usually present but often trailing edge of scales are only weakly raised, providing demarcation between dorsal and lateral surface. Pre-cloacal pores 2; femoral pores 0.

Variable patterning from strongly patterned to plain individuals. In patterned individuals, 5–7 dark brown transverse bands ranging from narrower to wider than pale background. Dark bands are offset to each other on either side of a narrow greyish or cream vertebral stripe and intersected two pale dorsolateral stripes. In plain individuals, dark dorsal transverse bands are faint or absent, vertebral stripe may be absent but there are usually still the pale dorsolateral stripes from neck to at least level of mid-dorsum. However, dorsolateral stripes are also absent in a few animals. Granular scales on flanks around arm are usually dark brown, extending posteriorly onto flanks that have speckled appearance due to scattered white scales on a dark background. These scattered pale scales sometimes form vertical lines. No white markings on face, labial scales speckled with light brown flecks. Usually faint or no banding on legs but in some more patterned animals banding present. Ventral surface cream, usually plain but some individuals have faint longitudinal stripes on ventral surface of head. Males with breeding colouration tend to lose some of their dorsal patterning, having a yellow wash over the head and upper body with a large black patch in axilla that extends onto shoulder.

**Distribution and ecology.** *Diporiphora bilineata* is widely distributed across the Top End of NT. It occurs sympatrically with *D. magna* in the Pine Creek area. It is a common generalist that occurs throughout the tropical savannah woodlands and grasslands of this region, and is often seen perching on low vegetation, rocks or termite mounds.

**Comparison with other species.** The distribution of *D. bilineata* overlaps with two other *Diporiphora* species. *Diporiphora bilineata* can be distinguished from *D. magna* in usually having fewer pre-cloacal pores (2 vs. 4), lacking a post-auricular fold and by possessing heterogeneous dorsal scales, rows of enlarged vertebral scales and dark flanks with scattered white scales. *Diporiphora bilineata* can be distinguished from *D. sobria* in lacking a gular fold and femoral pores, and having single canines on either side of the upper jaw.

**Remarks.** This taxonomic revision has reduced the distribution of this species to the Top End of the NT, with overlap with *D. magna* in the Pine Creek area. Previously, adult males of *D. bilineata* in breeding colouration may have been mistaken for *D. magna*, and *D. jugularis* has been resurrected that was often attributed to *D. bilineata*, further reducing this species' range. Genetic work has shown that these two species do not overlap extensively (Smith et al., 2011).

### *Diporiphora lalliae* Storr, 1974

**Common name.** Northern deserts dragon.

Figure 16, Tables 3, 4

*Diporiphora lalliae* Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146 [138]. Type data: holotype – WAM R23020, Langey Crossing, WA [17° 39' S, 123° 34' E].

**Diagnosis.** Body size moderately large (to 62 mm SVL) with very long tail (2.6–3.4 × SVL). Gular, post-auricular and scapular folds present. Small scales in axilla but usually not granular. Homogeneous dorsal scales between pale dorsolateral lines that usually lack raised scales in outer row, providing little demarcation between dorsal and lateral scales. Pre-cloacal pores 4; femoral pores 0.

**Description of holotype.** Male; 62 mm SVL; 152 mm tail length. Medium-large *Diporiphora* with long tail and long limbs. One canine on either side of upper jaw. Gular fold present. Strong scapular and post-auricular folds. Dorsal scales homogeneous, relatively large and strongly keeled. At the shoulder, dorsal scales are raised and strongly keeled (but not enlarged) in a longitudinal series of paravertebral and dorsolateral scales that fade by midbody. Scales on flanks homogeneous. Single white spinose scale at back of head sitting on ventral end of post-auricular fold, lacks spinose scales limbs or tail. Small scales in axilla but not granular. Ventral scales strongly keeled. Pre-cloacal pores 4; femoral pores 0.

Dorsum strongly patterned. Wide grey vertebral stripe (~4 scales wide at middle of dorsum), extending from back of head onto base of tail. Prominent pale dorsolateral stripes from shoulder to mid-dorsum, fading into background patterning; these scales form the enlarged longitudinal row of dorsolateral scales at the shoulder. Six dark transverse bands between head and pelvis, approximately the same width as the pale background. Head relatively plain with little patterning, labials similar colour to rest of head but have faint pale line between eye and ear. Dark smudge on posterior of tympanum absent.

Flanks pale in colour, similar to dorsum. Lateral stripe between axilla and groin absent. Dark patch in axilla absent. Arms with faint dark banding. Strong well-defined alternating light and dark bands on legs; dark bands on tail, continuing to near end of tail, with dark bands being a similar width to the light bands. Ventral surface white and unpatterned.

**Variation.** 49–62 mm SVL; 130–194 mm tail length. Very long tail, ranging from 2.7–3.4 × SVL. Gular fold always present, although weak in some individuals. Scapular fold strong and post-auricular fold usually strong, although weak in some individuals. No enlarged spinose scales above tympanum or along post-auricular fold, although the latter may have several slightly enlarged scales. Very low nuchal crest. Outer raised trailing edge of scales on outer row of dorsolateral stripes usually absent, but in some individuals, the trailing edge of scales are weakly raised, particularly over shoulder, providing weak demarcation between dorsal and lateral surface. Pre-cloacal pores 4; femoral pores 0.

Dorsal patterning variable from strongly patterned to little patterning. In strongly patterned individuals, there are 6–8 wide, dark brown transverse bars between shoulders and pelvis, intersected by a wide grey vertebral stripe; pale dorsolateral

stripes from neck and usually extending onto tail. At the shoulder, these dorsolateral stripes consist of an enlarged longitudinal row of scales. Usually no patterning on the head, but in some individuals a white stripe between the eye and ear. In more plain individuals, dark transverse bars faint or absent, and vertebral stripe often absent. Pale dorsolateral stripes from neck to tail usually present, even in unpatterned animals. Dark bands on tail, continuing to near tip. Usually well-defined alternating light and dark bands on upper and lower legs. Dark spot in axillary region absent and flanks usually pale, but some individuals have dark lateral spot above and slightly posterior to shoulder. Ventrums plain.

**Distribution and ecology.** The distribution of *D. lalliae* spans the northern extent of the arid zone along the western deserts, from the southern Kimberley in WA to the far west of Queensland. It extends into the southern reaches of the AMT but does not occur in the central arid zone as occasionally depicted (e.g. Cogger, 2014).

This species occurs in a variety of habitats from savannah woodlands and grasslands to arid habitats. It is a generalist species that is found in many habitats, often seen perching on small rocks, termite mounds or clumps of earth.

**Comparison to other species.** *Diporiphora lalliae* is sympatric with *D. magna*, *D. gracilis* sp. nov. and *D. granulifera* sp. nov. in the northern parts of its range, occurring in similar habitats and is superficially similar in appearance. However, *D. lalliae* can be distinguished from these species by the presence of a gular fold, which is unique in the *D. bilineata* species group (Table 2). The distribution of *D. lalliae* also overlaps with *D. sobria*, from which it can be distinguished in having single canine teeth on each side of upper jaw and lacking femoral pores. In the southern Kimberley region, *D. lalliae* can be distinguished from *D. pindan* in having a gular fold and strong post-auricular and scapular folds.

**Remarks.** This species has previously been confused with numerous other species owing to its generalised appearance. Phylogenetic work has confirmed that it is a member of the *D. bilineata* species group (Smith et al., 2011) but is unique in this group due to the presence of a gular fold.

#### *Diporiphora magna* Storr, 1974

**Common name.** Yellow-sided two-lined dragon.

Figure 17, Tables 3, 4

*Diporiphora magna* Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146 [137]. Type data: holotype – WAM R42786, Old Lissadell (now submerged by Lake Argyle), WA [16° 30' S, 128° 41' E].

**Diagnosis.** Body size moderately large (to 77 mm SVL) with very long tail (to 3 × SVL). Gular fold absent, post-auricular and scapular folds strong. Granular scales in axilla, extending over arm but not extending onto sides of neck. Homogeneous dorsal scales between pale dorsolateral lines that usually lack raised scales in outer row, providing little demarcation between dorsal and lateral scales. Pre-cloacal pores 4; femoral pores 0.

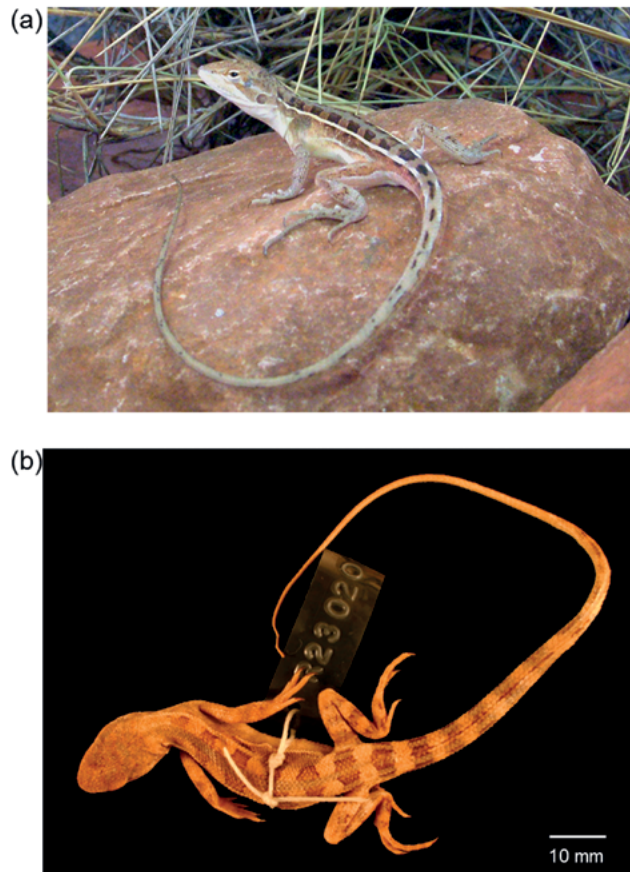


Figure 16. *Diporiphora lalliae*: a, adult male, Three Ways, Northern Territory (photo: S. Wilson); b, holotype – WAM R23020, Langley Crossing, Western Australia.

*Description of holotype.* Female; 47 mm SVL; 141 mm tail length. Medium *Diporiphora*, moderately gracile with long limbs and very long tail. One canine on either side of upper jaw. Gular fold absent. Post-auricular and scapular folds strong. Dorsal scales strongly keeled, relatively small and homogeneous. Scales on flanks homogeneous, although changing from small granular scales in axilla to small but non-granular scales on the posterior two-thirds of flanks. Cluster of spinose scales at back of head on each side, lacks spinose scales on limbs and tail. Granular scales in axilla, extending over arm but not extending onto sides of neck. Ventral scales strongly keeled. Pre-cloacal pores 3 (2 on right; 1 on left); femoral pores 0.

Dorsum strongly patterned. Wide grey vertebral stripe (~2 scales wide at mid-dorsum), extending from back of head onto base of tail, and prominent pale dorsolateral stripes from shoulder to base of tail, fading into background patterning. Seven dark transverse bands between head and pelvis, narrower than the pale background and offset across the vertebral stripe. Head relatively plain with little patterning,

labials similar colour to rest of head and lacking pale line between eye and ear. Dark smudge on posterior of tympanum absent. On flanks, granular scales in axilla are dark brown and strongly defined with an abrupt transition to pale flanks with little patterning. Lateral stripe between axilla and groin absent. Dark patch in axilla extending up onto shoulder. Faint banding on hind limbs; dark bands on anterior two-thirds of tail that are wider than the light bands, fading to unbanding light colouration for remainder of tail. Arms and legs with faint dark banding. Ventral surface cream with a few very faint longitudinal stripes on ventral surface of head.

*Variation.* 54–77 mm SVL; 145–209 mm tail length. Very long tail, ranging from 2.6–3.0 × SVL. Gular fold always absent, post-auricular and scapular strong. In a few individuals, the post-auricular fold, although strong, may be short (<2 mm). Low nuchal crest, more prominent in males. One spinose scale above tympanum and one on post-auricular fold with from 0–3 additional spines on post-auricular fold. Scales rows of dorsolateral stripes on neck and above arms with raised posterior edges. All individuals examined have pre-cloacal pores 4 and femoral pores 0, except for one individual: large male (NMV D73812) from the southern Kimberley has a small indistinct femoral pore on each side.

Variable patterning from strongly patterned individuals to plain individuals. In patterned individuals, 5–7 dark brown transverse bands ranging from narrower to wider than pale interspaces of background colour. Dark bands are often offset to each other on either side of a broad greyish or cream vertebral stripe 3–4 scales wide and two pale dorsolateral stripes usually present. In more plain individuals, dark dorsal transverse bands are faint or absent, vertebral stripe may be absent but with pale dorsolateral stripes from neck to at least level of mid-dorsum. However, dorsolateral stripes are also absent in a few individuals, particularly breeding males. Granular scales in or near the axilla are dark brown, flanks cream, grey, light brown with little patterning. No white markings on face, labial scales speckled with light brown flecks. Faint or no banding on legs. Ventral surface cream, usually plain but some individuals have faint longitudinal stripes in gular region. Males with breeding colouration tend to lose some of their dorsal patterning, having a yellow wash over the head and upper body with a large back patch in axilla that extends onto shoulder.

*Distribution and ecology.* *Diporiphora magna* is widely distributed across the tropical savannah region of northern Australia, from the central Kimberley, WA, through the NT and just over the Queensland border at Lawn Hill National Park. It appears to have been replaced by other *D. bilineata* species group members as follows: to the south by *D. lalliae*, which occupies the northern deserts, to the west in the Kimberley by *D. margaretae* and *D. gracilis* sp. nov., and in the Top End of the NT by *D. bilineata*, although there is a wide (~100 km) area of sympatry between roughly Pine Creek and Katherine.

A habitat generalist occurring in tropical savannah woodlands and grasslands, individuals have been observed to perch on low vegetation, rocks or termite mounds.

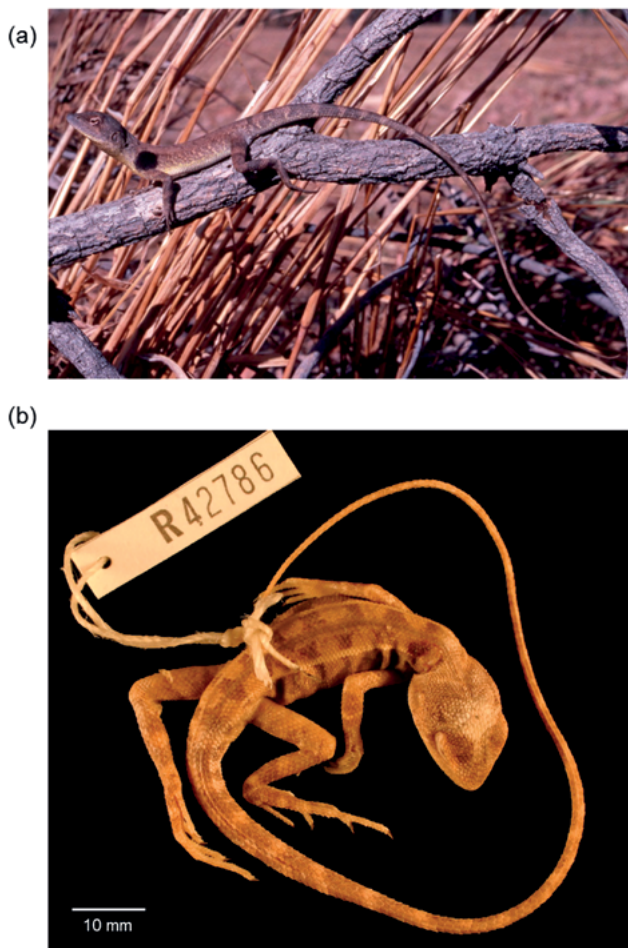


Figure 17. *Diporiphora magna*: a, adult male, Larrimah, Northern Territory (photo: S. Wilson); b, holotype WAM R42786, Old Lissadell (now submerged by Lake Argyle), Western Australia.

*Comparison to other species.* The distribution of *D. magna* overlaps with numerous other *Diporiphora* species across the tropical savannahs of northern Australia. In the Kimberley region, *D. magna* differs from *D. margaretae* in having a smaller body size (to 77 vs. 55 mm SVL), stronger post-auricular and scapular folds, a longer tail and flanks lacking speckled appearance (scattered white scales on a dark background). In the northern NT, *D. magna* differs from *D. bilineata* in having a post-auricular fold and homogenous dorsal scales, lacking rows of enlarged vertebral scales and lacking dark flanks with scattered white scales. In the southern part of its range, *D. magna* can be distinguished from *D. lalliae* in lacking a gular fold, a longer tail in proportion to body and granular scales in axilla. Across its range, *D. magna* can be distinguished from *D. albilabris*, *D. bennettii*, *D. sobria* and *D. perplexa* sp. nov. in lacking a gular fold, lacking femoral pores and having single canines on either side of the upper jaw.

*Remarks.* Phylogenetic work has redefined the distribution of this species (Smith et al., 2011). Specimens of *D. margaretae* were formerly assigned to *D. magna*, meaning now that *D. magna* does not occur in the north-west Kimberley region. This taxon is diverse and exhibits morphological variation in colour patterning and overlaps or contacts a number of phylogenetically close species. Where it occurs in close proximity to these species, it can be distinguished on the basis of scalation.

#### *Diporiphora margaretae* Storr, 1974

*Common name.* Northwest Kimberley two-lined Dragon.

Figure 18, Tables 3, 4

*Diporiphora bilineata margaretae* Storr, G.M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146 [143]. Type data: holotype – WAM R27648, Kalumburu, WA [14° 18' S, 126° 30' E].

*Diagnosis.* Body size small to moderate (to 55 mm SVL) with long tail ( $2.5\text{--}2.7 \times \text{SVL}$ ). Gular fold absent, post-auricular fold weak to moderate, scapular fold moderate to strong. Granular scales in axilla, extending over arm onto neck to posterior edge of the scapular fold. Scales on outer rows of dorsolateral stripes have raised trailing edge in some individuals, particularly over shoulder, giving moderate demarcation between dorsal and lateral surfaces. Enlarged pale scales on sides tending to form vertical bars. Pre-cloacal pores 4; femoral pores 0.

*Description of holotype.* Female; 55 mm SVL; 128 mm tail length. A medium-sized *Diporiphora*, moderately gracile with long limbs and tail. One canine on either side of upper jaw. Gular, post-auricular and scapular folds absent. Dorsal scales strongly keeled, relatively large and homogenous, although band of smaller homogenous scales across back of head and neck. Longitudinal series of raised, but not enlarged, pale paravertebral and dorsolateral scales at the shoulder, not extending down dorsum. Scales on flanks homogeneous, although changing from small granular scales in axilla to small, non-granular scales on the posterior two-thirds of flanks. A few small pale spinose scales at back of head on each side, lacks spinose scales limbs on

tail. Granular scales in axilla, extending over arm onto neck to posterior edge of the scapular fold. Ventral scales strongly keeled. Pre-cloacal pores 4; femoral pores 0.

Dorsum strongly patterned. Six irregular dark brown squares (rather than transverse bands) between head and pelvis either side of a broad grey vertebral stripe, intersected by poorly defined, light brown dorsolateral stripes. Dark brown squares are narrower than the pale background. Head relatively plain with little patterning, labials similar colour to rest of head and lacking pale line between eye and ear. Dark smudge on posterior of tympanum absent. Complex patterning on flanks; granular scales on flanks around arm are dark brown, extending posteriorly onto flanks that have speckled appearance due to seemingly random assortment of scale colours from white, cream, grey, light brown and dark brown; dark dorsal squares also extend as dark patches onto flanks. Lateral stripe between axilla and groin absent. Darker scales in axilla not extending up onto shoulder. Arms with faint dark banding. Banding on legs not well defined, with light bands narrower than dark bands. Dark bands on anterior third of tail, fading to unbanded light colouration for remainder of tail. Ventral surface cream with a few scattered fleck of light brown on ventrum, throat and head.

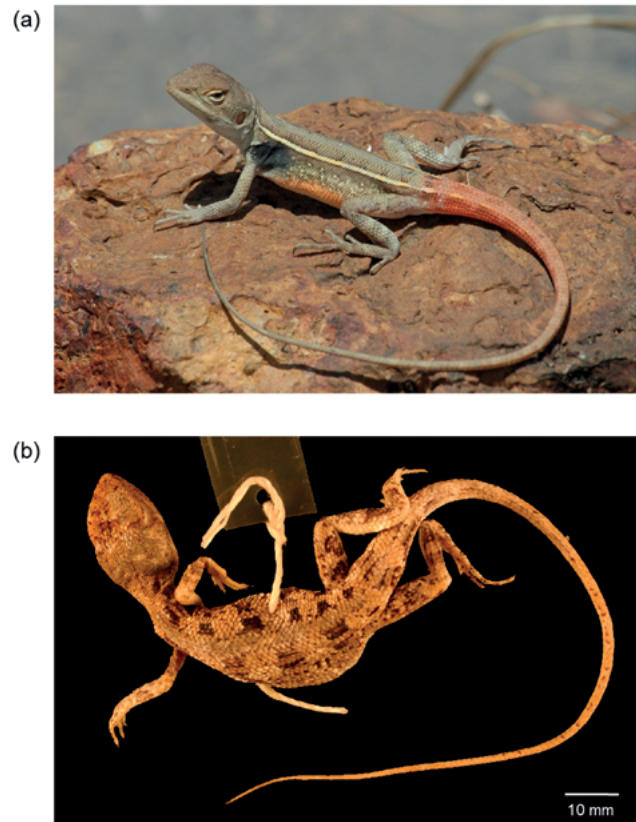


Figure 18. *Diporiphora margaretae*: a, adult male (NMV D73834), King Edward River, Kimberley, Western Australia (photo: J. Melville); b, holotype WAM R27648, Kalumburu, Western Australia.

*Variation.* 44–55 mm SVL; 110–135 mm tail length. Tail long, ranging from 2.5–2.7 × SVL. Gular fold always absent, post-auricular and scapular vary from weak to moderate. Low nuchal crest present. Spinose scale above tympanum, with 1–4 low spines on post-auricular fold. On dorsolateral row on neck, scales with posterior edges raised. Dorsal scales relatively homogeneous; an exception is the 2nd paravertebral row tending to be slightly enlarged. On flanks, keels of scales angled dorsally and posteriorly; flanks with scattered enlarged scales, tending to align vertically. Pre-cloacal pores 4; femoral pores 0.

Dorsal colour pattern variable. In patterned individuals, cream, grey, light brown to dark brown complex pattern with white dorsolateral stripes. Five or six irregular dark brown bands either side of a broad greyish vertebral stripe 3–5 scales wide. Granular scales on flanks around arm are usually dark brown, extending posteriorly onto flanks. Sides with speckled appearance due to scattered pale scales on enlarged scales on a dark background, often forming vertical rows. The dark bands on the dorsal surface do not extend laterally on the body and in most individuals the bands do not extend beyond the white dorsolateral stripes. In small heavily marked individuals, there is often a dark-edged pale lateral stripe. In plainer individuals, often adult males, dark transverse bands across the dorsum are either absent or faint. Lateral surfaces not as dark and speckled as for patterned individuals. No white markings on face, labial scales speckled with dark brown flecks. Banding on limbs not well defined, with light bands narrower than dark bands. Dark bands on anterior third of tail, fading to unbanded light colouration for remainder of tail. Ventral surface cream sometimes with a few scattered flecks of light brown on gular region and ventrum; occasionally several pairs of lines in gular region.

*Distribution and ecology.* Restricted to the far north Kimberley region, with records from the Anjo Peninsula and Sir Graham Moore Island in the extreme north, Kalumburu, Mitchell Plateau, Prince Regent River and Drysdale River National Parks, and on Mary Island.

This species has been recorded from Eucalyptus woodland, cane grass, triodia on sandstone and other rocky areas.

*Comparison to other species.* The distribution of *D. margaretae* overlaps with a number of other *Diporiphora* species, including *D. albilabris*, *D. bennettii*, *D. perplexa* sp. nov., *D. magna* and *D. pallida* sp. nov. *Diporiphora margaretae* differs from *D. magna* in having weak or absent post-auricular and scapular folds (as opposed to consistently strong folds), and having flanks that have a speckled or barred appearance due to scattered pale scales on a dark background. *Diporiphora margaretae* can be distinguished from *D. albilabris*, *D. bennettii* and *D. perplexa* sp. nov. in lacking a gular fold and femoral pores, and having single canines on either side of the upper jaw. *Diporiphora margaretae* differs from *D. pallida* sp. nov. in possessing a more gracile habitus with longer limbs and tail, lacking a gular fold and having granular scales in axilla.

*Remarks.* This species was originally described as a subspecies on *D. bilineata* (Storr, 1974) but was subsumed into *D. magna*

without comment in Storr et al. (1983), despite having the largest difference in body size of any species pair within the *D. bilineata* species group. Genetic work, across multiple genes (Smith et al. 2011), demonstrated the distinctiveness of this species relative to *D. bilineata* and *D. magna*. Phylogenetic analyses support it being the sister species to *D. gracilis* sp. nov. (fig. 1c).

***Diporiphora gracilis* sp. nov.**

ZooBank LSID: <http://zoobank.org/urn:lsid:zoobank.org:act:F3BB16E0-259E-4396-AD68-FFE06A0FE624>

*Common name.* Gracile two-lined dragon.

Figure 19, Tables 3, 4

*Holotype.* WAM R177291 (formerly NMV D75540) (adult male), Fairfield-Leopold Downs Road, south of Gibb River Road, WA (17° 29' 37.0" S, 125° 2' 17.7" E). Collected by P. Oliver on 2 November 2013.

*Paratypes.* NMV D75541 (adult females), as for holotype; NMV D73901 (adult male), as for holotype; WAM R163503 (female) and WAM R163504 (male), Mornington Station, WA (17° 30' 23" S, 126° 02' 07" E); WAM R177952 (formerly NMV D75542) (adult female), as for holotype.

*Diagnosis.* Body size moderately long (to 61 mm SVL) with elongate and gracile body shape and very long tail (to 3 × SVL). Gular fold absent, post-auricular and scapular folds weak. Granular scales in axilla, extending over arm to scapular fold. Homogeneous dorsal scales between pale dorsolateral lines that usually lack raised scales in outer row, providing little demarcation between dorsal and lateral scales. Pre-cloacal pores 4; femoral pores 0.

*Description of holotype.* Male; 57 mm SVL; tail length 165 mm. A medium-sized gracile *Diporiphora*, with long limbs and a very long tail. One canine on either side of upper jaw. Gular fold absent; post-auricular and scapular folds weak. Dorsal scales on torso strongly keeled, parallel to midline and homogenous; heterogeneous scales on head with wide band of smaller scales across back of head and neck. Low nuchal crest of ~8 scales. Granular scales in axilla, extending over arm to the weak scapular fold. Scales on flanks homogeneous, although changing from small granular scales in axilla to small but non-granular scales on the posterior two-thirds of flanks. Lacks spinose scales on limbs or tail. Ventral scales weakly keeled on head and throat, strongly keeled on body. Pre-cloacal pores 4; femoral pores 0.

Dorsal colour greyish-brown without patterning. Dorsolateral and vertebral stripes absent. Dark transverse bands between head and pelvis absent. Head relatively plain, labials similar colour to rest of head and lacking pale line between eye and ear; lateral portions of snout paler than dorsal surface of snout. Dark smudge on posterior of tympanum absent. Granular scales on axilla dark brown, posterior two-thirds of flanks same colour as dorsal surface. Lateral stripe between axilla and groin absent. Dark patch in axilla, not extending up onto shoulder. Faint banding on hind limbs; tail plain without banding. Arms lack dark banding. Ventral surface cream with no patterning, lower labials faintly stippled.



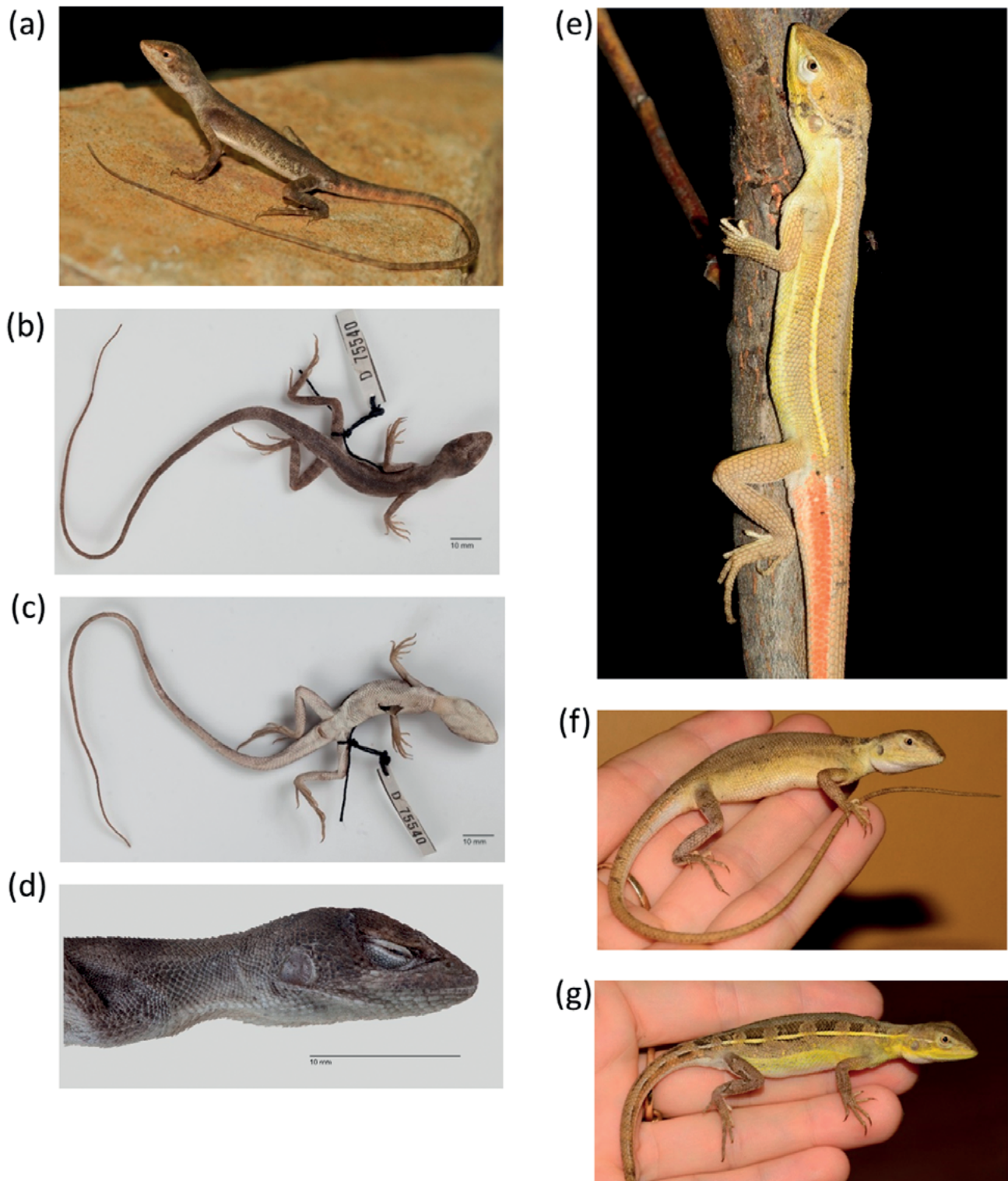


Figure 19. *Diporiphora gracilis* sp. nov. Images of holotype (WAM R177291, formerly NMV D77540), Fairfield-Leopold Downs Road, south of Gibb River Road, Western Australia: a, in life (photo: J. Sumner); b, c, d, dorsal, ventral and lateral (head) views. Pattern variation (individuals from Mornington Station, Western Australia: e, adult male with breeding colour; f, gravid female (plain); g, gravid female (patterned) (photos: Melissa Bruton, Australian Wildlife Conservancy).

*Variation.* 52–61 mm SVL; 140–185 mm tail length. Very long tail, ranging from 2.7–3.0 × SVL. Gular fold always absent, post-auricular fold weak or absent, and scapular fold weak. At most, a single small spinose scale above tympanum and one on post-auricular fold. Dorsal scales homogeneous. Presence of outer raised trailing edge of scales on outer row of dorsolateral stripes variable – usually absent in more plain individuals but present in those with strong patterning, providing weak demarcation between dorsal and lateral surface. Gulars smooth. Pre-cloacal pores 4; femoral pores 0.

Variable patterning from strongly patterned individuals to plain individuals. In patterned individuals, dark brown bands offset each other to either side of a broad greyish vertebral stripe, pale well-defined dorsolateral stripes (approximately two scales wide) that extend from back of head to hind legs, where stripes continue as broken stripes down a third of the tail. Dark dorsal cross-bands continue beyond dorsolateral stripes to a narrow pale lateral stripe. Below lateral stripes is plain with start of cream ventral colour. No patterning on head, lacks pale stripe between eye and ear. Faint banding on limbs and banding on anterior third of tail. In plain individuals, there is no patterning on body or head, including no dorsolateral or vertebral stripes. In these plain individuals, granular scales in axilla are dark brown and in life have a well-defined black spot on sides and a greenish-yellow hue to body. No white markings on face, labial scales speckled with light brown flecks. Faint or no banding on limbs. Ventral surface cream, without markings. In life, males with breeding colouration have a well-defined black spot on sides, a greenish-yellow hue to body and a pink flush on the tail.

*Etymology.* Named for the gracile body shape, with noticeably long and slender body, limbs and tail. Used as a noun in apposition.

*Distribution and ecology.* Restricted to the south-western Kimberley region (fig. 14). Currently only known from two locations, the type location on the Fairfield-Leopold Downs Road and further east on Mornington Station, approximately 80 km apart.

*Diporiphora gracilis* sp. nov. appears to be a grassland specialist, occupying savannah grasslands on clay soils associated with the floodplain of the Lennard River. More collecting is required to determine how far the distribution of this species extends and whether it is only associated with grasslands on clay soils.

*Comparison with other species.* The distribution of *D. gracilis* sp. nov. overlaps numerous other *Diporiphora* species. The distribution of *D. pindan* overlaps with *D. gracilis* sp. nov. but they appear to occupy different habitats (*D. gracilis* sp. nov. in grasslands on floodplains; *D. pindan* in shrubs and spinifex). *Diporiphora pindan* can be distinguished from *D. gracilis* sp. nov., with the latter lacking a well-defined white stripe between eye and ear, having strongly keeled dorsal scales where keels form longitudinal ridges running along torso and having a very long tail in proportion to body size. Differs from *D. magna* in lacking strong post-auricular and scapular folds, and having a more gracile habitus. Differs from *D. lalliae* in lacking gular fold and possessing granular scales in axilla. Differs from *D.*

*albilabris*, *D. bennettii*, *D. sobria* and *D. perplexa* sp. nov. in lacking femoral pores, lacking a gular fold and having single canines on each side of the upper jaw.

*Remarks.* This species is sister to *D. margaretae* from the northern Kimberley, both of which form a Kimberley endemic lineage compared to the next closely related species, *D. lalliae* and *D. magna*, which both extend across the Kimberley and NT to just inside the Queensland border.

*Diporiphora gracilis* sp. nov. was first collected on Mornington Station in 2004. The collection of further individuals by J. Melville that had tissues taken establishes this species' distinctiveness, and the morphology of these specimens is shared by the two Mornington specimens.

#### *Diporiphora granulifera* sp. nov.

ZooBank LSID: <http://zoobank.org/urn:lsid:zoobank.org:act:B6B3DAEB-9D8E-4D5A-A53B-04BF6962C3B1>

*Common name.* Granulated two-lined dragon.

Figure 20, Tables 3, 4

*Holotype.* QM J96362 (formerly NMV D74060) (adult male), Downs Road, 2 km from Barkly Highway, Queensland (20.3714° S, 139.1529° E). Collected by K. Smith in October 2005.

*Paratypes.* NMV D74047 (adult female), Lawn Hill Station, Queensland (18.6536° S, 138.5653° E); NMV D74054 (adult male), Carpentaria Highway, west of Burketown, Queensland (18.0242° S, 139.0077° E); NMV D74062 (adult male), Downs Road, 2 km from Barkly Highway, Queensland (20.3717° S, 139.1525° E).

*Diagnosis.* Medium-large species (to 68 mm SVL) with a very long tail (>2.5 × SVL). Gular fold absent, post-auricular fold weak and scapular fold strong. Granular scales in axilla, extending over arm and along the full length of the scapular fold. Scales on neck anterior to scapular fold small and slightly granular. Outer scale row in dorsolateral stripes have raised posterior edge, particularly over shoulder, giving strong demarcation between dorsal and lateral surfaces. Pre-cloacal pores 4–6 (usually 4); femoral pores 0.

*Description of holotype.* Male; 65 mm SVL; 176 mm tail length. Medium-large *Diporiphora*, moderately gracile with long limbs and very long tail. One canine on either side of upper jaw. Gular fold absent. Post-auricular and scapular folds strong. Dorsal scales strongly keeled, relatively homogenous. Longitudinal series of raised but unenlarged pale dorsolateral scales at the shoulder, extending down posteriorly along dorsum to base of tail. Scales on flanks homogeneous, although changing from small granular scales in axilla to small but not granular scales on the posterior two-thirds of flanks. Lacking cluster of spinose scales at rear of head on the post-auricular fold, lacks spinose scales limbs or tail. Small granular scales in axilla, extending up over shoulder and along under full extent of the scapular fold. Scales on sides of neck anterior to scapular fold small and slightly granular. Ventral scales strongly keeled. Pre-cloacal pores 6; femoral pores 0.

Dorsum light brown with little patterning. Faint broad grey vertebral stripe; well-defined cream dorsolateral stripes running from back of head to base of tail and associated with

raised but not enlarged longitudinal scales. Dark transverse bands absent. Head relatively plain with little patterning; labials similar colour to rest of head, although posterior third paler than anterior; poorly defined, faint pale stripe from eye



Figure 20. *Diporiphora granulifera* sp. nov.: a, in life, Lawn Hill, Queensland (photo: S. Wilson). b, c, d, dorsal, ventral and lateral (head) views of holotype QM J96362 (formerly NMV D74060) Downs Road, 2 km from Barkly Highway, Queensland.

to top of ear. Dark smudge on posterior of tympanum absent. On flanks, granular scales in axilla are dark brown then transition posteriorly into cream, grey and light brown with little patterning; flanks have darker dorsal patterning above and pale cream ventrally; flecked with a few light brown scattered scales. Lateral stripe between axilla and groin absent. Dark patch in axilla extending up over shoulder and down full length of scapular fold. Arms lack dark banding. No patterning on legs, faint banding on anterior third of tail with dark bands wider than pale bands. Ventral surface cream with no patterning.

**Variation.** 44–68 mm SVL; 121–179 mm tail length. Very long tail, ranging from 2.7–3.0 × SVL. Gular fold always absent, post-auricular fold weak to present, scapular fold strong, extending onto edges of ventrum. In some animals, enlarged scales on post-auricular fold has an enlarged cluster of scales at the ventral extent but without a single spinose scale. Pre-cloacal pores variable from 4–6 (usually 4); femoral pores always 0.

Variable patterning from strongly patterned individuals to plain individuals. In patterned individuals, approximately 6–8 dark brown bands slightly offset to each other on either side of a broad undefined greyish vertebral stripe. Banding extends onto tail, fading out half way down tail. Well-defined pale dorsolateral stripes, running from back of head to base of tail and becoming interrupted by banding pattern of tail. Flanks have a faint, poorly defined light brown lateral stripe, with darker dorsal patterning above and pale cream below. Flanks flecked with a few light brown scattered scales. In more plain individuals, pale dorsolateral stripes from neck onto base of tail. Granular scales in axilla are dark brown; flanks cream, grey or light brown with little patterning. No white markings on face, labial scales speckled with light brown flecks. Faint or no banding on limbs. Ventral surface cream, usually plain but some individuals have faint dark flecking on ventral surface of head. Males with breeding colouration tend to lose some of their dorsal patterning, having a large black patch in axilla extending on to shoulder and some having a pink flush on base of tail.

**Etymology.** Named for the extensive granulated scales on sides of body.

**Distribution and ecology.** Restricted to the far north-west Gulf of Carpentaria region of Queensland. More collecting is required to determine how far east this species extends and whether it extends west into the NT. A habitat generalist occurring in tropical savannah woodlands and grasslands. Has been observed perching on low vegetation, rocks or termite mounds.

**Comparison to other species.** The distribution of *D. granulifera* sp. nov. contacts a number of other *Diporiphora* species in the western Gulf of Carpentaria region. Very similar morphologically to *D. carpentariensis* sp. nov. and it remains unclear whether they come into contact in the central Gulf of Carpentaria region, but can be distinguished from this species in lacking or having weak spinose scales on the post-auricular fold and in having granular scales extending anteriorly to the scapular fold, with scales on the sides of neck more homogenous and outer scale row in dorsolateral stripes having raised trailing

edge, particularly over shoulder, giving strong definition between dorsal and lateral surface. Differs from *D. magna* in having granular scales extending over shoulder and along scapular fold, slightly onto ventral surface of neck. Differs from *D. lalliae* in lacking a gular fold. Can be distinguished from *D. sobria* in lacking a gular fold and femoral pores, and having single canines on either side of the upper jaw.

**Remarks.** Although very similar morphologically to *D. carpentariensis* sp. nov., the genetic analysis of Smith et al. (2011) across multiple genes distinguished these two species as divergent lineages that are not each other's closest relatives. It remains to be determined if these two species contact in the central Gulf of Carpentaria region.

Recent unpublished phylogenomic research using single-nucleotide polymorphisms shows that *D. granulifera* sp. nov. is highly divergent and genetically distinguishable from *D. magna* (as defined above) (J. Fenker, unpublished data). However, there is evidence of gene flow and mtDNA introgression between these two species in areas of contact, including along the Barkly Highway, Queensland. The holotype (QM J96362), which was included in this genomic analysis, was confirmed as being *D. granulifera* sp. nov. and is not a hybrid animal, with no evidence of genomic contribution from *D. magna*.

*Diporiphora granulifera* sp. nov. contributes to a small number of endemic lizard and frog species from the Gulf of Carpentaria region, including *Cryptoblepharus zoticus* Horner, *Oedura bella* Oliver and Doughty and *Litoria electrica* Ingram and Corben. Further genetic and morphological work on species that span the Gulf of Carpentaria area may reveal further interesting phylogenetic patterns in this poorly sampled region.

#### *Diporiphora carpentariensis* sp. nov.

ZooBank LSID: <http://zoobank.org/urn:lsid:zoobank.org:act:6795AD24-03D8-4E4E-9FD8-4757AEE964C5>

**Common name.** Gulf two-lined dragon.

Figure 21, Tables 3, 4

**Holotype.** QM J88197 (adult male), Littleton National Park, northern Queensland (18.2243°S, 142.7489°E). Collected by E. Vanderduys on 20 November 2008.

**Paratypes.** NMV D74080 (adult female), Mt Turner Road, 5 km north of Gulf Development Road, Queensland (18.2692° S, 143.3647° E); NMV D74079 (adult male), Mt Turner Road, 20 km north of Gulf Development Road, Queensland (18.2733° S, 143.3656° E); NMV D74076 (adult female), road to Strathmore, 3 km north of Gulf Development Road, Queensland (18.1783° S, 142.8844° E); NMV D74068 (adult male), Bourke Development Road, 25 km NE of Karumba turnoff, Queensland (17.3931° S, 141.3989° E).

**Diagnosis.** Moderately large body size (to 68 mm SVL), with adult males with very long tails (to 3 × SVL) and females with shorter tails (to 2.3 × SVL). Gular fold absent, post-auricular fold weak to strong, scapular fold strong. Granular scales in axilla, extending over arm and along the full length of the scapular fold. Scales on neck in anterior to scapular fold small but not granular. Outer scale row in dorsolateral stripes lack raised trailing edge, without strong delimitation between dorsal and lateral surface. Pre-cloacal pores 4 or 5 (usually 4); femoral pores 0.

**Description of holotype.** Male; 62 mm SVL; 185 mm tail length. Medium-large *Diporiphora*, gracile with long limbs and very long tail. One canine on either side of upper jaw. Gular fold absent, post-auricular fold weak and scapular fold strong, extending onto edges of ventrum. Dorsal scales strongly keeled, relatively homogenous. Longitudinal series of raised but not enlarged pale paravertebral and dorsolateral scales at the

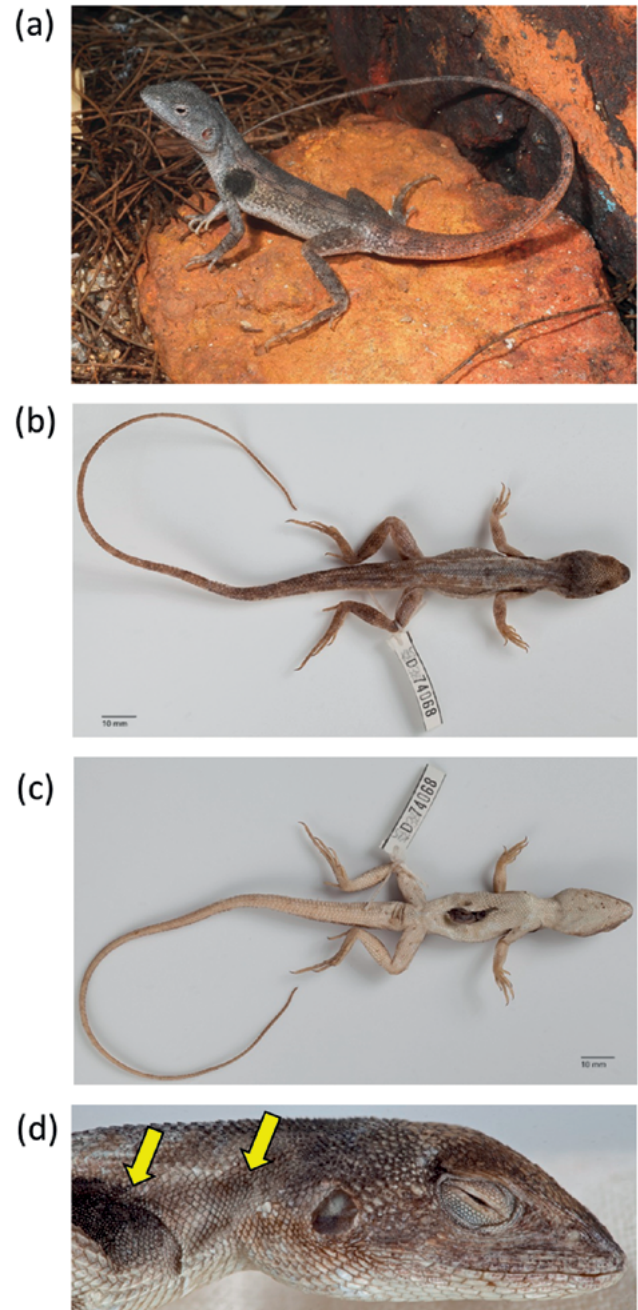


Figure 21. *Diporiphora carpentariensis* sp. nov. Image of holotype (QM J88197), Littleton National Park, northern Queensland, a, in life (photo: E. Vanderduys); b, c, d, dorsal, ventral and lateral (head) view of paratype NMV D74068.

shoulder, extending down back to base of tail. Scales on flanks homogeneous, although changing from small granular scales in axilla to small but non-granular scales on the posterior two-thirds of flanks. Cluster of small spinose scales on post-auricular fold with one cream-coloured spine being clearly larger than the others. Lacks spinose scales on limbs or tail. Granular scales in axilla, extending over arm and along the full length of the scapular fold. Scales on neck, anterior to scapular fold small but not granular. Ventral scales strongly keeled. Pre-cloacal pores 5 (2 on right; 3 on left); femoral pores 0.

Dorsum light brown with little patterning. Faint, broad grey vertebral stripe; well-defined cream dorsolateral stripes running from back of head to base of tail, associated with raised but not enlarged longitudinal scales. Dark transverse bands absent. Head relatively plain with little patterning, labials similar colour to rest of head and lacking pale line between eye and ear. Dark smudge on posterior of tympanum absent. On flanks, granular scales in axilla are dark brown then transition posteriorly into cream, grey and light brown without patterning; flanks have darker dorsal patterning above and pale cream ventrally; flecked with a few light brown scattered scales. Lateral stripe between axilla and groin absent. Dark patch in axilla, associated with granular scales, continues up over shoulder and down full length of scapular fold. Banding on limbs absent; faint banding on anterior third of tail, with dark bands narrower than the light bands. Ventral surface cream with no patterning.

*Variation.* 52–65 mm SVL; 118–187 mm tail length. Very long tail, ranging from 2.1–3.0 × SVL. Tail length appears to be sexually dimorphic with adult male tails ranging from 2.7–3.0 × SVL, while adult female tails ranging from 2.1–2.3 × SVL. Gular fold always absent, post-auricular fold weak to present, scapular fold strong, extending onto edges of ventrum. In some animals, a cluster of small spinose scales on post-auricular fold has an enlarged scales that is not obviously spinous. Pre-cloacal pores variable from 4–5 (usually 4); femoral pores always 0.

Variable patterning from strongly patterned individuals to plain individuals. In patterned individuals, eight or nine dark brown bands slightly offset to each other on either side of a broad undefined greyish vertebral stripe. Banding extends onto tail, fading out halfway down tail. Well-defined pale dorsolateral stripes, running from back of head to base of tail and becoming interrupted by banding pattern of tail. Flanks have faint poorly defined light brown lateral stripe, with darker dorsal patterning above and dark background colour extending slightly below stripe. Flanks flecked with a few light brown scattered scales. In more plain individuals, pale dorsolateral stripes from neck onto base of tail. Granular scales in axilla are dark brown or black, flanks cream, grey, light brown with little patterning. No white markings on head, labial scales speckled with light brown flecks. Faint or no banding on legs and tail. Ventral surface cream, usually plain but some individuals have faint dark flecking on ventral surface of head. Males with breeding colouration tend to lose some of their dorsal patterning, having a large back patch in axilla extending onto shoulder but not anteriorly of the scapular fold, and some males have a pink flush on base of tail.

*Etymology.* Named for the region in which this two-lined dragon occurs on the Gulf of Carpentaria.

*Distribution and ecology.* *Diporiphora carpentariensis* sp. nov. is restricted to the far north-east Gulf of Carpentaria region of Queensland at the western extent of Cape York Peninsula. More collecting is required to determine whether this species extends further west into the Gulf of Carpentaria region. It appears to be habitat generalist, occurring in tropical savannah woodlands and grasslands. Little is known about this species and further field-based work is needed to determine the extent of its distribution and its ecological requirements, habitat preferences and behaviour.

*Comparison to other species.* The distribution of *D. carpentariensis* sp. nov. overlaps a number of other *Diporiphora* species in the Gulf of Carpentaria region. Very similar morphologically to *D. granulifera* sp. nov. and remains unclear whether they contact in the central Gulf of Carpentaria region but can be distinguished from this species in having spinose scales on the post-auricular fold, with a single spine clearly larger than the others, and in lacking granular scales extending anteriorly from the scapular fold, and outer scale row in dorsolateral stripes lack raised trailing edge without a strong demarcation from the dorsal to lateral surface. *Diporiphora carpentariensis* sp. nov. differs from *D. jugularis* in having a strong scapular fold, granular scales in axilla that extend over shoulder and along scapular fold, scales on flanks relatively homogeneous and lacking a black gular band or black spot on sides of neck. *Diporiphora carpentariensis* sp. nov. can be distinguished from *D. australis* in lacking a gular fold and having granular scales in axilla that extend over shoulder and along scapular fold.

*Remarks.* This species has previously been identified as *Diporiphora bilineata*. It is probable that animals previously identified as *D. bilineata* on Cape York Peninsula actually comprise two species: *D. carpentariensis* sp. nov. and *D. jugularis*. Phylogenetic work (Smith et al., 2011) clearly shows that this species is unrelated to either *D. bilineata* or *D. jugularis* (fig. 1).

#### (d) Arid zone species group

*Content:*

- D. adductus* Doughty, Kealley and Melville, 2012
- D. ameliae* Emmott, Couper, Melville and Chapple, 2012
- D. linga* Houston, 1977
- D. paraconvergens* Doughty, Kealley and Melville, 2012
- D. pindan* Storr, 1980
- D. valens* Storr, 1980
- D. vesus* Doughty, Kealley and Melville, 2012
- D. winnecke* Lucas and Frost, 1896
- D. pallida* sp. nov.

*Diagnostic characters for group in north-western Kimberley:*

- one canine tooth on each side of upper jaw
- axilla granular scales absent
- lateral dark spot absent
- femoral pores absent.

### Remarks

The arid zone species group is widely distributed across arid WA (Couper et al., 2012; Doughty et al., 2012a), with highest species diversity in the Pilbara region but extending north to the southern Kimberley (*D. pindan*) and east into the arid interior (*D. paraconvergens*), crossing into South Australia and the NT. However, *D. pallida* sp. nov. is from the Mitchell Plateau (fig. 22), north-western Kimberley, more than 450 km north of the nearest member of this species group (*D. pindan*). *Diporiphora pallida* sp. nov. expands the bioclimatic and distributional limits of the arid zone species group. Key characters in distinguishing the arid zone species group from the other species groups in northern Australia is the number of canine teeth on each side of the upper jaw combined with the absence of granular scales in the axilla. In addition to these characters, in the Kimberley region this species group can be distinguished from *D. lalliae* (a member of the *D. bilineata* species group) by species-specific characters: the lack of a gular fold for *D. pindan* and a short tail for *D. pallida* sp. nov.

### *Diporiphora pallida* sp. nov.

ZooBank LSID: <http://zoobank.org/urn:lsid:zoobank.org:act:7967A170-9260-40F9-A895-D5C5041E4729>

**Common name.** Pale two-pored dragon.

Figure 22, Tables 3, 4

**Holotype.** WAM R177292 (formerly NMV D73853) (adult male), Mitchell Plateau, WA (14° 49.45' S, 125° 42.12' E). Collected by J. Melville on 12 September 2005.

**Diagnosis.** Small body size (to 46 mm SVL), short tail (2.0 × SVL), robust head and prominent brow above eye. Gular fold strong, post-auricular fold weak, scapular fold present. Single canine in upper jaw, no granular scales in axilla. Pre-cloacal pores 2; femoral pores 0.

**Description.** Male; 46 mm SVL; 91 mm tail length. Small *Diporiphora*, robust head with relatively short tail (~2.0 × SVL) and limbs. One canine on either side of upper jaw. Gular fold strong, post-auricular fold weak and scapular fold present. Prominent ridges above eye, extending along canthal ridge to dorsal corner of nasal scale, with short tapered snout. Dorsal scales strongly keeled and homogenous, running parallel to the midline. Scales on flanks homogeneous, keels angled posteriorly and dorsally. One small white spinose scale at back of head sitting on ventral end of post-auricular fold. Lacks spinose scales on limbs or tail. Small scales in axilla but not granular. Ventral scales strongly keeled. Pre-cloacal pores 2; femoral pores 0.

Dorsum relatively plain with little patterning. Broad (~4 scales wide) greyish indistinct vertebral stripe and broad yellow-cream dorsolateral stripes (~3 scales wide) running from back of head to base of tail; dorsolateral stripes continuous from head to mid-dorsum, and from there broken into sections by background colour. Dark transverse bands absent. Head relatively plain with little patterning, labials similar colour to rest of head and lacking pale line between eye and ear. Dark smudge on posterior of tympanum absent. Flanks pale without patterning. Lateral stripe between axilla and groin absent.

Dark patch in axilla absent. Banding on limbs and tail absent. Ventral surface cream with no patterning.

**Variation.** This description is based on a single specimen collected on the Mitchell Plateau, thus the variation in this species is unknown.

**Etymology.** Named for the pale appearance of this species in life. Used as an adjective.

**Distribution and ecology.** Based on a single animal, *D. pallida* sp. nov. occurs on the Mitchell Plateau in the northwest Kimberley. This animal was found perched in spinifex grass on a rocky outcrop (pictured in fig. 22). Little is known of this species but it appears to be associated with spinifex grasses on rocky substrates.

**Comparison to other species.** Unlike other dragons found in the northwest Kimberley, *D. pallida* sp. nov. appears to be a habitat specialist in spinifex grasses and has a distinctive morphology. Its distribution overlaps with *D. margaretae*, but differs in having a gular fold. It also differs from *D. albilabris*, *D. bennettii* and *D. perplexa* sp. nov. in having a single canine on either side of upper jaw and further differs from *D. albilabris* in lacking femoral pores.

**Remarks.** Genetic analyses indicate that this species is not related to other *Diporiphora* species in the Kimberley but instead belonging to the arid zone species group containing other spinifex specialist species (e.g. *D. linga* and *D. winneckeii*), which occur in arid central Australia. In mtDNA phylogenetic analysis, this species was resolved as the sister to *D. paraconvergens*, but this relationship was not strongly supported (fig. 1). *Diporiphora pallida* sp. nov. can be readily distinguished from *D. paraconvergens* by dorsal scales that run parallel to the midline (vs. converging) and by having a short tail (vs. very long). Based on genetic results and morphological distinctiveness we feel confident that this a new species for the Kimberley region, joining *D. convergens* as another *Diporiphora* species known only from the holotype. Further sampling is required to gain a better understanding of the ecology, biology and evolutionary relationships of this little-known species.

### Discussion

Our study provides the first comprehensive taxonomic treatment of *Diporiphora* species across northern Australia since Storr's revision in 1974. Using an understanding of relationships based on genetic data and a re-examination of newly collected and historical specimens, we describe five new species, raise a further two taxa to full species status and redefine six existing species. This work significantly increases the species diversity of *Diporiphora*, and agamid lizards, in the AMT.

*Diporiphora* species occur in most habitats in the AMT and are one of the most common and abundant lizards in the tropical savannah woodlands and grasslands. The Australian tropical savannah is one of the largest and most intact in the world (Bowman et al., 2010; Laver et al., 2018), and is globally significant. Despite this importance, we are only beginning to document the true species diversity of many vertebrate groups (e.g. Afonso Silva et al., 2017; Doughty 2011; Doughty et al.,

2012b, 2018; Laver et al., 2018; Melville et al., 2018; Pepper et al., 2011; Potter et al., 2012). With these recent studies and our taxonomic treatment documenting lizard diversity patterns in geckos, skinks and agamids, we can start to look for concordant patterns of diversity between these lineages. Three clear patterns are apparent across these major lineages: (1) greater species diversity in the northern extent of the AMT, particularly the Kimberley region; (2) fewer and more widely distributed species in southerly portions of the AMT; and (3) consistent major biogeographic breaks across terrestrial vertebrate groups.

A consistent pattern in studies investigating phylogeographic structuring and species diversity across the AMT is a north–south gradient of diversity in lizard lineages. In the northern parts of the AMT, species diversity is greatest, with particular diversity hotspots in the north-western Kimberley and Arnhem Land regions (e.g. Powney et al., 2010). In addition to higher species diversity, there are higher numbers of short-range endemic species in these northern hotspots. For example, in the *Oedura* geckos of the AMT, genetic evidence suggests that microendemism and diversity is highest in the northern AMT high-rainfall regions (Laver et al., 2018), while the most widespread lineages occur in the more southerly boundary between the AMT and Australian arid zone. Similarly, in *Diporiphora* the highest species diversity is in the Kimberley, with three lineages (*D. bilineata*, *D. bennettii* and arid zone species groups) occurring in the region. Each of these species groups contain more than one species in the Kimberley, with all four species from the *D. bennettii* species group occurring in the region, including two locally endemic (*D. bennettii* and *D. albilaris*). In contrast, the southern region of the AMT has fewer *Diporiphora* species but they have broad east–west distributions (*D. sobria*, *D. magna* and *D. lalliae*), with the later of these encroaching into the Australian arid zone. This north–south pattern of species diversity, which appears across multiple groups, has been attributed to an aridity gradient, climate stability or instability, and historical refugia in mesic areas (Afonso Silva et al., 2017; Laver et al., 2018; Palmer et al., 2013). The hypothesis that the presence of rocky refugia drives patterns of diversity is supported by higher diversity along the barrier ranges in the southern Kimberley (Doughty et al., 2018; Oliver et al., 2014, 2016).

In addition to documenting greater species diversity in *Diporiphora*, our work also demonstrates that there is high diversity in body size and ecology within the Kimberley region, with large and small sympatric species within each species group and with ecological variation. In the *D. bennettii* species group, there are two rock-specialist species, one large (*D. perplexa* sp. nov.) and one small (*D. bennettii*), and a smaller generalist woodland species (*D. albilaris*). Similar body size divergence in sympatric rock-dwelling *Gehyra* species has been documented in the Kimberley (Moritz et al., 2018; Oliver et al., 2016). In the *D. bilineata* species group, there is a generalist woodland species (*D. margaretae*) with smaller body size in the northern Kimberley and a gracile species found in grasslands on river floodplains in the southern Kimberley (*D. gracilis* sp. nov.), although it is unlikely these species are sympatric. These patterns suggest that more than



Figure 22. *Diporiphora pallida* sp. nov. Images of holotype (WAM R177292, formerly MNV D73853), Mitchell Plateau, Western Australia: a, in life (photo: J. Melville); b, c, dorsal and ventral views; d, collection location.

mesic refugia and aridity gradients are shaping diversity in Kimberley *Diporiphora* species, and that ecological and morphological diversification through processes other than evolutionary drift may drive diversity patterns. Regardless of the mechanisms, there is a clear pattern for high species diversity in the Kimberley, with more widespread species within the AMT appearing to arise within these Kimberley species groups.

In the more southerly regions of the AMT, this diversity in body size is not apparent in *Diporiphora*. Across the east–west span of the AMT, past climatic fluctuations and aridity gradients have probably shaped species diversity. A number of major biogeographic breaks have been identified in different lizard lineages, several which appear to be relatively consistent across groups (e.g. Noble et al., 2018). Genetic differentiation across two biogeographic barriers – the Carpentaria Gap in the Gulf of Carpentaria region of Queensland and the Ord River region between the Kimberley region and the Top End of the NT – has been well documented across numerous taxa (Catullo et al., 2014; Noble et al., 2018; Potter et al., 2012), including agamid lizards (see Pepper et al., 2017). In *Diporiphora*, the divergence across the Carpentaria Gap appears to be most dramatic. For example, in the *D. bilineata* species group, the distributions of *D. bilineata*, *D. magna* and *D. granulifera* sp. nov. appear to truncate at the western portions of the Carpentaria Gap, while *D. carpentariensis* sp. nov. is to the east of this biogeographic barrier. In addition, the *D. australis* species group is only found to the east of the Carpentaria Gap (see Edwards and Melville, 2010, 2011). The divergence of species across the Gulf of Carpentaria region has been attributed to increased aridity in these regions compared to adjacent topographic uplands (Pepper et al., 2017). It remains unclear as to whether AMT *Diporiphora* species groups have a distributional gap in the Gulf of Carpentaria region of Queensland, as is currently suggested by maps, or is this due to a lack of sampling and records in this region. Further field-based research is needed to fully elucidate the distributions of *Diporiphora* species across this biogeographic barrier.

#### Acknowledgements

JM, PD and PH examined specimens at the following institutions: Australian Museum, Sydney; Western Australian Museum; Museums Victoria; Queensland Museum; Museum and Art Gallery of the Northern Territory; Natural History Museum, United Kingdom, Naturhistorisches Museum, Vienna and Naturhistoriska Riksmuseet, Stockholm. We would like to thank staff and researchers from these institutions for their help and assistance, in particular, P. Wagner (Bonn, Germany) for organising type loans to be examined. We thank S. Wilson, E. Vanderduys, M. Bruton and the Australian Wildlife Conservancy for the use of images. We thank G. Shea for advice on nomenclature and discussions regarding synonymies and we thank A. Bauer for providing a high-resolution scan of the *D. australis* syntype from the original species description. Research funding provided to JM by the Australian Research Council.

#### References

- Afonso Silva, A.C., Bragg, J.G., Potter, S., Fernandes, C., Coelho, M.M., and Moritz, C. 2017. Tropical specialist vs. climate generalist: diversification and demographic history of sister species of *Carlia* skinks from northwestern Australia. *Molecular Ecology* 26: 4045–4058. <https://doi.org/10.1111/mec.14185>
- Bowman, D.M.J.S., Brown, G.K., Braby, M.F., Brown, J.R., Cook, L.G., Crisp, M.D., Ford, F., Haberle, S., Hughes, J., Isagi, Y., Joseph, L., McBride, J., Nelson, G., and Ladiges, P.Y. 2010. Biogeography of the Australian monsoon tropics. *Journal of Biogeography* 37: 201–216. <https://doi.org/10.1111/j.1365-2699.2009.02210.x>
- Catullo, R.A., Lanfear, R., Doughty, P., and Keogh, J.S. 2014. The biogeographical boundaries of northern Australia: evidence from ecological niche models and a multi-locus phylogeny of *Uperoleia* toadlets (Anura: Myobatrachidae). *Journal of Biogeography* 41: 659–672. <https://doi.org/10.1111/jbi.12230>
- Cogger, H. G., Cameron, E. E., and Cogger, H. M. 1983. *Amphibia and reptilia* (Vol. 1). Australian Government Publishing Service: Canberra. 313 pp.
- Cogger, H. 2014. *Reptiles and amphibians of Australia*. 7th edition. CSIRO Publishing: Melbourne. 1033 pp.
- Couper, P., Melville, J., Emmott, A. and Chapple, S.N.J., 2012. A new species of *Diporiphora* from the Goneaway Tablelands of Western Queensland. *Zootaxa*, 3556: 39–54.
- Doughty, P. 2011. An emerging frog diversity hotspot in the northwest Kimberley of Western Australia: another new frog species from the high rainfall zone. *Records of the Western Australian Museum* 26: 209–216. [https://doi.org/10.18195/issn.0312-3162.26\(2\).2011.209-216](https://doi.org/10.18195/issn.0312-3162.26(2).2011.209-216)
- Doughty, P., Kealley, L., and Melville, J. 2012a. Taxonomic assessment of *Diporiphora* (Reptilia: Agamidae) dragon lizards from the western arid zone of Australia. *Zootaxa* 3518: 1–24.
- Doughty, P., Palmer, R., Sistrom, M., Bauer, A.M., and Donnellan, S.C. 2012b. Two new species of *Gehyra* from the north-west Kimberley, Western Australia. *Records of the Western Australian Museum* 27: 117–134. [https://doi.org/10.18195/issn.0312-3162.27\(2\).2012.117-134](https://doi.org/10.18195/issn.0312-3162.27(2).2012.117-134)
- Doughty, P., Bourke, G., Tedeschi, L.G., Pratt, R.C., Oliver, P.M., Palmer, R.A., and Moritz, C. 2018. Species delimitation in the *Gehyra nana* (Squamata: Gekkonidae) complex: cryptic and divergent morphological evolution in the Australian Monsoonal Tropics, with the description of four new species. *Zootaxa* 4403: 201–244. <https://doi.org/10.11646/zootaxa.4403.2.1>
- Edwards, D.L., and Melville, J. 2010. Phylogeographic analysis detects congruent biogeographic patterns between a woodland agamid and Australian wet tropics taxa despite disparate evolutionary trajectories. *Journal of Biogeography* 37: 1543–1556. <https://doi.org/10.1111/j.1365-2699.2010.02293.x>
- Edwards, D.L., and Melville, J. 2011. Extensive phylogeographic and morphological diversity in *Diporiphora nobbi* (Agamidae) leads to a taxonomic review and a new species description. *Journal of Herpetology* 45: 530–546. <https://doi.org/10.1670/10-115.1>
- Günther, A. 1867. VIII.—Additions to the knowledge of Australian reptiles and fishes. *Annals and Magazine of Natural History* 20: 45–68. <https://doi.org/10.1080/00222936708562716>
- Huelsenbeck, J.P., and Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755. <https://doi.org/10.1093/bioinformatics/17.8.754>
- Kutt, A.S., Bateman, B.L., and Vanderduys, E.P. 2011. Lizard diversity on a rainforest–savanna altitude gradient in north-eastern Australia. *Australian Journal of Zoology* 59: 86–94. <https://doi.org/10.1071/ZO11036>



- Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T., and Calcott, B. 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 34: 772–773. <https://doi.org/10.1093/molbev/msw260>
- Laver, R.J., Doughty, P., and Oliver, P.M., 2018. Origins and patterns of endemic diversity in two specialized lizard lineages from the Australian Monsoonal Tropics (*Oedura* spp.). *Journal of Biogeography* 45: 142–153. <https://doi.org/10.1111/jbi.13127>
- Melville, J., Ritchie, E.G., Chapple, S.N.J., Glor, R.E., and Schulte, II, J.A. 2011. Evolutionary origins and diversification of dragon lizards in Australia's tropical savannas. *Molecular Phylogenetics and Evolution* 58: 257–270.
- Melville, J., Ritchie, E.G., Chapple, S.N.J., Glor, R.E., and Schulte, II, J.A. 2018. Diversity in Australia's tropical savannas: an integrative taxonomic revision of agamid lizards from the genera *Amphibolurus* and *Lophognathus* (Lacertilia: Agamidae). *Memoirs of Museum Victoria* 77: 41–61. <https://doi.org/10.24199/jmmv.2018.77.04>
- Moritz, C.C., Pratt, R.C., Bank, S., Bourke, G., Bragg, J.G., Doughty, P., Keogh, J.S., Laver, R.J., Potter, S., Teasdale, L.C., Tedeschi, L.G., and Oliver, P.M. 2018. Cryptic lineage diversity, body size divergence, and sympatry in a species complex of Australian lizards (*Gehyra*). *Evolution* 72: 54–66. <https://doi.org/10.1111/evo.13380>
- Noble, C., Laver, R. J., Rosauer, D. F., Ferrier, S., and Moritz, C. 2018. Phylogeographic evidence for evolutionary refugia in the Gulf sandstone ranges of northern Australia. *Australian Journal of Zoology* 65: 408–416. <https://doi.org/10.1071/ZO17079>
- Oliver, P.M., Laver, R., Melville, J., and Doughty, P. 2014. A new species of Velvet Gecko (*Oedura*: Diplodactylidae) from the limestone ranges of the southern Kimberley, Western Australia. *Zootaxa* 3873: 49–61. <https://doi.org/10.11646/zootaxa.3873.1.4>
- Oliver, P.M., Bourke, G., Pratt, R.C., Doughty, P., and Moritz, C. 2016. Systematics of small *Gehyra* (Squamata: Gekkonidae) of the southern Kimberley, Western Australia: redescription of *G. kimberleyi* Börner & Schüttler, 1983 and description of a new restricted range species. *Zootaxa* 4107: 49–64. <https://doi.org/10.11646/zootaxa.4107.1.2>
- Palmer, R., Pearson, D.J., Cowan, M.A., and Doughty, P. 2013. Islands and scales: a biogeographic survey of reptiles on Kimberley islands, Western Australia. *Records of the Western Australian Museum Supplement* 81: 183–204. <https://doi.org/10.18195/issn.0313-122x.81.2013.183-204>
- Pepper, M., Ho, S.Y., Fujita, M.K., and Keogh, J.S. 2011. The genetic legacy of aridification: climate cycling fostered lizard diversification in Australian montane refugia and left low-lying deserts genetically depauperate. *Molecular Phylogenetics and Evolution* 61: 750–759. <https://doi.org/10.1016/j.ympev.2011.08.009>
- Pepper, M., Hamilton, D.G., Merklings, T., Svedin, N., Cser, B., Catullo, R.A., Pryke, S.R., and Keogh, J.S. 2017. Phylogeographic structure across one of the largest intact tropical savannahs: molecular and morphological analysis of Australia's iconic frilled lizard *Chlamydosaurus kingii*. *Molecular Phylogenetics and Evolution* 106: 217–227. <https://doi.org/10.1016/j.ympev.2016.09.002>
- Potter, S., Eldridge, M.D.B., Taggart, D.A., and Cooper, S.J.B. 2012. Multiple biogeographic barriers identified across the monsoon tropics of northern Australia: phylogeographic analysis of the *brachyotis* group of rock-wallabies. *Molecular Ecology* 21: 2254–2269. <https://doi.org/10.1111/j.1365-294X.2012.05523.x>
- Powney, G.D., Grenyer, R., Orme, C.D.L., Owens, I.P.F., and Meiri, S. 2010. Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. *Global Ecology and Biogeography* 19: 386–396. <https://doi.org/10.1111/j.1466-8238.2009.00521.x>
- Richman, J. M., and Handrigan, G. R. 2011. Reptilian tooth development. *Genesis* 49: 247–260. <https://doi.org/10.1002/dvg.20721>
- Smith, K. L., Harmon, L. J., Shoo, L. P., and Melville, J. 2011. Evidence of constrained phenotypic evolution in a cryptic species complex of agamid lizards. *Evolution* 65: 976–992. <https://doi.org/10.1111/j.1558-5646.2010.01211.x>
- Storr, G. M. 1974. Agamid lizards of the genera *Caimanops*, *Physignathus* and *Diporiphora* in Western Australia and Northern Territory. *Records of the Western Australian Museum* 3: 121–146.
- Storr, G. M., Johnstone, R. E., and Smith, L. A. 1983. *Lizards of Western Australia. II. Dragons and monitors*. Western Australian Museum: Perth. 113 pp.
- Wilson, S., and Swan, G. 2017. *A complete guide to reptiles of Australia*. 5th edition. New Holland Publishers: Sydney. 560 pp.