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Systematic revision of the marbled velvet geckos (*Oedura marmorata* species complex, Diplodactylidae) from the Australian arid and semi-arid zones

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Abstract

Lizards restricted to rocky habitats often comprise numerous deeply divergent lineages, reflecting the disjunct nature of their preferred habitat and the capacity of rocky habitats to function as evolutionary refugia. Here we review the systematics and diversity of the predominantly saxicoline Australian marbled velvet geckos (genus *Oedura*) in the Australian arid and semi-arid zones using newly-gathered morphological data and previously published genetic data. Earlier work showed that four largely allopatric and genetically divergent lineages are present: Western (Pilbara and Gascoyne regions), Gulf (west and south of the Gulf of Carpentaria), Central (central ranges) and Eastern (Cooper and Darling Basins). None of these four populations are conspecific with true *O. marmorata*, a seperate species complex that is restricted to the Top End region of the Northern Territory. Top End forms share a short, bulbous tail whereas the other four lineages treated here possess a long, tapering tail. Morphological differences among the arid and semi-arid lineages include smaller body size, tapering lamellae and a shorter tail for the Gulf population, and a partially divided rostral scale in the Western population compared to the Central and Eastern populations. Accordingly, we resurrect *O. cincta* de Vis from synonymy for the Central and Eastern lineages, and regard this species as being comprised of two evolutionary significant units. We also describe the Gulf and Western lineages as new species: *Oedura bella* **sp. nov.** and *O. fimbria* **sp. nov.**, respectively. We note that a predominantly arboreal lineage (the Eastern lineage of *O. cincta*) is more widely distributed than the other lineages and is phylogenetically nested within a saxicoline clade, but tends to have a deeper head and shorter limbs, consistent with morphological variation observed in other lizard radiations including both saxicoline and arboreal taxa.

Key words: arboreal, central ranges, Cooper Basin, gecko, de Vis, Gulf Country, new species, *Oedura cincta*, *Oedura bella* **sp. nov.**, *Oedura fimbria* **sp. nov.**, Pilbara, saxicoline, taxonomy

Introduction

Large areas of rocky outcropping in many areas of the world are inhabited by specialised lineages of saxicoline lizards (Couper & Hoskin 2008; Pepper *et al.* 2011; Stanley *et al.* 2011; Jacobsen *et al*. 2014; Oliver *et al.* 2014a). Many of these lizards (but certainly not all) show a suite of morphological characters that are associated with this lifestyle—most notably dorso-ventral flattening and increased limb length (Doughty & Shine 1995; Vitt *et al*. 1997; Goodman & Isaac 2008; Goodman *et al*. 2008; Hoskin & Couper 2013). Saxicoline lizard 'species' also frequently comprise multiple deeply divergent evolutionary lineages—perhaps to some extent reflecting the inherently 'insular' distribution of their habitat (Oliver *et al*. 2010; Grismer *et al*. 2012; Werneck *et al*. 2012; Jacobsen *et al*. 2014). These apparent genetic and morphological correlates of specialisation suggest saxicoline lizards offer opportunities to better understand how non-adaptive (e.g. isolation) and adaptive (e.g. habitat structure) evolutionary processes can interact to shape biodiversity (Oliver *et al*. 2010; Grismer *et al*. 2012; Werneck *et al*. 2012; Jacobsen *et al*. 2014). Their propensity to consist of divergent, morphologically cryptic and overlooked lineages also has important implications for efforts to manage and conserve evolutionary biodiversity.
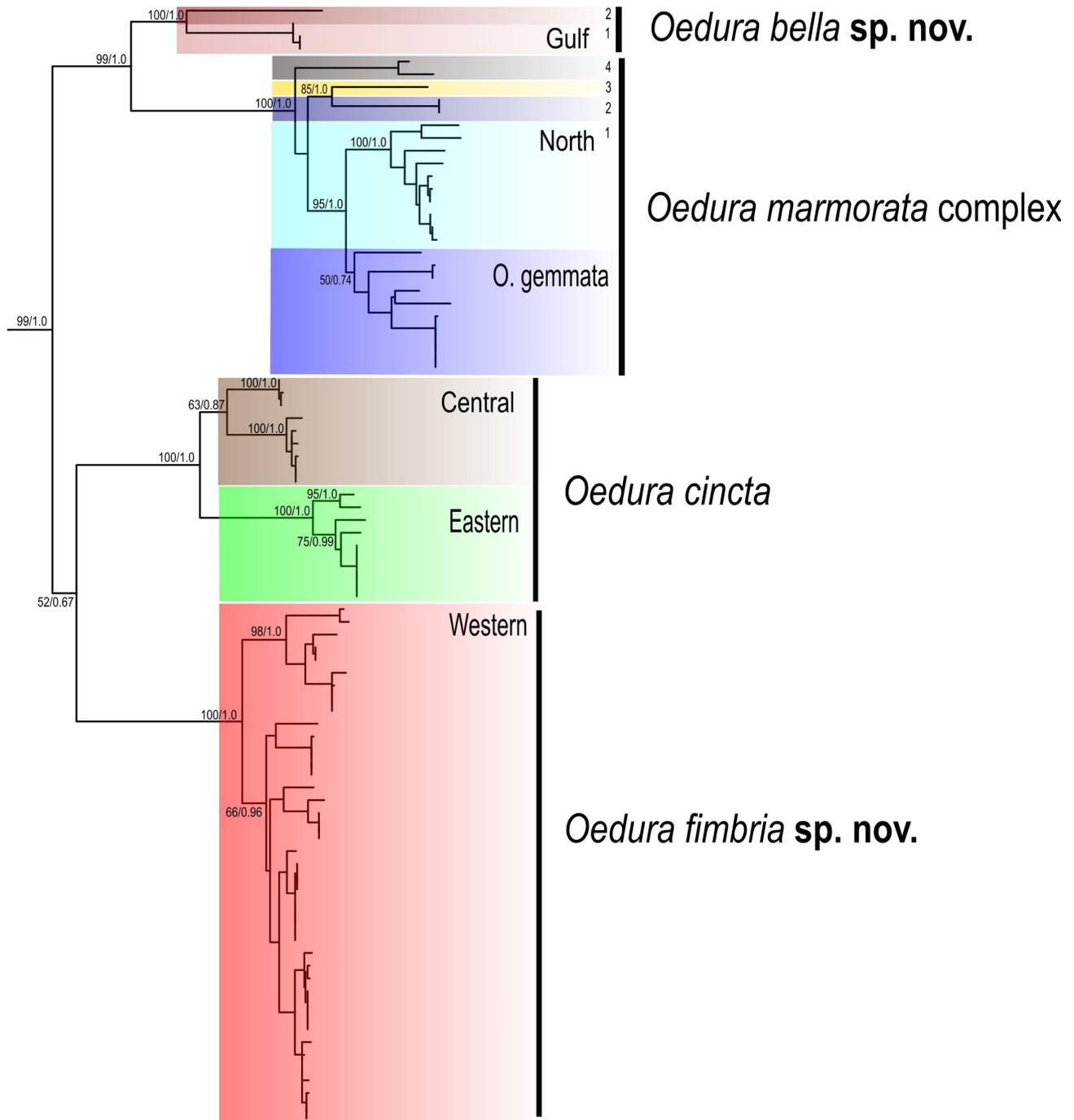
FIGURE 1. Summary of major lineages with *Oedura marmorata* complex and their interrelationships based on *ND2* data - including both informal lineage names from Oliver *et al.* (2014a) and new taxonomic designations presented in this paper. From top to bottom: *O. bella* **sp. nov.** (Gulf), the residual *O. marmorata* complex (including *O. gemmata*, true *O. marmorata* and related lineages), *O. cincta* (comprising Central and Eastern ESUs) and *O. fimbria* **sp. nov.**

The exceptionally diverse lizard fauna of the vast Australian arid zone (Pianka 1986; Powney *et al.* 2010) includes numerous lineages that are closely associated with rocky habitats. Recent detailed analyses of saxicoline taxa from the arid zone have revealed deep phylogenetic divergences, and indicated that these areas have mediated the evolution and/or persistence of localized endemic lineages (Fujita *et al.* 2010; Oliver *et al.* 2010, 2014a; Pepper *et al.* 2013a,b). The rocky Pilbara region in the western arid zone is a special case, with many new endemics described recently (e.g. Aplin *et al.* 2006; Doughty *et al.* 2010, 2011, 2012; Doughty & Oliver 2011; Maryan *et al.*

2014; Oliver *et al*. 2014b). However, previously unknown divergent lineages have also been recently detected from other rocky areas including the Central Ranges (Pepper *et al*. 2013b; Sistrom *et al*. 2013; Hutchinson *et al.* 2014), the Gulf Country at the northern edge of the arid zone (Fujita *et al*. 2010), and the Andamooka and Barrier Ranges in the southern arid zone (Oliver *et al.* 2009; McLean *et al*. 2013).

Oedura Gray, 1842 are relatively large-bodied saxicoline or arboreal geckos with well-developed toe pads. *Oedura* species occur throughout the Australian monsoonal tropics, where nearly all the currently-recognized diversity resides. In contrast, the diversity of *Oedura* in the arid zone is depauperate, with only a single recognized species, *O. marmorata* Gray, 1842, which also occurs in the monsoonal tropics. A recent study by Oliver *et al*. (2014a), however, found high genetic diversity across isolated populations in the arid and semi-arid zones currently referred to this species (summarised in Fig. 1). The type locality of *O. marmorata* is Port Essington on the Coburg Peninsula, near Darwin in the 'Top End' region of the Northern Territory, with true *O. marmorata* appearing to be part of a complex of related northern lineages restricted to the Top End. In arid and semi-arid regions of Australia, four additional largely allopatric populations occur: Gulf, Central, Eastern and Western (Fig. 2). With the exception of the Eastern group, all of these lineages are predominantly saxicoline. Oliver *et al*. (2014a) focused on broader biogeographic considerations, and the taxonomic status of the recovered lineages was not addressed.

Herein we present a more detailed morphological analysis of the systematics of the *O. marmorata* species complex in and around the Australian arid zone. We summarize patterns of morphological variation in the main lineages recovered from the genetic analyses to determine if there is further evidence to consistently differentiate them. On the basis of our data and analyses we conclude that: a) none of the arid or semi-arid lineages represent true *O. marmorata*, b) *O. cincta* de Vis, 1888 is applicable to the Eastern and Central lineages and c) the Gulf and Western lineages both represent new species, which we describe here.
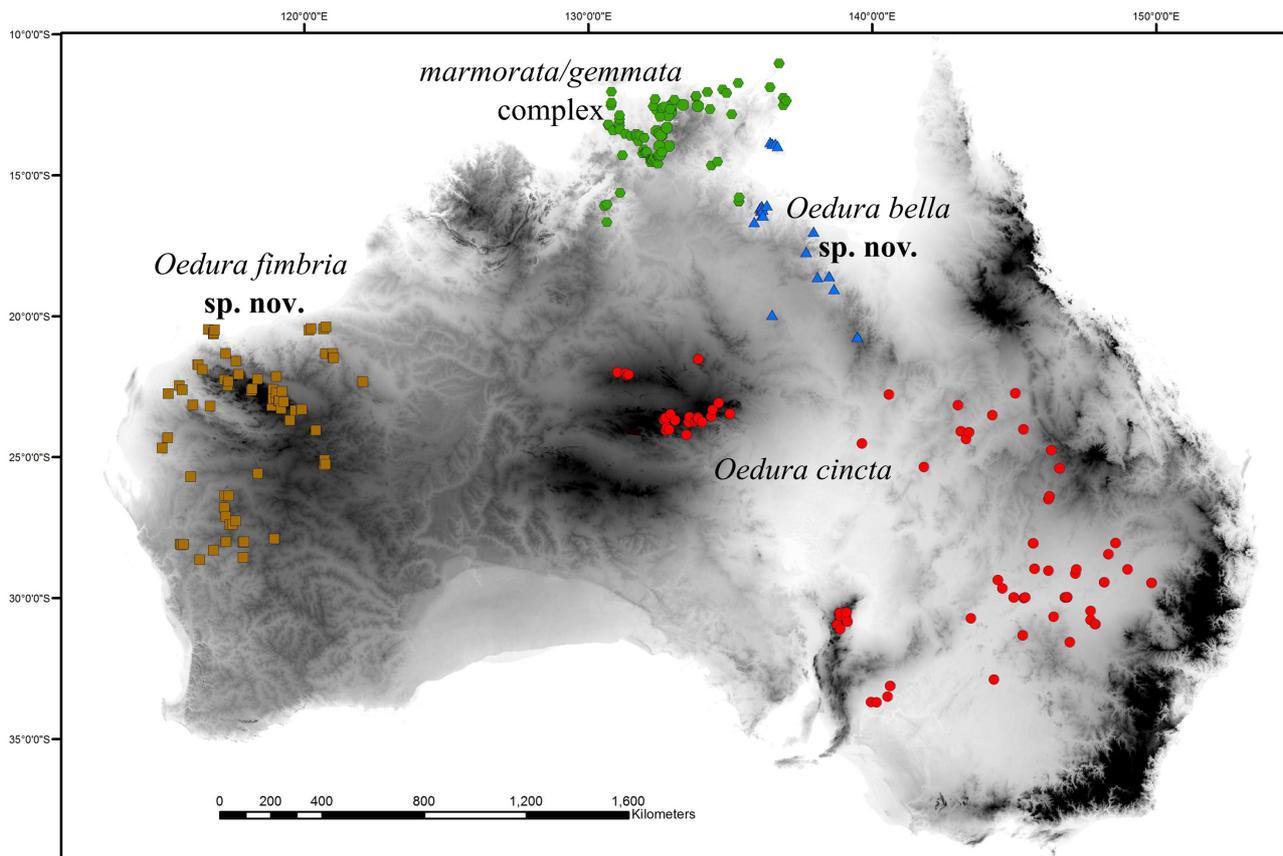

FIGURE 2. Distribution of three *Oedura* species resurrected or described in this paper: *O. bella* **sp. nov.** (blue, Gulf) from the Gulf Country, *O. cincta* (red, comprising Central and Eastern ESUs), and *O. fimbria* **sp. nov.** (yellow-brown, Western) from mid-western Australia. The distribution of the residual *O. marmorata* complex (green, comprising *O. gemmata*, true *O. marmorata*, and related lineages) in the Top End of northern Australia is also indicated. Darker regions indicate greater topographic complexity.

Methods

Genetic data. A multilocus genetic investigation of the systematics of the *O. marmorata* complex is presented elsewhere (Oliver *et al.* 2014a). A summary of phylogenetic relationships based on the mitochindrial *ND2* is presented in Fig. 1. To briefly reiterate the main findings of this study, all three of the datasets examined (allozymes, mtDNA, nDNA) support the existence of three main groups in the *O. marmorata* species complex: i) Top End+Gulf, ii) Central+Eastern, iii) Western. The allozyme and mtDNA data provided evidence for further major subdivisions: two divergent groups of lineages in the north (northern lineages [including *O. gemmata* King and Gow, 1983] and Gulf), and more shallow divergences between the Central and Eastern populations. For this initial continent-wide assessment of taxonomic diversity based on the observed genetic divergences, we consider the distinctiveness and diagnosabilty of the four allopatric or parapatric clades that occur in or close to the Australian arid zone: Gulf, Central, Eastern and Western. The remaining northern populations (including the nominal species *O. gemmata*) comprise several parapatric lineages and are currently the focus of more detailed analysis (P. Skipworth, unpublished data) and are not considered in detail here beyond providing sufficient characters to allow effective diagnosis.

Morphology. We examined material, including type material, held in the in the Australian Museum (AMS), Museum Victoria (NMV), Northern Territory Museum and Art Gallery (NTM), Queensland Museum (QM), South Australian Museum (SAMA) and Western Australian Museum (WAM). Where possible, specimens included in the genetic analyses were included in the morphological analyses. Type material of *O. marmorata* held at the Natural History Museum, London (BMNH) was also examined.

We chose adult specimens for measurements, as determined by large body size, presence of enlarged follicles or eggs in females, extended hemipenes in males or by direct examination of gonads), but we generally chose the largest, best-preserved specimens available. Measurements taken were as follows: snout-vent length (SVL), total length from tip of snout to the anterior edge of vent; head width (HW), maximum width of the head; head depth (HD), maximum depth of the head just posterior to the orbitals; head length (HL), from anterior edge of ear to tip of snout; eye to naris distance (EN), from anterior corner of eye to posterior edge of naris; internarial distance (IN), from inner edge of the nares; interorbital distance (IO), from the anterior-dorsal edge of the orbitals; transverse length of eye (EYE); axilla to groin (trunk) distance (Trk), from posterior edge of forelimb insertion to anterior edge of hindlimb insertion with limbs held at right angles; length of lower arm (ArmL), from posterior edge of bent elbow to base of bent wrist; length of lower leg (LegL), from anterior edge of bent knee to base of heel with foot bent; maximum width (including lamellae) of the third finger (3FW) and 3rd toe (3TW); tail length (TL), from posterior edge of cloaca to tip of tail; maximum tail width (TW) and tail depth (TD). Both original and regrown tails were measured, and are reported separately.

The following details of scalation were also recorded: number of supralabials (SuL), more than twice the size of surrounding granular scales (both total number and number to mid-point of eye); number of infralabials (InL), more than twice size of surrounding granular scales; number of small scales contacting the dorsal edge of nasals between the enlarged left and right supranasals (InN); length of rostral crease (RC), at the midpoint of the rostral from the dorsal edge downwards as a percentage of rostral height; total number of expressed precloacal pores (PP) on males; number of enlarged cloacal spurs (CS) on each of the right side and on the left side; and number of enlarged lamellae (more than twice the width of surrounding scales) in series under the third finger (3FL) and also of the third toe (3TL) (taken on left side only).

Results

Table 1 summarizes the morphological information for all populations measured. Top End *O. marmorata* and *O. gemmata* differ from all other arid and semi-arid populations of *O. marmorata senso lato* (Gulf, Central, Eastern and Western) in possessing a tail that is always more swollen in appearance; specifically it is very wide (usually wider than the head—TW/HW 0.83–1.30), often flattened, and always sharply tapered at the tip (Table 1; Figs. 3, 4). All other populations have tails narrower than the head (TW/HW 0.44–0.77), tending towards cylindrical in cross-section and not sharply tapered towards the tip (Figs. 5–10). This difference holds for both original and regenerated tails (Table 1; Figs. 3, 4). Coupled with the strong genetic divergence (more than seven fixed allozyme differences; > 15% mtDNA divergence), these morphological differences suggest that none of the four major lineages of *O. marmorata s.l.* from the arid zone and semi-arid regions considered here represent true *O. marmorata*.

TABLE 1. Summary meristic data (mean±S.D., ranges in parentheses) for the main lineages of the *Oedura marmorata* complex investigated in this study. Differing traits in bold.

	Oedura marmorata n = 9	*Oedura gemmata* n = 11	*Oedura cincta* (eastern) n = 32	*Oedura cincta* (central) n = 23	*Oedura bella* **sp. nov.** n = 20	*Oedura fimbria* **sp. nov.** n = 28
SVL	89.0±6.7 (77.0–97.0)	93.5±5.6 (84.0–103.0)	90.6±6.0 (78.0–100.0)	95.5±7.2 (82.0–108.0)	**78.8±7.4 (64.0–92.0)**	94.3±6.7 (71.0–104.0)
HW	17.5±1.6 (14.8–19.8)	17.5±0.7 (16.6–18.4)	16.3±1.1 (14.1–18.5)	17.7±1.1 (15.9–20.0)	15.8±1.6 (12.6–18.5)	18.1±1.3 (14.3–20.3)
HD	9.9±0.8 (8.6–10.9)	8.3±0.5 (7.5–9.1)	9.6±0.6 (8.3–10.5)	9.1±0.7 (7.6–10.1)	8.3±0.9 (7.4–10.0)	9.6±0.9 (7.2–11.3)
HL	22.3±1.1 (20.5–23.8)	22.8±0.8 (21.6–24.4)	20.5±1.3 (18.5–22.9)	22.3±1.2 (19.7–24.3)	20.5±1.5 (17.5–23.8)	23.3±1.3 (18.6–24.9)
SuL	10.1±0.9 (8.0–14.0)	10.5±1.0 (8.0–13.0)	10.4±0.8 (9.0–13.0)	9.7±0.6 (9.0–11.0)	10.8±0.6 (9.0–13.0)	11.1±0.6 (9.0–14.0)
InL	10.0±1.0 (8.0–11.0)	10.6±1.1 (9.0–12.0)	11.2±0.9 (10.0–13.0)	12.0±0.9 (10.0–14.0)	11.0±1.0 (9.0–13.0)	11.4±1.0 (10.0–13.0)
EN	7.6±0.3 (7.2–8.0)	7.9±0.4 (7.4–8.6)	7.0±0.6 (6.0–8.3)	7.6±0.5 (6.8–8.7)	6.9±0.6 (5.8–8.0)	8.1±0.5 (6.6–8.6)
IN	3.3±0.2 (3.1–3.8)	3.3±0.2 (2.9–3.8)	3.2±0.3 (2.7–3.7)	3.2±0.3 (2.7–3.8)	3.0±0.3 (2.6–3.7)	3.3±0.3 (2.9–3.7)
IO	7.3±0.5 (6.7–7.8)	7.3±0.3 (6.5–7.7)	6.9±0.4 (6.2–7.3)	7.4±0.5 (6.4–8.3)	7.0±0.6 (5.7–7.9)	7.8±0.6 (6.1–8.8)
EYE	5.6±0.3 (5.0–5.9)	5.7±0.3 (5.2–6.1)	5.0±0.4 (4.4–5.9)	5.6±0.5 (5.0–6.8)	5.1±0.5 (4.6–6.4)	5.3±0.4 (4.4–6.1)
Trk	39.6±4.4 (32.5–45.4)	40.8±3.0 (36.5–44.9)	44.2±3.9 (38.3–52.6)	46.3±4.3 (38.7–54.8)	36.3±4.1 (32.3–44.1)	44.7±4.6 (34.1–54.3)
ArmL	11.5±0.9 (9.8–13.1)	12.5±0.9 (11.6–14.7)	11.1±0.9 (9.6–12.9)	12.2±0.9 (10.8–13.6)	10.6±1.3 (8.0–12.8)	12.5±1.0 (8.7–14.1)
LegL	13.2±0.9 (11.7–14.5)	14.1±1.1 (13.1–16.7)	12.5±0.8 (11.0–14.3)	14.0±1.0 (11.8–15.9)	11.7±1.2 (9.7–13.4)	14.3±1.3 (9.9–16.7)
3FW	2.1±0.2 (1.8–2.4)	2.1±0.2 (1.8–2.2)	2.3±0.2 (1.7–2.7)	2.6±0.4 (1.9–3.3)	1.8±0.2 (1.5–2.3)	2.7±0.3 (1.8–3.3)
3TW	2.4±0.2 (2.0–2.6)	2.3±0.2 (1.9–2.5)	2.6±0.3 (2.1–3.0)	2.9±0.4 (2.1–3.5)	2.0±0.2 (1.7–2.3)	3.0±0.4 (1.9–3.6)
3FL	7.8±0.7 (7.0–8.0)	8.1±0.3 (8.0–9.0)	7.8±0.5 (6.0–8.0)	8.1±0.5 (7.0–9.0)	7.8±0.6 (7.0–8.0)	8.4±0.8 (7.0–10.0)
3TL	8.1±0.6 (7.0–9.0)	8.6±0.7 (8.0–10.0)	8.1±0.3 (8.0–9.0)	9.0±0.6 (8.0–10.0)	8.1±0.5 (7.0–9.0)	9.0±0.5 (8.0–10.0)
Ratios						
HW/SVL	0.20±0.01 (0.19–0.20)	0.19±0.01 (0.18–0.20)	**0.18±0.01 (0.17–0.20)**	**0.19±0.01 (0.17–0.20)**	**0.20±0.01 (0.19–0.23)**	**0.19±0.01 (0.18–0.21)**
HD/SVL	0.11±0.01 (0.10–0.12)	0.09±0.00 (0.08–0.09)	**0.11±0.01 (0.09–0.12)**	**0.10±0.01 (0.09–0.11)**	**0.11±0.01 (0.10–0.12)**	0.10±0.01 (0.09–0.13)
HL/SVL	0.25±0.01 (0.24–0.27)	0.24±0.01 (0.24–0.26)	0.23±0.01 (0.22–0.25)	0.23±0.01 (0.22–0.25)	0.26±0.01 (0.25–0.28)	0.25±0.01 (0.24–0.27)
EN/SVL	0.086±0.006 (0.077–0.095)	0.084±0.003 (0.081–0.090)	0.081±0.005 (0.072–0.090)	0.080±0.004 (0.072–0.089)	0.087±0.005 (0.073–0.095)	0.086±0.003 (0.078–0.093)

TABLE 1. (Continued)

	Oedura marmorata n = 9	*Oedura gemmata* n = 11	*Oedura cincta* (eastern) n = 32	*Oedura cincta* (central) n = 23	*Oedura bella* **sp. nov.** n = 20	*Oedura fimbria* **sp. nov.** n = 28
EYE/SVL	0.063±0.003 (0.058–0.067)	0.061±0.004 (0.058–0.069)	0.059±0.006 (0.049–0.068)	0.059±0.005 (0.049–0.068)	0.065±0.003 (0.058–0.071)	0.057±0.004 (0.051–0.064)
Trk/SVL	0.44±0.03 (0.39–0.47)	0.44±0.03 (0.39–0.48)	0.49±0.02 (0.45–0.53)	0.48±0.02 (0.42–0.51)	**0.46±0.02 (0.41–0.49)**	**0.47±0.03 (0.42–0.53)**
ArmL/SVL	0.13±0.00 (0.12–0.14)	0.13±0.01 (0.13–0.16)	**0.12±0.01 (0.11–0.13)**	0.13±0.01 (0.12–0.14)	0.13±0.01 (0.12–0.15)	0.13±0.01 (0.12–0.15)
LegL/SVL	0.15±0.01 (0.14–0.16)	0.15±0.01 (0.14–0.16)	**0.14±0.01 (0.12–0.15)**	0.15±0.01 (0.13–0.16)	0.15±0.01 (0.14–0.16)	0.15±0.01 (0.14–0.17)
3TW/SVL	**0.027±0.002 (0.023–0.031)**	0.025±0.002 (0.022–0.026)	0.030±0.002 (0.023–0.034)	0.031±0.003 (0.023–0.036)	**0.025±0.002 (0.021–0.030)**	0.032±0.003 (0.027–0.036)
Original tail	n = 4	n = 5	n = 20	n = 13	n = 15	n = 9
TL	49.0±2.3 (47.0–51.0)	50.8±3.3 (48.0–56.0)	64.7±5.7 (56.0–77.0)	65.8±7.2 (57.0–82.0)	44.1±7.8 (33.0–55.5)	65.8±8.9 (60.0–77.0)
TW	18.9±1.3 (17.4–20.5)	15.8±1.4 (13.8–17.3)	11.0±1.5 (7.8–13.6)	10.6±1.4 (8.3–12.9)	10.2±1.6 (7.4–12.6)	10.1±2.1 (5.8–13.3)
TD	8.1±0.8 (6.9–8.7)	6.2±0.2 (6.0–6.4)	8.7±1.2 (7.1–11.4)	7.5±1.4 (5.6–10.1)	6.5±1.1 (4.4–8.9)	7.7±1.8 (4.9–10.2)
TL/SVL	**0.56±0.03 (0.53–0.61)**	**0.57±0.04 (0.53–0.63)**	0.72±0.05 (0.64–0.79)	0.70±0.05 (0.61–0.78)	**0.55±0.05 (0.49–0.65)**	0.71±0.04 (0.65–0.80)
TW/SVL	**0.21±0.01 (0.20–0.22)**	**0.18±0.02 (0.16–0.20)**	0.12±0.02 (0.10–0.15)	0.11±0.01 (0.09–0.13)	0.13±0.01 (0.10–0.15)	0.11±0.01 (0.08–0.14)
TW/TL	**0.39±0.02 (0.36–0.41)**	**0.31±0.05 (0.28–0.35)**	0.17±0.03 (0.14–0.22)	0.16±0.02 (0.13–0.19)	**0.23±0.03 (0.18–0.28)**	0.15±0.01 (0.13–0.17)
Regrown tail	n = 5	n = 6	n = 11	n = 8	n = 5	n = 17
TL	33.0±6.7 (30.0–38.2)	48.3±4.6 (43.1–54.6)	50.5±6.3 (38.0–58.0)	68.0±13.0 (27.1–68.0)	37.0±3.1 (33.0–41.0)	56.8±7.0 (49.0–73.0)
TW	19.6±2.5 (17.1–23.2)	16.4±3.8 (12.2–20.4)	10.8±1.2 (9.1–12.6)	11.9±1.0 (8.9–11.9)	9.7±1.2 (8.2–11.0)	12.3±1.1 (10.4–14.5)
TD	10.2±1.5 (8.3–12.1)	7.0±0.9 (5.7–8.3)	8.2±0.9 (6.1–9.3)	10.2±1.0 (7.1–10.2)	6.3±1.0 (5.3–8.0)	8.8±0.8 (7.5–10.1)
TL/SVL	0.37±0.08 (0.23–0.45)	0.50±0.05 (0.44–0.56)	0.55±0.05 (0.43–0.62)	0.72±0.13 (0.30–0.72)	0.48±0.04 (0.44–0.53)	0.59±0.05 (0.51–0.66)
TW/SVL	0.22±0.03 (0.18–0.25)	0.17±0.03 (0.14–0.21)	0.12±0.01 (0.10–0.13)	0.13±0.01 (0.09–0.13)	0.13±0.01 (0.11–0.15)	0.13±0.01 (0.12–0.15)
TW/TL	0.63±0.23 (0.47–1.02)	0.34±0.06 (0.24–0.40)	0.22±0.04 (0.16–0.30)	0.37±0.07 (0.13–0.37)	0.26±0.03 (0.21–0.31)	0.22±0.02 (0.18–0.26)

Of the four arid and semi-arid populations, the Gulf animals can be distinguished from all others by the following traits (full details of ranges are given in Table 1): smaller size (max mean SVL 78 mm *versus* >90 mm), shorter body (mean Trk/SVL 0.46 *versus* 0.47–0.49), narrower apical lamellae (mean 3TW/SVL 0.025 *versus* 0.030–0.032), less prominently flared lamellae series on fingers (at most equal in width to ultimate pair and generally narrower *versus* distinctly flared and sometimes wider than ultimate lamellae) and tail that tends to be slightly flattened in cross-section (*versus* more cylindrical) and relatively short (mean TL/SVL 0.55 *versus* 0.70–0.72).

FIGURE 3. Preserved specimens of *Oedura marmorata* from the Top End of the Northern Territory, Australia, showing wide tail and pattern. From top to bottom: NTM R6890; SAMA R36709; NTM R6283. Scale bar = 1 cm.
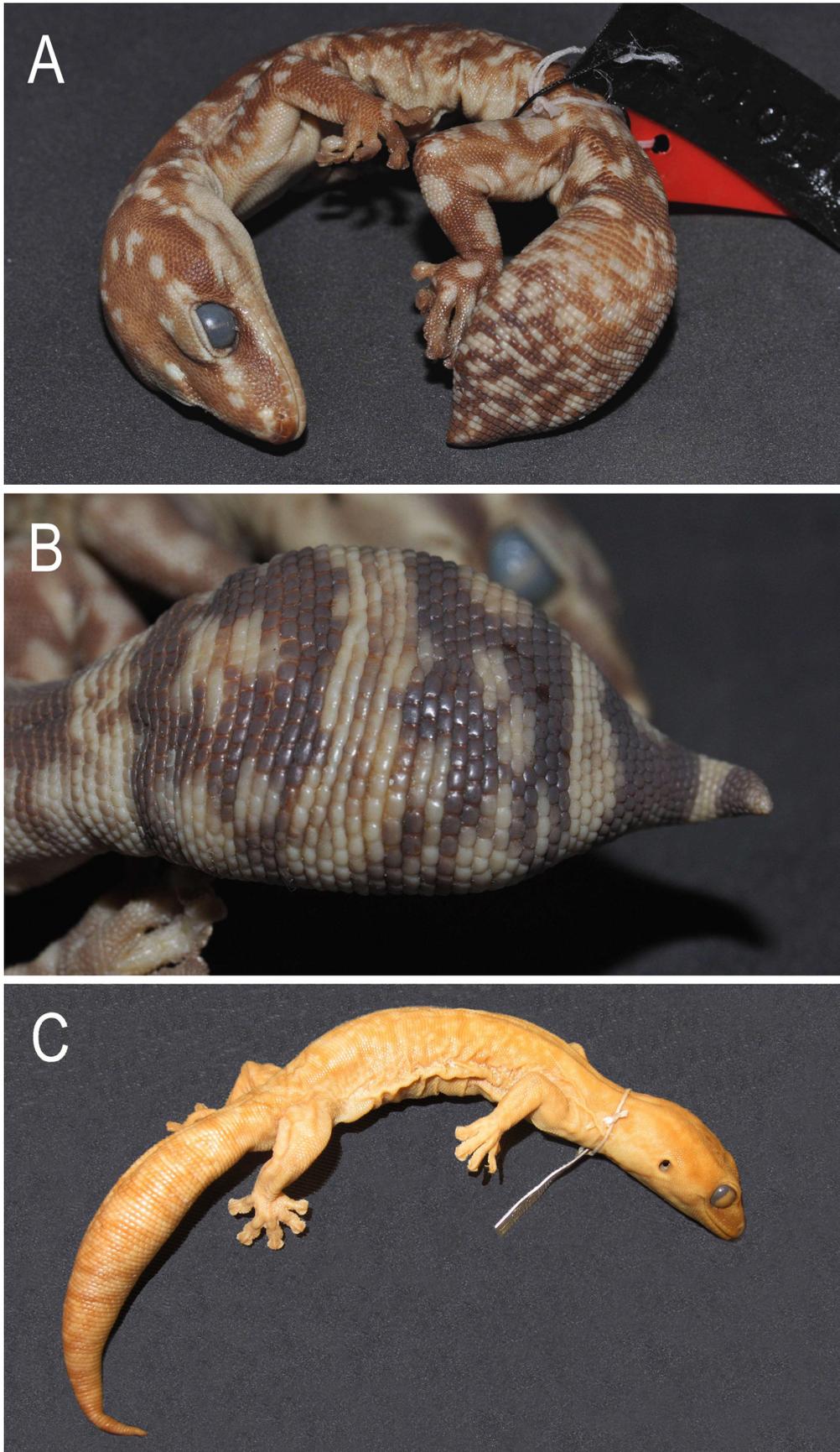
FIGURE 4. A) Lectotype of *Oedura marmorata* with regrown tail (BMNH xxii.2b). B) Original tail of *O. marmorata* paralectotype BMNH xxii.2c. C) Lectotype of *O. cincta* QM J226.
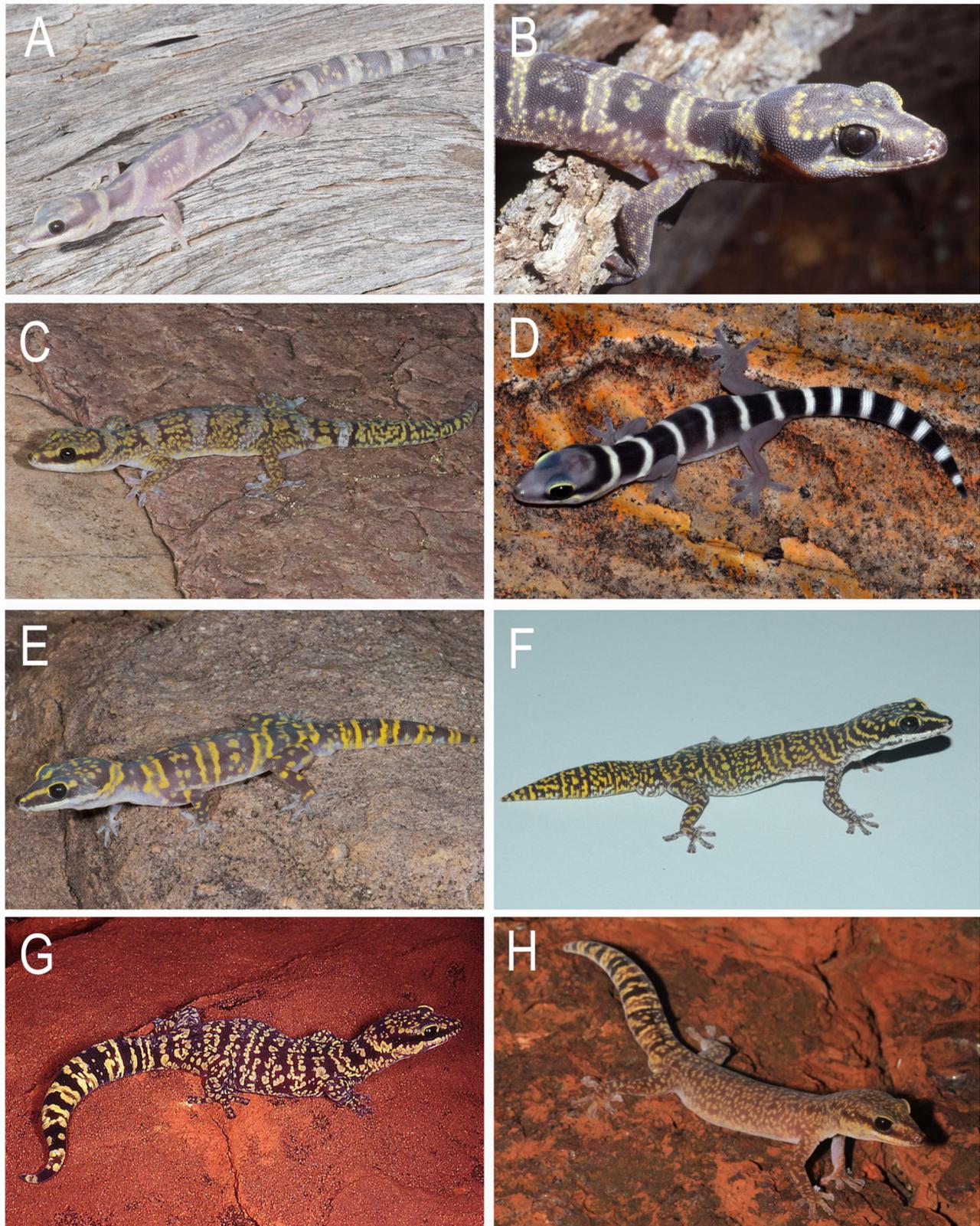
FIGURE 5. Species in the *Oedura marmorata* complex in life: **A.** *O. cincta*, Eastern ESU, Winton Region, Queensland; **B.** *O. cincta*, Eastern ESU, Danggalli Conservation Park, South Australia; **C.** *O. cincta*, central ESU, Simpson's Gap, Northern Territory; **D.** *O. cincta*, central ESU, hatchling, Simpson's Gap, Northern Territory; **E.** *O. bella* **sp. nov.**, Doomadgee area, Queensland; **F.** *O. bella* **sp. nov.** holotype, 10 km south of Mt Isa, Queensland; **G.** *O. fimbria* **sp. nov.**, Little Sandy Desert, Western Australia; **H.** *O. fimbria* **sp. nov.**, Pannawonnica, Western Australia. Photographs: **A, C–E.** S. Macdonald; **B.** M. Hutchinson; **F.** P.M. Oliver; **G.** B. Maryan; **H.** R. Ellis.

The three remaining populations are similar to each other in overall proportions. The Eastern animals tend to be smaller, and possess deeper heads and shorter limbs than Central and Western lineages (see Table 1). In comparison with these other two lineages, Western specimens tend to have a proportionally shorter body and longer and wider head, although there is extensive overlap among the ranges (Table 1). Western animals, however, can be consistently differentiated from both Central and Eastern by having a rostral scale that is only partially divided by a medial crease (crease <60% of rostral height *versus* typically l00%).

All lineages show variation in dorsal colour pattern (Fig. 5), although much of this is associated with a dramatic ontological colour transition from strongly contrasting bands on hatchlings to an increasingly subdued pattern of much more extensive pale spotting and increasingly faint bands on adults. Once ontogenetic changes are taken into account, there are few clear geographic patterns in colouration with respect to the major genetic lineages. The dorsal pattern of adult Gulf animals ranges from clearly banded to reticulated with bright yellow flecks or lines. Central animals tend to have a dorsal colouration with extensive yellow spotting and wider light bands, whereas in Eastern animals the light colouration on the dorsum tends to be more whitish and less extensive, often with narrower bands. Within the Western population, animals from the southern half of the range tend to be more heavily banded and coarsely spotted or blotched with yellow as adults, whereas northern animals tend to be more finely spotted and less bright, although occasional strongly banded adults do occur. Overall, however, there is considerable overlap between most of these colour pattern elements, and many animals are difficult to assign to a particular population based on colour pattern alone, especially in preservative.

Taxonomic conclusions

Morphologically, the Gulf, Eastern, Central and Western lineages can be distinguished from all Top End populations of *O. marmorata*, including type material (lectotype—BMNH xxii.2b; Fig. 3) and the nominal taxon *O. gemmata*, by their narrower tails. Type material of *O. marmorata* from Port Essington on the Coburg Peninsula (Fig. 4) and other recent material from proximate localities in the Top End can be further distinguished from all lineages under consideration here by their very bulbous (much wider and deeper than the head) and sharply tapered tail. These specimens also tend to have only one small scale between the enlarged supranasals (*versus* usually two or more in arid zone *Oedura*). On this basis, we are confident that while the status of the various genetic lineages from the north requires further work, morphology supports the geographic and genetic evidence that none of the species from the arid zone considered here are true *O. marmorata*.

A suite of morphological characters, including small size, tapering lamellae, and shorter tail, coupled with the previous genetic data (Oliver *et al.* 2014a), distinguish the Gulf animals from all others, indicating they are a distinct species. The remaining three populations show extensive overlap of most major morphological characters. However, the Western lineage is genetically diagnosable via three independent molecular datasets (allozymes, mtDNA, nDNA; Oliver *et al.* 2014a) and also possesses a diagnostic morphological character (rostral partially divided *versus* fully divided), making this lineage recognizable as a distinct evolutionary lineage (species).

The Central and Eastern populations show some evidence of morphological divergence, with Eastern animals tending to have longer bodies (Trk/SVL) and proportionally shorter legs, possibly deeper heads and less light flecking and narrower bands on the dorsum; however, these two populations still extensively overlap in most characters. Variation in head and body proportions can accumulate rapidly in closely related lineages with differing ecologies, and do not nessecarily imply that they represent separate evolutionary species (Vitt *et al.* 1997; Sistrom *et al.* 2012). These two lineages are not as genetically divergent as other lineages considered here (no fixed allozyme differences, no differentiation at the nuclear genes we sequenced and lower mtDNA divergences) (Oliver *et al.* 2014a). Mitochondrial divergences within the Central populations are also almost as high as those between Eastern and Central populations. Our geographic coverage of genetic samples of these two lineages is poor, especially from potential areas of contact such as the Simpson Desert. Thus we conservatively consider these two populations to be conspecific, but given the evidence for some genetic and morphologicial differentiation, we regard them as two evolutionary significant units (ESUs; *sensu* Moritz 1994).

Nomenclature

Several names are currently in the synonymy of *O. marmorata*. Of these, the type material of the two oldest names (*O. verrillii* Cope, 1869 and *O. fracticolor* de Vis, 1884) appears to have been lost.

Oedura verrillii is characterized by few characters with the type location 'Australia'. The identity of this form was considered to be suspect by Boulenger (1885) and was later considered a *nomen dubium* by Kluge (1965). Cogger *et al.* (1983) did not list this taxon in their catalogue on the basis that it was probably not an *Oedura* (H.G. Cogger, pers. comm.). Some of the characters given in the diagnosis are inconsistent with this form being a member of the *O. marmorata* complex; specifically an undivided rostral and only two pairs of divided scansors on the toes (Boulenger 1885). Bauer & Henle (1994), however, did regard this taxon as a member of the *O. marmorata* complex based on the presence of six dark cross-bands and a single postcloacal tubercle. Owing to the vague description and type location and lack of type specimens, we maintain *O. verrillii* as a junior synonym of *O. marmorata*. This maintains some stability in that it is not possible to precisely apply the name to any of the new *Oedura* taxa in the absence of further information.

The type locality of *O. fracticolor* de Vis, 1884 was given as 'Kimberley' (currently Normanton) at the mouth of the Norman River on the Gulf of Carpentaria in Queensland. Normanton is outside the known range of any of the *O. marmorata* complex taxa under consideration here, but is geographically closest to the Gulf population (although still over 200 km distant). The type material for *O. fracticolor* was collected by Kendall Broadbent who worked for the Queensland Museum as their zoological collector. The original description of *O. fracticolor* lists a series of characters that suggest it is an *Oedura*: 'The chevron plates, on the outer toes, in six, on the other toes in nine pairs' and 'Total length 9.3 c.m. Tail 4. Head 1.4'. The colour pattern is also described in some detail:

'Grey; a darker grey stripe runs from the angle of the mouth to the shoulder: above it, a second from the middle of the orbit to and along the side of the back; a third from the upper orbit to and along the side of the back: a third from the upper part of the orbit goes to the nape, and is continuous with its fellow of the opposite side. These lateral stripes are joined by backwardly curved transverse bands, which alone are continued to the tail. All these are linear, and in the brightest specimens are edged posteriorly with white spots, most evident on the tail, which is thus crossed by pairs of short black and white bars. In most examples the spots are obsolete, and the lines are broken up into irregular streaks and spots. In some the grey ground colour is by the disappearance of the lines, almost uninterrupted.' (p. 160)

This colour pattern description does not clearly match the colour pattern of the Gulf form which tends to have at most a single light band on the head, and relatively indistinct and thin transverse bands that are not 'backwardly curved' (see more detail below). Loosely interpreted, the description could correspond to *O. castelnaui* (Thominot, 1889), a large-bodied arboreal species that has been recorded just over 100 km from the area around Kimberley/ Normanton (e.g. Croydon tip, AMS R63355), and possesses distinctive 'backwardly curved' dorsal bands. The collector Broadbent visited Somerset in Cape York just prior to his collecting trip to Kimberley, making a mixing of specimens possible (although he likely sent his Cape York collections to Brisbane prior to his departure; G. Shea, pers. comm.). Based on the locality and morphological data we consider it possible that *O. fracticolor* is a senior synonym of *O. castelnaui*. In the absence of the type specimens or recent collections around Normanton, however, we refrain from taking taxonomic action on *O. fracticolor* pending further work on *Oedura* in Queensland (C. Hoskin, pers. comm.). Regardless of the status of *O. castelnaui* and *O. fracticolor*, on the basis of distribution and dorsal colour patterns observed, we consider that the Gulf lineage is not *O. fracticolor* and represents an unnamed taxon.

Oedura cincta de Vis, 1888 was described from Charleville, Queensland. There is one specimen in the Queensland Museum (QM J226) and two more specimens held in the Australian Museum (AMS R5602, R5603) that are considered to be probable syntypes. Based on their morphology and geography, this taxon is clearly applicable to Central and Eastern populations, and we nominate a lectotype in the taxonomic section, below.

Wells and Wellington (1985) proposed three names for species resembling *O. marmorata*. *Oedura greeri* Wells & Wellington, 1985 (holotype: AMS R87677) was described without diagnosis and is regarded as a *nomen nudum* (Shea & Sadlier 1999). *Oedura attenboroughi* Wells & Wellington, 1985 (holotype: NTM R4816) has been referred to *O. marmorata* by Shea & Sadlier (1999), however, the type specimen has distinctive dark-edged dorsal ocelli and is relatively small, indicating that it is part of the *O. monilis* de Vis, 1888 species complex from eastern Australia. *Oedura derelicta* Wells & Wellington, 1985 (holotype: NTM R11413, Jessie Gap, Alice Springs,

Northern Territory) was diagnosed from *O. marmorata* by 'the lack of transverse banding' in the latter species. This diagnosis was made citing photographs of *Oedura* 'derelicta' in Bustard (1970b, Plate 24) and *O.* 'marmorata' in Cogger (1983, Plate 1983). In contrast to this statement, relative to other populations in the *O. marmorata* species complex, adult central Australian specimens often have weak or no transverse bands (Fig. 5), and the specimen figured by Bustard appears to be a subadult. The specimen of '*O. marmorata*' figured by Cogger (1983) from Mt Brockman in the Northern Territory represents the species described as *O. gemmata* by King and Gow in 1983, one of the few members of the *O. marmorata* species complex that lacks transverse bands at all size classes. In our treatment here, however, *O. derelicta* is a junior synonym of *O. cincta*.

Systematics

Oedura Gray, 1842

Type species: *O. marmorata* Gray, 1842, by monotypy.

Generic diagnosis. A genus of the Diplodactylidae distinguished from all related genera by the possession of enlarged juxtaposed dorsal scales approximately the same size as the ventrals (*versus* much smaller in related genera). Further distinguished from other taxa formerly placed in *Oedura* (*Amalosia*, *Hesperoedura* and *Nebulifera*; Oliver *et al*. 2012), by the combination of large size (adult SVL >60 mm), usually more than one cloacal spur per side, and dorsal pattern generally including a weak to bold series of transverse bands or disjunct blotches and no evidence of a vertebral stripe.

Oedura cincta de Vis, 1888
Inland marbled velvet gecko
Figs. 3, 5–6

Lectotype. QM J226, Charleville, Queensland, Australia (collected by Kendall Broadbent in 1885).
Paralectotypes. AMS R5602, AMS R5603, as for lectotype.
Synonomy. *Oedura derelicta* Wells & Wellington, 1985, holotype—NTM R11413, Jessie Gap, Alice Springs, Northern Territory.

Diagnosis. A large-bodied (SVL: mean 90 mm, max 108 mm) species in the *O. marmorata* complex, with a moderately broad head (HW/SVL 0.17–0.21), moderately long body length (Trk/SVL 0.42–0.53), moderately long tail (original TL/SVL 0.61–0.79) narrower than head and roughly circular in cross-section, rostral usually completely divided, apical lamellae wide (ToeW/SVL 0.023–0.036), subdigital lamellae in a flared series that on fingers 3 and 4 is wider than apical pair, 9–21 precloacal pores in adult males and dorsal pattern (especially conspicuous on juveniles) of 5 or 6 light transverse bands on purplish-brown background.

Description. A large (max SVL 108 mm) and moderately elongate *Oedura* (Trk/SVL 0.42–0.53). Head moderately wide (HW/SVL 0.17–0.21) and deep (HD/SVL 0.07–0.12). Rostral usually fully (n = 39) or near fully divided (n = 5), bordered dorsally by two internasals, internasal bordered dorsally by two relatively small, roundish supranasals and 3–5 (mode = 3) small intervening scales. Enlarged supralabials 9–11 to midpoint of eye, 9–13 in total, second supralabial equal to or slightly higher than first, infralabials 10–15. Limbs moderately long (ArmL/SVL 0.11–0.14, LegL/SVL 0.12–0.16). Subdigital lamellae expanded and prominent, 6–9 under third finger, 8–10 under third toe, distal lamellae on digits either divided or deeply notched, apical pair distinctly larger (but not always wider) than and separated from other pairs, penultimate pair slightly narrower, subsequent lamellae on digits two to five forming distinctly flared series, proximal lamellae undivided.

Enlarged postcloacal spurs in a single cluster of between 1–4 (mode 2). Original tail moderately long (TL/SVL 0.58–0.79) and narrow (TW/SVL 0.07–0.15) with a slight ventral groove, varying from somewhat depressed to almost circular in cross section, width and depth varies greatly depending on body condition, caudal scalation homogeneous, squarish flat scales arranged in regular rows. Fully regrown tails shorter (TL/SVL 0.43–0.65) than original tails but comparably wide (TW/SVL 0.09–0.13).

FIGURE 6. Preserved specimens of *Oedura cincta*. From top to bottom: SAMA R38843; SAMA R65905 (Central ESU); SAMA R38900; SAMA R51833 (Eastern ESU). Scale bar = 1 cm.

In preservative, base colouration of dorsum usually dark purplish brown, with a nuchal band and 5 further narrow pale buff transverse bands between the limbs, and a further 5–8 similar bands on the tail. Pale bands often with dark brown regions within them. Nuchal band usually joins a light lateral band extending from the supralabial scales and above the tympanum. Bands usually become indistinct with increasing size, especially on the tail, and are not or only faintly apparent on larger specimens, especially the Central lineage. Extensive further light flecks and blotches are also present between the bands, and elsewhere on the dorsal and lateral surfaces of the torso, limbs and tail. Larger specimens can be heavily mottled with equal amounts of light buff and brown, with no obvious transverse banding. Top of head usually with light to heavy pale mottling and a distinct to indistinct canthal stripe. Venter relatively plain light buff with a faint to distinct wash of light brown, particularly towards the lateral extremities and under head and limbs. Regrown tails dark brown and mottled with varying amounts of light flecking.

Hatchlings and juveniles lack light flecking and usually have a very simple pattern of sharply defined light bands separated by wide plain dark brown regions, and a thin white labial stripe. As specimens increase in size, the sharp definition of light and dark regions decreases, and the amount of light flecking and blotching across the body increases.

In life, adults possess base colouration of dark purplish-brown during the day, washed out grey at night; light bands and flecks tend to be light grey or buff in the Eastern population, but tend to be more yellow in Central population. Iris dark brown.

Particulars of syntypes. QM J226, female with original tail (in mm): SVL 88.0, HW 15.3, HD 9.8, HL 19.2, EN 6.6, IN 2.9, IO 6.9, EYE 4.4, TrK 39.3, ArmL 9.9, LegL 11.4, TL 66.0, TW 12.4, TD 9.8, 3FW 2.4, 3TW 2.7. Scales: RC 100%, SuL 9 (10), InF 12, CS 2/3, 3FL 8, 3TL 8.

AMS R5602, male with original tail: SVL 79.0, HW 15.8, HD 9.8, HL 18.5, EN 6.4, IN 2.7, IO 6.8, EYE 4.5, Trk 39.4, ArmL 10.5, LegL 12.2, TL 56.0, TW 11.0, TD 8.1, 3FW 2.2, 3TW 2.2. Scales: RC 100%, SuL 10(10), InF 12, CS 2/2, 3FL 7, 3TL 8, precloacal pores 23.

AMS R5603, male with original tail: SVL 78, HW 16.0, HD 9.7, HL 18.8, EN 6.8, IN 2.9, IO 7.3, EYE 4.6, TrK 39.1, ArmL 10.2, LegL 11.9, TL 62.0, TW 8.7, TD 9.0, 3FW 2.3, 3TW 2.7. Scales: RC 100%, SuL 11 (12), InF 12, CS 2/2, 3FL 8, 3TL 8, precloacal pores 11.

All three syntypes have original tails and completely divided rostrals. Colour pattern is greatly faded, although indistinct dark bands, blotches and flecks are faintly discernable to a varying extent across the dorsal surfaces of the head, torso and especially tail.

Distribution and habitat. The Eastern population occurs in woodlands throughout the channels and floodplains of the Cooper and Darling Basins in western Queensland and New South Wales. Apparently isolated populations occur from the northern Flinders Ranges and just north of the Murray River in South Australia (Fig. 2). Eastern animals are usually associated with exfoliating bark and hollows in small trees (both living and dead), especially Bulloaks in the genus *Casuarina*, but may also use rocks when available (Miller 1980; P.M. Oliver, pers. obs.; D. Armstrong, pers. comm.). In areas with a high density of suitable trees *O. cincta* can be abundant, and large numbers can be collected in small periods of time. Specimens have also been reported from under exfoliating rock in the Flinders Ranges (Miller 1980; D. Armstrong, pers. comm.).

The Central population is known from two apparently isolated subpopulations centred on the MacDonnell and Reynolds Ranges in the southern Northern Territory. The accuracy of an additional old record (Museum Victoria) from the Tennant Creek area requires verification through additional recent samples. Populations of this species from the Central Ranges are associated with gorges and other range country and are usually found while foraging on and around rock faces.

Comparisons. *Oedura cincta* is very similar the Western lineage (see below) and shares with that taxon a combination of moderately large size (average SVL > 90 mm SVL), moderately long tail which tends to be rounded in cross-section and not wider than the head, prominently flared subdigital lamellae series (on fingers 3 and 4 of equal or greater width to the apical lamellae) and dorsal pattern usually consisting of numerous poorly-defined light flecks and blotches, and often thin light bands. *Oedura cincta*, however, has a longer rostral crease (60–100% *versus* 25–60% of the rostral height in the Western lineage).

Oedura cincta can be specifically distinguished from lineages in the *O. marmorata* species complex from northern Australia by possessing a longer (TL/SVL 0.65–0.80 *versus* 0.53–0.63) and narrower tail (always narrower than the head), a longer body (Trk/SVL 0.42–0.53 *versus* 0.39–0.49), slightly wider apical lamellae

(0.23–0.36 *versus* 0.21–0.31) and a distinctly flared subdigital lamellae series on fingers 3–4 wider than the apical pair (*versus* not wider).

Oedura cincta can be specifically distinguished from most other *Oedura* from eastern Australia by the presence of a subdigital lamellae series on digits 2–5 that is prominently expanded at its midpoint (*versus* tapering or slightly expanded), higher number of postcloacal tubercles per side (mode of 2 *versus* 1) and dorsal colour pattern consisting of 5–6 distinct to indistinct narrow light bands with poorly defined light flecking (*versus* wide pale transverse bands in *O. castelnaui*, distinct dark-edged ocelli or transverse bands of varying size in *O. coggeri* Bustard, 1966, *O. monilis* and *O. tryoni* de Vis, 1884, or two pale bands across the nape and base of tail in *O. jowalbinna* Hoskin & Higgie, 2008). Further distinguished from the Gulf lineage by larger body size (SVL 78–106 mm *versus* 64–92 mm), longer original tail (TL/SVL 0.58–0.79 *versus* 0.49–0.65), wider terminal lamellae and wider lamellae series on fingers (see details below).

Oedura bella sp. nov.
Gulf marbled velvet gecko
Figs. 5, 7, 8

Holotype. QM J94016 (field number—OMAR #001), adult male with original tail, 10 km south of Mt Isa on Boulia Road, Queensland, Australia (20.8617°S, 139.4617°E), collected by P.M. Oliver, M. Vucko and M. Vickers, on 20 February 2007.

Paratypes. Northern Territory: AMS R53437–8, 37 km north of McArthur River base camp on Borroloola Road (16.10°S, 136.12°E); AMS R53467, Caranbirini Water Hole, 21 km north of McArthur River base camp (16.22°S, 136.15°E); AMS R53643, Glyde River, 10 km east of McArthur River base camp (16.43°S, 136.17°E); AMS R53782, 37 km north of McArthur River Camp (16.10°S, 136.12°E); SAMA R34188, McArthur River Station (16.67°S, 135.85°E). Queensland: NTM R21288, Musselbrook Reservoir (18.61°S, 138.08°E); SAMA R34208–9, SAMA R35425, Lawn Hill NP (18.58°S, 138.50°E); QM J52748, Lawn Hill Station, Century Project Site (18.75°S, 138.58°E); QM J74927, Hells Gate (17.47°S; 138.37°E); QM J75207–8, Lawn Hill (18.71°S, 138.48°E).

Referred material. AMS R138727–8, Groote Eylandt (13.83°S, 136.42°E); NTM R7494–5, Umbakumba Rd (13.88°S, 136.50°E); NTM R7541, Ayakamindadina (13.97°S, 136.60°E).

Diagnosis. A medium-sized (SVL: mean 78 mm, max 92 mm) species in the *O. marmorata* complex with a wide (HW/SVL 0.19–0.23) and moderately deep head (HD/SVL 0.10–0.12), short body (Trk/SVL 0.41–0.49), short original tail (TL/SVL 0.49–0.65) that is narrower than head and slightly depressed, rostral usually less than half divided, terminal lamellae moderately wide (ToeW/SVL 0.021–0.030), proximal subdigital lamellae of all fingers not wider than apical pair, 12–17 precloacal pores in males and base colouration dark purplish brown with 5 distinct to faint light dorsal bands from nape to hindlimbs.

Description. A medium-sized (to 92.0 mm SVL) and moderately robust *Oedura* (Trk/SVL 0.41–0.49). Head moderately narrow (HW/SVL 0.19–0.23) and not strongly depressed (HD/SVL 0.10–0.12). Rostral 25–50% divided, bordered dorsally by two internasals, internasals bordered dorsally by two oblong moderately enlarged supranasals and 1–3 (mode 1) smaller intervening scales. Enlarged supralabials 9–10 to midpoint of eye, 11–13 in total; infralabials 9–13. Limbs moderately long (ArmL/SVL 0.12–0.15; LegL/SVL 0.14–0.16). Subdigital lamellae moderately expanded and prominent, 7–8 rows (mode 8) under finger three and 7–9 toe three, distal lamellae on all digits either divided or deeply notched, apical distinctly larger and generally wider than more proximal pairs—especially on fingers, proximal lamellae undivided. Enlarged postcloacal spurs 2 or 3, in a single cluster per side. Original tail relatively short (TL/SVL 0.49–0.65) and wide (TW/TL 0.18–0.28), gradually tapering to a point, slightly depressed in cross-section and slightly concave ventrally; moderately wide but shows considerable variation depending on body condition (TW/SVL 0.10–0.15), scalation relatively homogeneous with dorsal and ventral scales of similar size. Fully regrown tails shorter (TL/SVL 0.44–0.53) and wider (TW/TD 0.21–0.31) than original tails.

FIGURE 7. Holotype of *Oedura bella* **sp. nov.** (QM J94016) in dorsal and ventral views. Scale bar = 1 cm.

In preservative, dorsal colouration of adults variable; base colouration dark purplish brown, with 5 distinct to very indistinct broad light bands from nape to hindlimbs, with a further 4–7 similar bands on the tail. Light bands with little to extensive dark brown flecking or blotches; on larger specimens dark brown pigmentation is extensive such that the broad light bands are reduced to two narrow indistinct and often broken bands. The anterior (nuchal) light band extends across the nape and joins or approaches a light lateral band extending from the labial scales and above the tympanum. The canthal stripe ranges from distinct to indistinct. Dark brown regions between light bands and elsewhere on the dorsal and lateral surfaces of the head, torso, limbs and tail, with extensive further light flecking and blotches. Venter relatively plain light buff with a very faint wash of light brown, particularly towards the lateral extremities and on the head and limbs, more extensive brown mottling also present along the ventrolateral edges of the tail. Regrown tails dark brown with varying amounts of light flecking, but no clear pattern.

Hatchlings and small juveniles lack light flecking and generally have a very simple pattern of five sharply-defined light bands on the neck and body, and 5–7 light bands on the tail, separated by broad plain dark brown regions. As specimens grow, the sharp definition of light and dark regions decreases, and the amount of light flecking and blotching across the body increases.

In life, the base colouration of adults is dark purplish brown during the day, washed out grey at night; light

bands and flecks ranges tend to be bright yellow. The canthal stripe tends to be very strongly defined and a white labial stripe is also sometimes clearly apparent. Iris very dark brown.

Particulars of holotype. QM J94016 (field tag number—OMAR#001), male with original tail (in mm): SVL 77.0, HW 14.6, HD 7.4, HL 19.6, EN 6.3, IN 2.8, IO 6.7, EYE 5.0, TrK 31.0, ArmL 10.1, LegL 10.9, TL 38.0, TW 8.3, TD 5.6, 3FW 1.8, 3TW 2.3. Scales: RC 25%, SuL 12(10), InF 11, CS , 3FL 7, 3TL 8, precloacal pores 16.

FIGURE 8. Preserved specimens of *Oedura bella* **sp. nov.** showing range of variation in dorsal patterning. From top to bottom: SAMA R35425; NTM R7541; SAMA R34188. Scale bar = 1 cm.

Distribution and habitat. Restricted to the ranges around the south and western edges of the Gulf of Carpentaria; from the Selwyn Range around Mt Isa in the southeast, north to Riversleigh and Musselbrook regions in the Queensland-Northern Territory border, as far west as the McArthur River and Borroloola regions of Northern Territory, with a further apparently isolated insular population on Groote Eylandt to the north (see comments), and another isolated record from the northern edge of the Barkly Tablelands (Fig. 2).

Field observations suggest this species is primarily saxicoline, using both horizontal screes and vertical faces (including road cuttings), however, it has also been recorded under bark around the base of trees (but in rocky country) (G. Bourke, pers. comm.).

Etymology. From the Latin masculine adjective *bellum* (used in its feminine form), meaning amongst other things pretty, handsome, charming, fine, lovely, neat, pleasant, agreeable, active, gallant or good. In reference to the very attractive contrasting yellow and dark colour pattern of this species.

Comparisons. *Oedura bella* is similar to parapatric populations of *O. marmorata* in northern Australia (although it differs in both nuclear and mitochondrial loci). It differs in external morphology by possessing an original or regrown tail that is much narrower (TW/SVL 0.10–0.15 *versus* 0.19–0.24) and generally less than the width of head, and *O. bella* also reaches a smaller maximum size, although adult sizes overlap (adult SVL usually 77–92 mm *versus* 77–97 mm) and sample sizes are low.

Oedura bella differs from *O. cincta* and Western (see below) by the combination of its smaller maximum size (SVL 64–92 mm *versus* 77–106 mm), shorter original tail (TL/SVL 0.49–0.65 *versus* 0.58–0.80), and its narrower terminal lamellae (0.21–0.30 *versus* 0.23–0.36) and narrower lamellae series on the fingers (not wider than terminal lamellae *versus* wider on digits 3 and 4). It further differs from the geographically proximate *Oedura cincta* by generally having a rostral partially divided by a crease (*versus* usually fully divided).

Oedura bella can be distinguished from the three species of *Oedura* in the Kimberley region in Western Australia by having subdigital lamellae that are slightly expanded around the midpoint of the digit (*versus* strongly tapering in *O. gracilis* King, 1984, or obviously flared and often as wider or wider than the apical lamellae in *O. filicipoda* King, 1984 and *O. murrumanu* Oliver, Laver, Melville & Doughty, 2014), and its moderately long and slightly swollen tail (*versus* very long [approaching length of body] and tapering in *gracilis*, or greatly flattened and wider than body in *O. filicipoda* and *O. murrumanu*). With a maximum SVL of 92 mm, *O. bella* is also smaller than *O. filicipoda* and *O. murrumanu* (which both regularly exceed 100 mm).

Oedura bella differs from all other *Oedura* in eastern Australia by possessing more than one postcloacal tubercle and in having a base colouration of five relatively thin dorsal bands. The latter character distinguishes it from two other small saxicoline *Oedura* in eastern Australia: *O. coggeri* has large ocelli on limbs and torso and *O. jowalbinna* has a pale pinkish gray dorsum with distinct dark-edged bands across the neck and base of tail and a plain yellow original tail (Hoskin & Higgie 2008). All other *Oedura* in eastern Australia tend to be larger (SVL > 90 mm) and also have dorsal patterns that do not feature thin light bands; specifically, *O. castelnaui* has wide bands, *O. monilis* has blotches or ocelli, and *O. tryoni* has dense small spots.

Remarks. No genetic samples were available from the Groote Eylandt samples that we refer to this species. Given their geographic disjunction from all other material, the distinctiveness of this population warrants further investigation.

Oedura fimbria **sp. nov.**
Western marbled velvet gecko
Figs. 5, 9, 10

Holotype. WAM R154783, adult male with original tail, Brockman Ridge, Western Australia, 23.3108°S, 119.9169°E, Western Australia, collected by J. Fraser on 5 April 2004.

Paratypes. All from Western Australia: WAM R105965, 7 km north of Mount Magnet (28.00°S, 117.88°E); WAM R119991, Hope Downs (23.01°S, 119.10°E); WAM R119993, Hope Downs (23.00°S, 119.12°E); WAM R129595, 120 km north-west of Newman (22.92°S, 118.88°E); WAM R129635, 120 km north-west of Newman (22.92°S, 119.02°E); WAM R135369, Mount Brockman (22.31°S, 117.32°E); WAM R154796–7, Walga Rock (27.40°S, 117.47°E); WAM R157504, WAM R157508, WAM R157516, Packsaddle Range (22.92°S, 118.89°E); WAM R157595, West Angelas (23.19°S, 118.86°E); WAM R160074, 32.5 km east-south-east of Meentheena Outcamp (21.33°S, 120.750°E); WAM R165150, 5 km north-north-west Python Pool (21.32°S, 117.23°E).

Referred material. All from Western Australia: WAM R52852, 12 km east of Tallering Peak (28.10°S, 115.75E); WAM R84004, 6 km north of Mount Magnet (28.03°S, 117.85°E); WAM R84365, WAM R84366, 17 km north-north-east Anketell homestead (27.90°S, 118.95°E); WAM R87544, 30 km south-south-west Glenburgh homestead (24.68°S, 115.00°E); WAM R97012, Woolgerong Rock (27.40°S, 117.38°E); WAM R106289, 7 km north Mount Magnet (28.00°S, 117.88°E); WAM R119086, Virgin Springs, Carnarvon Range (25.10°S, 120.72°E); WAM R119837, Yandicoogina (22.72°S, 119.02°E); WAM R129622, 120 km north-west Newman (22.92°S, 118.88°E); WAM R132296, Ulongunna Rock (27.12°S, 117.23°E); WAM R132626, Burrup Peninsula (20.60°S, 116.81°E); WAM R135445, Mount Brockman (22.31°S, 117.32°E); WAM R146593, WAM R146594, 40 km south-east Pouyouwuncubban (22.15°S, 119.02°E); WAM R157508, Packsaddle Range (22.92°S, 118.89°E); WAM R160066 58 km east-south-east Meentheema Outcamp (21.32°S, 121.00°E); WAM R165150, 5 km north-north-west Python Pool (21.32°S, 117.23°E).

FIGURE 9. Holotype (WAM R154783) of *Oedura fimbria* **sp. nov.** in dorsal and ventral view. Scale bar = 1 cm.

Diagnosis. A large (mean SVL 94 mm, max 104 mm) species in the *O. marmorata* complex, with a moderately broad head (HW/SVL 0.18–0.21), moderately long body length (Trk/SVL 0.42–0.53), tail moderately long (TL/SVL 0.65–0.80), narrower than head and roughly circular in cross-section, rostral 25–60% divided, apical lamellae wide (TW/SVL 0.027–0.036), subdigital lamellae in a flared series wider than apical pair on fingers 3–4, 13–26 precloacal pores in adult males, and basic dorsal colouration (especially on juveniles) usually including 5 light transverse bands.

Description. A large (to 104 mm SVL) and moderately elongate *Oedura* (Trk/SVL 0.40–0.53); head moderately wide (HW/SVL 0.18–0.21) and deep (HD/SVL 0.09–0.13). Rostral 25 to 60% divided, bordered dorsally by two nasals, nasals bordered dorsally by two relatively small supranasals and 2–4 (mode 3) small intervening scales. Supralabials 9–11 to midpoint of eye, 11–13 in total; infralabials 10–13. Limbs moderate (ArmL/SVL 0.12–0.15, LegL/SVL 0.14–0.17). Subdigital lamellae expanded and prominent, 7–10 under third

finger, 8–10 under third toe, distal lamellae on digits either divided or deeply notched, apical pair distinctly larger (but not always wider) than and separated from other pairs, penultimate pair slightly narrower, subsequent pairs on digits 2–5 distinctly flared, proximal lamellae undivided. Original tail moderately long (TL/SVL 0.65–0.80) and narrow (TW/TL 0.13–0.17) with a slight ventral groove, varying from somewhat depressed to almost circular in cross-section, relative width and depth varies greatly depending on body condition; caudal scalation homogeneous. Fully regrown tails shorter (TL/SVL 0.51–0.66) and wider (TW/TL 0.18–0.26) than original tails.

FIGURE 10. Preserved specimens of *Oedura fimbria* **sp. nov.**, showing range of variation in dorsal patterning. From top to bottom: WAM R105965; WAM R119991; WAM R157595. Scale bar = 1 cm.

In preservative, base colouration of dorsum dark purplish brown, with a highly variable amount of light cream flecking or blotching. Most adult specimens have 5–6 distinct to very indistinct pale light transverse dorsal bands with wide brown central regions, with a further 5–8 similar bands on the tail. In larger specimens, however, all traces of bands have been lost. The anterior (nuchal) light band generally joins or approaches a light lateral stripe that extends from the labial scales and above the tympanum. Bands are typically very faded and indistinct on adult specimens from the north of the range, but remain more conspicuous in specimens of all sizes from the south. Extensive further light flecking and blotches are present between the bands, and elsewhere on the dorsal and lateral surfaces of the head, torso and limbs; northern specimens tend to have many smaller flecks, while southern specimens have fewer larger flecks or reticulate blotches. On a small number of apparently aberrant specimens, the light pigmentation is very extensive and brown areas form narrow transverse bands. Venter plain light buff, sometimes with faint brownish tinge on the throat and the terminal lamellae. Regrown tails dark brown with varying amounts of light flecking, but no clear bands.

Hatchlings and small juveniles are dark purplish brown dorsally, with 5 sharply-defined light cream transverse bands on the torso, 5–7 additional light bands on the tail, and a narrow white labial stripe. The dorsum of the head tends to be lighter brown than the remainder of the body. With increasing size, the light transverse bands become less clearly defined and usually develop a wide brown mid-region. An additional very light creamish transverse band or series of blotches also develops at the approximate midpoint of the pre-existing light bands; light flecking and blotching across the body, limbs and tail also becomes increasingly apparent.

In life, the basic pattern and colouration of adults matches those of preserved specimens, however, the darker regions are purplish during the day, silvery grey at night, and light regions tend to be whitish to relatively bright yellow. Iris very dark brown.

Particulars of the holotype. WAM R154783, adult male with original tail (in mm): SVL 104.0, HW 19.3, HD 10.9, HL 24.6, EN 8.1, IN 3.7, IO 8.5, EYE 5.4, TrK 49.0, ArmL 13.2, LegL 16.4, TL 74, TW 12.2, TD 10.2, 3FW 3.1, 3TW 3.6. Scale counts: SuL 10(12), InF 10, CS 2/3, 3FL 9, 3TL 8, precloacal pores 26. Hemipenes everted, right 10.2 mm long, left 7.6 mm long, pores in an almost continuous curved series separated by 2 poreless medial scales, two additional pore-bearing scales are also present posterior to the main series in the precloacal region.

Distribution and habitat. Occurs in the Pilbara, Gascoyne and Murchison regions of mid-western Western Australia (Fig. 2). In the north (Pilbara), this species extends to the southern edge of the Great Sandy Desert, east to Karlamilyi National Park, and west to the Burrup Peninsula. In the south it occurs in the Gascoyne, western Murchison and Yalgoo regions, east as far as the Barlee Range, south to Mt Magnet and Gullwa, and east to the Little Sandy Desert. From collector's notes associated with voucher specimens, this species was recorded as occurring on relatively massive ranges, rocky outcrops and breakaways, caves and gorges 114 times, whereas there are only 4 occurrences on trees and one under tin. We have only observed this species on rocky outcrops with large boulders (Pilbara) or on cliff faces (Kennedy Range).

Etymology. *Fimbria* is Latin for fringe in reference to the lateral fringes of expanded lamellae along the sides of the digits. Used as a noun in apposition.

Comparisons. *Oedura fimbria* **sp. nov.** is most similar to *O. cincta* and shares moderately large size (SVL > 100 mm), moderately long tail which tends towards rounded in cross-section and is not wider than the head, wide flared subdigital lamellae, dorsal pattern usually consisting of numerous poorly-defined light flecks and blotches and often thin light bands. The only clear diagnostic morphological character between the two speices is an incomplete rostral crease on O. *fimbria* **sp. nov.** (25–60% *versus* 60 [rarely]–100% [usually] of the rostral height). There are some differences in average for relative head length and body length, but ranges overlap extensively (see Table 1).

Oedura fimbria **sp. nov.** can be distinguished from other lineages in the *O. marmorata* species complex from northern Australia by possessing a longer (TL/SVL 0.65–0.80 *versus* 0.53–0.63) and narrower tail (always narrower than the head). It differs from *O. bella* in its larger size (max SVL 104 mm *versus* 92 mm), longer tail (TL/SVL 0.65–0.80 *versus* 0.49–0.65), wider terminal lamellae (3TW/SVL 0.23–0.36 *versus* 0.21–0.30) and prominently flared subdigital lamellae series—especially on fingers 3 and 4 (proximal lamellae wider than apical lamellae *versus* not wider).

Oedura fimbria **sp. nov.** can be distinguished from the three other species of *Oedura* in the Kimberley region in Western Australia as follows: from *O. gracilis* by its moderately long and swollen tail (*versus* very long [approaching length of body] and tapering) and in having subdigital lamellae series that is flared around the

midpoint of the digit (*versus* tapering); from *O. filicipoda* in having a narrow tail that is not wider than the head and near circular in cross-section (*versus* wider and very flattened) and smaller eyes (EYE/SVL 0.051–0.064 *versus* 0.071–0.076); and from *O. murrumanu* in having a smaller eye (EYE/SVL 0.051–0.064 *versus* 0.067–0.069) and a longer rostral crease (> 25% [typically 40–60%] *versus* < 25% of rostral height).

Discussion

Our partitioning of the *O. marmorata* complex is conservative. We only recognize distinct taxa that are unambigiously delineated by multiple independent sources of data (three different lines of genetic data and several morphological characters for all taxa, except *O. cincta versus O. fimbria* which are separable only by the rostral crease). Additional data may provide stronger evidence for the evolutionary distinctiveness of the Central and Eastern ESUs that we have pooled into *O. cincta*. *Oedura fimbria* samples from the isolated Burrup Peninsula on the coast of northwest Pilbara showed fixed allozyme differences, but relatively shallow mtDNA divergences (Oliver *et al*. 2014a).

Sampling from new localities and morphological and molecular analyses have increased the total number of *Oedura* species from 8 to 13 in the last 10 years (Hoskin & Higgie 2008; Oliver *et al*. 2014c; this study). Almost all of these recently recognised species are associated with discrete blocks of suitable habitat, usually rocky isolates, and some of them are highly restricted (Hoskin & Higgie 2008; Oliver *et al*. 2014c). However, there remain additional unrecognised lineages that appear to be restricted to isolated patches of rocky country and islands across the Monsoon Tropics, and to a lesser extent the arid zone (Oliver *et al*. 2014a; R. Laver, C. Hoskin, pers. comm.). Resolving the systematics of these lineages will aid delineation of patterns of endemism across the Australian arid and monsoonal biomes, and provide a framework for an improved understanding of how climatic change and topographic variation have shaped the biota of these regions.

Most *Oedura* species are climbing geckos, but show variability in habitat use, ranging from exclusively saxicoline habits to predominantly arboreal (Bustard 1971; King & Gow 1983; King 1984; Greer 1989; Oliver *et al*. 2014c). The phylogeny of *Oedura* indicates that shifts between arboreal and saxicoline ecologies have occurred independently on a number of occasions (Oliver *et al*. 2012), however, the potential for morphological evolution to be tracking ecological shifts has not been investigated. Our morphological data was primarily collected for taxonomy, but suggests some interesting patterns. While ranges do overlap, the taxa largely recorded from rock (Central *O. cincta*, *O. gemmata* and *O. fimbria*) on average were found to have flatter heads than the arboreal or more generalist species (*O. marmorata*, Eastern *O. cincta* and *O. bella*). Our data also suggest that the predominantly arboreal eastern Australian *O. cincta* has shorter legs, and possibly a longer body. These observations are consistent with patterns observed in other lizard radiations. Saxicoline lizards often have longer legs and flatter heads than non-saxicoline relatives (Goodman *et al*. 2008), and some arboreal lizards have also been shown to have shorter legs than their nearest relatives (Kohlsdorf *et al*. 2001). These observations suggest that morphological differentiation between the populations of *Oedura* we have examined may be related to their differing ecologies. *Oedura* species show variation in other potentially significant morphological features such relative eye size, colour pattern (bands *versus* spots) and tail shape (King & Gow 1983; King 1984; Oliver *et al*. 2014c; this study). Ongoing work to resolve the systematics of *Oedura* will provide a framework to explore further if shifts in habitat use are predictably linked to patterns of morphological variation in this genus.

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APPENDIX 1. Additional material examined.

Oedura cincta

New South Wales: AMS R107176, Byrock (30.67°S, 146.40°E); AMS R127130 Barrakee Station, 3.2 km east of Main Entrance, via Bourke-Wanaaring Rd (29.98°S, 145.00°E); AMS R137613, Byerawering Property Homestead (29.13°S, 147.17°E); AMS R137634, Wanaaring, 53 km east of Bourke Rd (29.67°S, 144.60°E); AMS R138446, Bourke-Wanaaring Rd, 1.2 km west Warrego River Bridge (30.00°S, 145.35°E).

Northern Territory: AMS R87680–1, AMS R 87683–4, AMS R87687, Mt Doreen (22.03°S, 131.33°E); AMS R136049, vicinity of 8 Mile Bore, 49.7 km northwest of Yeunduma turnoff on Tanami Road (22.12°S, 131.37°E); NTM R1407, Wolfram Hill, 59.6 km west of Yuendumu (22.03°S, 131.33°E); NTM R11413, Jesse Gap, 17 km east of Alice Springs (23.75°S, 134.017°E); NTM R18172, Harts Range, Mt Riddock Station (23.08°S, 134.60°E); NTM R18278, Paddy's Rockhole (22.40°S, 137.67°E); NTM R35902, NTM R35912, NTM R35919, 10 km south of Mt Doreen ruins (22.11°S, 131.39°E); SAMA R38842–3, Honeymoon Gap, Alice Springs (23.75°S, 133.75°E); SAMA R38844–6, 3 km west of Standley Chasm turnoff on Larapinta Drive (23.77°S, 133.53°E); SAMA R65905–6, Emily Gap (23.74°S, 133.95°E).

Queensland: AMS R139806, 9.3 km south of Charleville on Mitchell Hwy (26.49°S, 146.22°E); SAMA R42883–4, 30 km east of Noonbah Station (24.12°S, 143.42°E); SAMA R42894–5, 5 km west of Noonbah Station (24.08°S, 143.13°E); SAMA R42913, 85 km west of Windorah (25.35°S, 141.83°E); SAMA R55903, 9 km north of NSW/QLD border on Mitchell highway (28.96°S, 145.73°E); SAMA R65405, 6.7 km east of Noonbah Homestead (24.10°S, 143.25°E); QM J46669, Victoria Downs, 7 km north of Charleville turnoff, Augathella Road (26.42°S, 147.03°E); QM J71840, QM J71842, Dynevor Downs, 64 km east of Thargomindah, Dynevor Lake (-28.12°S, 144.17); QM J88239, Culgoa Floodplain National Park (28.88°S, 146.99°E); QM J89717, Winton area (22.46°S, 142.97°E); QM J90783, Noonbah Dam (24.10°S, 143.16°E); QM J90798, Wondula House, 0.5 km west of Ballard Tank, Plevna Downs (26.74°S, 142.56°E).

South Australia: SAMA R38016, Faraway Bore, Danggali Conservation Park (33.50°S, 140.55°E); SAMA R38900–1, 0.5 km south of Angepena Homestead (30.58°S, 138.85°E); SAMA R50764, 1 km southwest of Mt Serle Homestead (30.53°S, 138.85°E); SAMA R51833, 0.5 km north-northwest of Crump Bore (30.64°S, 138.87°E); SAMA R52203, 2.7 km west of

Lance Bore, Narrina Station (30.96°S, 138.77°E); SAMA R52333, 6 km east-southeast of Blackwater Springs, Oratunga Station (31.10°S, 138.88°E); SAMA R54300, west of Bellbird Campsite, Gluepot Reserve (33.70°S, 140.16°E); SAMA R64526, 15.4 km north-northeast of Nantawarrina Homestead (30.70°S, 139.06°E); SAMA R64626, 11.3 km south-southwest of The John Crossing (30.70°S, 139.05°E).

Oedura filicipoda
   Western Australia: WAM R60685, WAM R83707–8 (holotype and paratypes)—Camp Creek, Mitchell Plateau (14.83°S, 125.83); WAM R86897—11 km SE Mount Daglish (16.38°S, 124.98E); WAM R167805—Surveyor's Pool (14.67°S, 125.73E); WAM R138874—4.1 km S Donkin's Hill (14.99°S, 125.51E); WAM R171552—Prince Regent Nature Reserve (15.76°S, 125.26E).

Oedura gemmata
   Northern Territory: NMV D72584, NMV D72598–600; NMV D72621, Near Kikiyown (also called 'Kikikyon') (12.19°S, 133.81°E); NTM R27383, Oenpelli (12.38°S, 133.02°E); NTM R27599, Kikikyaw (12.19°S, 133.81°E); NTM R34986–7, Mountain Valley Station (13.98°S, 133.18°E); NTM R35680, Kakadu National Park (13.86°S, 132.98°E); NTM R35753, Oenpelli Reservoir (12.38°S, 133.07°E); QM J83987–8, Kolorbidahdah (12.65°S, 134.29°E).

Oedura marmorata
   Northern Territory: NTM R13295, Victoria River Gregory National Park (15.94°S, 130.50°E); NTM R19029–31, North Marchinbar Island (11.28°S, 136.63°E); NTM R21895, Low Hill, Roper River (14.65°S, 134.35°E); NTM R22444, Limmen Gate National Park (15.78°S, 135.33°E); NTM R33814, Bauhinia Downs Station (15.93°S, 135.32°E); NTM R36709, Fish River Station (14.07°S, 130.79°E); NTM R36746, Wongalara (14.13°S, 134.34°E).

Oedura murrumanu
   Western Australia: WAM R173368 (holotype), WAM R173370, NMV D76948 (paratypes), Oscar Range, Western Australia (17.9166°S, 125.3024°E); NMV D77002, NMV D76947, WAM R173369 (paratypes), Oscar Range (17.9125°S, 125.2827°E).