Taxonomic assessment of two pygopodoid gecko subspecies from Western Australia

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Taxonomic assessment of two pygopodoid gecko subspecies from Western Australia

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Abstract Subspecies designations for herpetofauna in Western Australia were largely coined in the 20th century where rigorous evolutionary concepts to species were not consistently applied. Rather, subspecies tended to designate geographic populations of similar-looking taxa to nominate forms, usually differing in size, pattern or colour and, at best, a few scalation differences. Here we re-evaluate two pygopodoid taxa from Western Australia using a combination of published and original genetic data coupled with a reassessment of morphology. We review these differences in light of an integrative taxonomic approach that looks to find multiple independent lines of evidence to establish the evolutionary independence of populations. For the pygopod species *Pletholax gracilis*, we found consistent diagnostic characters (e.g. body size, visibility of ear opening, scalation) and a deep genetic divergence between the two subspecies. We therefore raise each subspecies to full species: *P. gracilis* and *P. edelensis*. The two subspecies of the carphodactylid gecko *Nephrurus wheeleri* were also assessed, and we found strong genetic and morphological evidence (e.g. body size, scalation, pattern) to raise these to full species: *N. wheeleri* and *N. cinctus*. By revisiting Storr's morphological insights and newly acquired genetic evidence, in addition to a thorough re-examination of morphological traits, our study provides a robust foundation to raise Storr's morphological subspecies into full species based upon multiple lines of evidence. Such an approach applied to other subspecies in the Australian herpetofauna also may result in revised taxonomies.

Keywords Australia; legless lizard; mitochondrial DNA; *Nephrurus wheeleri*; *Pletholax gracilis*

Introduction

South-western Australia is home to many endemic lizard species (Edwards et al., 2012; Rix et al., 2015), including a disproportionate number of pygopod (legless geckos: Pygopodidae) species as well as other carphodactylid and diplodactylid gekkotan species (e.g. Bush et al., 2007). Together, all three Gondwanan families form Pygopodoidea (Vidal and Hedges, 2009; Brennan and Oliver, 2017). Historically, many species from south-western Australia were described from early collecting efforts by English, French, Dutch and German naturalists in the 18th and 19th centuries (Cogger, 1993). In the mid to late 20th century, Glen Storr of the Western Australia Museum (WAM) described many species and subspecies of reptiles from Western Australia. Of these taxa, we focus attention here on two species, each with a subspecies added by Storr. As in other works by Storr, his descriptions of subspecies were extremely brief and relied heavily on pattern. Importance was placed on apparent geographic breaks in distributions that, in hindsight, may have been the result of gaps in sampling effort reflected in the early collections rather than disjunct populations. In addition, specimens of the new subspecies were usually few in number compared to present day numbers of specimens in museum collections. Storr never articulated a species or subspecies concept he was working from in his brief papers, but we can surmise that erection of a subspecies, rather than describing a new species, was based on a qualitative assessment of morphological divergence, which was in keeping with current 20th century ideas on taxonomy.

In this paper, we assess the taxonomic status of subspecies of *Pletholax gracilis* Cope, 1864 and *Nephrurus wheeleri* Loveridge, 1932 (Fig. 1). The *Pletholax* species is a pygopod (family Pygopodidae) and is endemic to south-western Australia. The legless gecko subspecies *Pletholax gracilis edelensis* Storr, 1978 occurs in the Shark Bay area and Storr based his description on five specimens that were available at the time. In contrast, the carphodatylid gecko subspecies *Nephrurus wheeleri cinctus* Storr, 1963 was based on a larger series of specimens (N = 20), and effectively divided the known range into a southern subspecies (type: Murchison region) and northern subspecies (*cinctus*: northern Gascoyne and southern Pilbara regions) (Fig. 2).

At the time of Storr's descriptions, molecular genetic evidence was not widely available. In this study, however, we evaluate recently published genetic data for *N. wheeleri*, and present original data for *P. gracilis*. Furthermore, we carried out a detailed morphological assessment with larger series of better preserved specimens, including consulting all available types at the WAM. We resolve the taxonomy of these taxa by leaving no subspecies extant by raising to full species *Pletholax edelensis* and *Nephrurus cinctus*.

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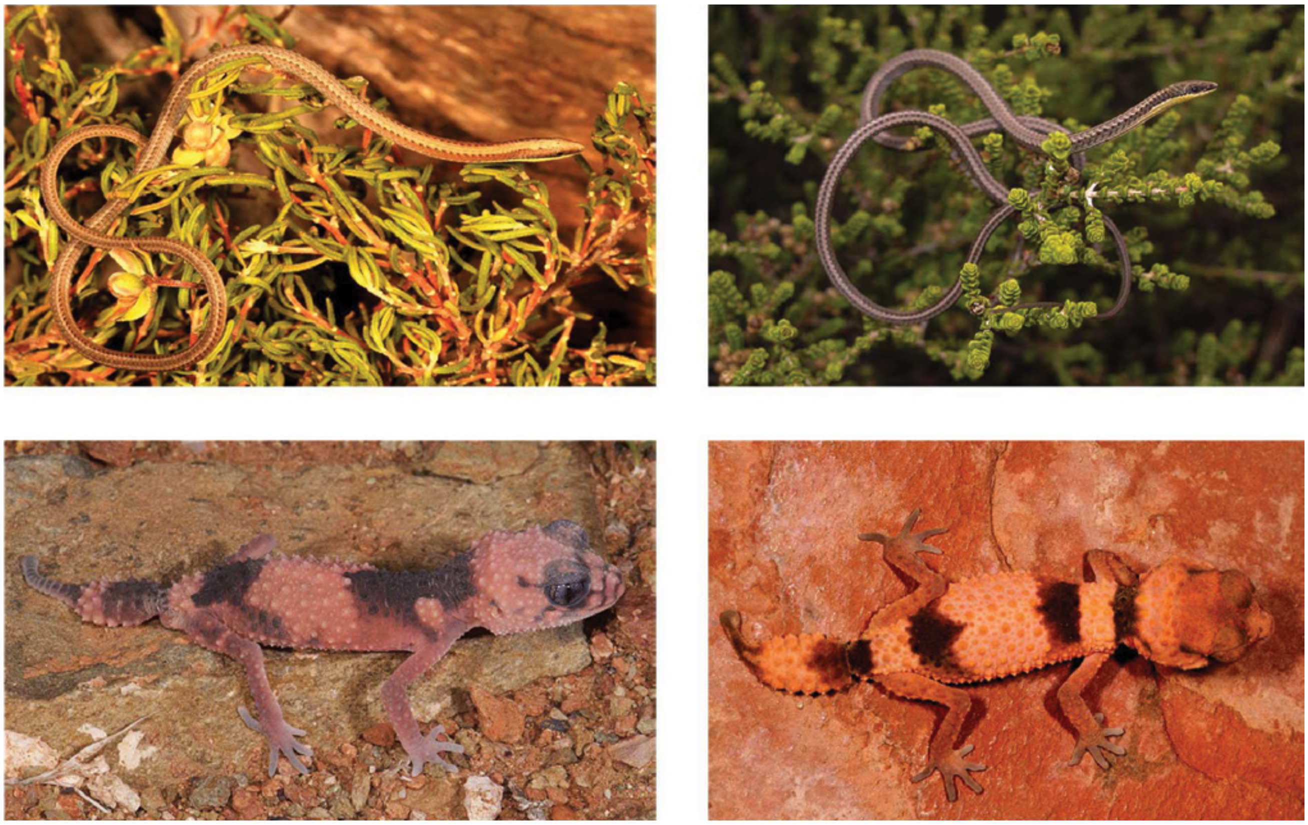


Figure 1. Photos in life of taxa evaluated here. Top row – *Pletholax gracilis* (left; photo credit – R.J. Ellis); *Pletholax edelensis* (right; R. Lloyd). Bottom row – *Nephrurus wheeleri* (left; S. MacDonald); *Nephrurus cinctus* (right; R.J. Ellis).

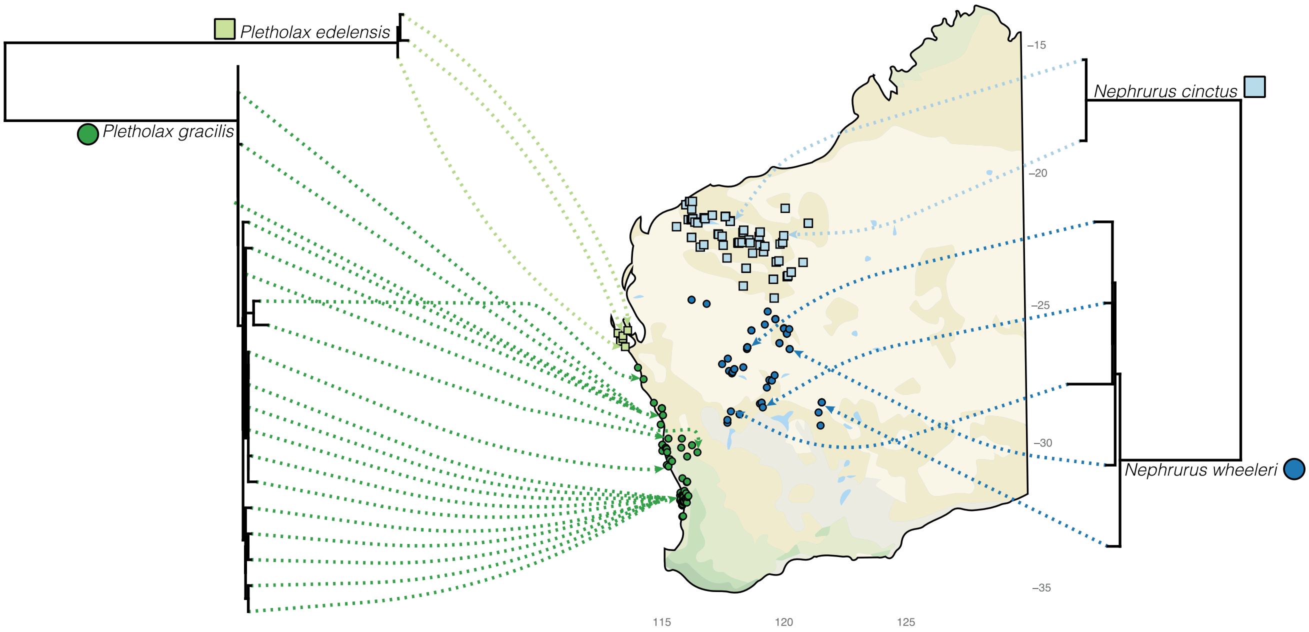


Figure 2. Distribution of *Pletholax gracilis* and *Nephrurus wheeleri* in Western Australia. Arrows point to where samples were drawn from. See Figs. 7 and 8 for more detailed phylograms.

Materials and methods

Taxonomic concepts and approaches

Overall, our approach was to investigate the subspecies designation, and to either elevate to full species or synonymise based on a thorough re-examination of morphological and genetic evidence. The category of subspecies in herpetological taxonomy usually tends to denote a morphologically distinct population and was generally based on a qualitative appraisal (Torstrom et al., 2014; see also Zink, 2004). However, with the insights from modern genetic techniques to examine evolutionary history, many subspecies in herpetology are being lost through elevation or synonymy (Torstrom et al., 2014). Furthermore, recent research is opting not to denote subspecies, as it is a vague and hard to define concept (cf. Couper and Hoskin [2013] vs. Hoskin [2019]). Compared to earlier centuries, very few subspecies are now coined, especially in studies using molecular genetic techniques (e.g. Couper and Hoskin, 2013). Owing to the frequently vague concept of subspecies, modern classifications will be most beneficial to users of taxonomy such as ecologists and conservation planners if taxonomic designations are underpinned by multiple lines of evidence (Isaac et al., 2004; Padial et al., 2010).

The operational approach to recognising species we apply herein is largely that of Padial et al. (2010)'s "integrative taxonomy" (see also Dayrat, 2005; De Queiroz, 2007; but see Valdecasas et al., 2008). For elevating subspecies to full species, we looked for a congruence of morphological (including body size, scalation, pattern and colouration) and especially genetic divergences. If the subspecies are actually isolated from each other, then the lineages should accumulate morphological differences in at least some of these characters. Cryptic species, however, possess similar morphologies despite quite deep genetic divergences, especially in highly conserved groups such as geckos (Oliver et al., 2009, 2012, 2019; Doughty et al., 2018a, b; Kealley et al., 2018). For a subspecies to be synonymised, then either little or no morphological differences occur between subspecies and additionally no species-level (relative to other congeneric pairs) genetic divergences are found. If two populations differ by only a single morphological character and lack molecular genetic differences, then we see little utility in continuing to recognise subspecies status in such cases (see Torstrom et al., 2014).

This is a useful methodology to take when assessing the subspecies pairs treated herein, given available data on distribution, morphology and genetics. The *Pletholax* subspecies are widely separated (~400 km) with no intervening populations, whereas the *Nephrurus* subspecies are separated by 85 km. However, there is the possible exception of an isolated population that shows features of both subspecies near Mt Augustus (the north-western dots in the Fig. 2, below), indicating a possible hybrid population. Alternatively, this region may be poorly sampled with *N. w. wheeleri* the likely taxon in this region based on the morphology of these two specimens. In the taxa considered here, genetic divergences were strong, i.e. in line with species differences elsewhere in the phylogram, which we deem to meet the criteria for recognising both subspecies as full species.

Molecular sampling and analyses

Genetic data were generated for this study or collected from GenBank based on previous studies of pygopodoid geckos (Jennings et al., 2003; Oliver and Bauer, 2011; Brennan and Oliver, 2017). Molecular sampling of *Nephrurus* includes five *N. wheeleri wheeleri* and two *N. wheeleri cinctus*. Molecular sampling of *Pletholax* includes 22 *P. gracilis gracilis* and three *P. gracilis edelensis*. New genetic material was extracted from ethanol-preserved liver samples using a traditional "salting-out" method, amplified using GoTaq and primers listed in the supplemental material, and sequenced on an ABI 3130. Molecular data and alignments of *Nephrurus* and associated carphodactylid outgroups follows Oliver and Bauer (2011) and includes the mitochondrial locus *ND2* (1087 bp), and the nuclear loci *RAG-1* (1071 bp) and *c-mos* (384 bp). Molecular data and alignments of *Pletholax* and associated pygopodid outgroups includes the mitochondrial locus *ND2* (1042 bp) and the trailing tRNAs (TRP, ALA), and nuclear loci *PRLR* (572 bp) and *PTPN12* (801 bp). Sequences were aligned using MAFFT and inspected by eye for consistency. We used the maximum likelihood method IQ-TREE (Nguyen et al., 2015) to estimate phylogenies, with sequence data partitioned by locus, allowing IQ-TREE to automatically choose the most appropriate model of molecular evolution per partition (--nt AUTO), and obtained branch support values using the ultrafast bootstrap (Hoang et al., 2018) (--bb 1000).

Morphology

We examined 25 *N. wheeleri* and 29 *P. gracilis* specimens in the collections of the Western Australian Museum (WAM) (Appendix 1). Table 1 presents the morphological variables assessed. To produce homogeneous samples, we measured adult specimens only: >60 mm SVL for the pygopod taxa and >70 mm SVL for *Nephrurus*. Measurements were made with an electronic calliper to the nearest 0.1 mm for SVL, and to nearest whole mm for tail length (TailL) using a ruler. We measured approximately 10–20 individuals from each genetic lineage (see Results, below), depending on the availability of specimens. For *N. wheeleri* we measured the limbs using electronic callipers and assessed the density of tubercles over the body visually.

Abbreviations: Australian Museum, Sydney (AMS); Northern Territory Museum and Art Gallery (NTM); South Australian Museum, Adelaide (SAMA); Naturalis Biodiversity Center, Leiden (RMNH).

Results

Morphology

We report morphological differences under the taxonomic accounts below, but provide a brief summary of our findings here and in Tables 1 and 2. For *P. gracilis*, a consistent difference in the ear opening was observed between subspecies, with *gracilis* possessing a visible opening, whereas in *edelensis* the opening was covered (Fig. 3). Furthermore, there were consistent differences in the number of supraciliaries, anterior temporals and the relative size of the posterior supraocular. The body size difference was also supported, with *edelensis* reaching a greater maximum SVL than *gracilis* (91 mm vs. 78 mm).

We consider Pletholax particularly narrow because its minimal width is exaggerated by its extremely long tail (up to 300% of the body length). Most other pygopod species are considerably broader/girthier (Pygopus > 5mm; Delma > 4 mm; Lialis > 5 mm), and those that are of similar width

Table 1. Summary of morphological characters of pygopodoid taxa. Figures represent means±S.D. (range). Abbreviations: snout-vent length – SVL; tail length (original tails only) – TailL; head length (measured obliquely from tip of snout to the skin covering the retroarticular process, mouth closed) – HeadL; head width (widest point posterior to eyes) – HeadW; head depth (deepest part behind eyes) – HeadD; supralabials (labial counted if bordering mouth and larger than background scales) – SupLab; infralabials – InfLab; superciliaries – Supercil; mid-body scale rows (encircling the body approximately midway between the head and cloaca) – MBSR; forearm length (elbow to base of wrist) – ArmL; crus length (knee to heel) – LegL; orbit length (widest distance inside bony orbit) – OrbitL; interorbital distance (measured at anterior edge) – IntOrb; nasal-eye distance (from posterior edge of nasal to anterior corner of eye) – NasEye; internasal distance (from medial edges of nasal) – IntNas; fourth finger length (from base of finger to base of claw) – 4FL; fourth toe length (from base of toe to base of claw) – 4TL.

A. *Pletholax* taxa.

	SVL	TailL	HeadL	Suplab	Inflab	Supercil	MBSR
gracilis N = 20	70.2±1.3 (60–78)	218±4 (192–242)	6.6±0.1 (5.5–7.3)	4.8±0.1 (3–5)	3.8±0.1 (3–4)	2.0±0 (2–2)	15.9±0.1 (15–17)
edenlensis N = 9	77.4±2.4 (68–91)	232±11 (197–302)	6.6±0.1 (6.1–7.3)	5.0±0 (5–5)	4.0±0 (4–4)	2.6±0.2 (2–3)	15.6±0.1 (15–16)

B. *Nephrurus* taxa.

	SVL	TrunkL	TailL	TailW	ArmL	LegL
wheeleri N = 13	81.5±2.0 (70.2–93.5)	37.8±1.7 (26.3–46.7)	27.1±1.1 (24.5–29.1)	9.2±0.4 (8.4–10.2)	12.2±0.3 (10.3–14.7)	14.7±0.4 (11.2–17.0)
cinctus N = 12	90.6±2.9 (73.3–102.1)	42.3±1.8 (32.3–49.8)	33.5±1.1 (28.8–38.9)	11.3±0.4 (9.9–13.2)	13.8±0.3 (12.6–16.0)	15.9±0.3 (14.4–17.8)

	HeadL	HeadW	HeadD	OrbitL	IntOrb	NasEye
wheeleri	24.9±0.5 (21.1–29.0)	18.8±0.4 (16.3–20.4)	10.7±0.2 (8.9–11.7)	6.6±0.2 (5.7–8.1)	8.4±0.4 (6.7–11.3)	5.8±0.2 (4.8–7.2)
cinctus	27.4±0.7 (23.7–31.1)	20.9±0.5 (17.6–23.0)	12.2±0.4 (10.1–14.2)	6.6±0.1 (6.0–7.4)	8.9±0.2 (7.6–10.1)	6.4±0.1 (5.5–7.1)

	IntNas	Suplab	Inflab	4FL	4TL
wheeleri	3.9±0.1 (3.3–4.9)	18.8±0.2 (18–20)	18.5±0.2 (18–20)	4.8±0.2 (4.2–6.7)	4.8±0.2 (4.0–6.2)
cinctus	4.3±0.1 (3.3–5.1)	19.3±0.3 (18–21)	18.5±0.3 (17–21)	5.0±0.1 (4.1–5.9)	5.1±0.1 (4.2–6.2)

Table 2. Summary of morphological differences between pygopodid subspecies considered herein.

Subspecies	Max. SVL	Pattern	Scalation
P. gracilis	78 mm	• Darker dorsal pattern • Subdued contrast between dorsal and lateral zones	• Ear opening visible • Posterior supraocular larger • Two supraciliaries • Three anterior temporals
P. edelensis	91 mm	• Lighter dorsal pattern • Greater contrast between dorsal and lateral zones	• Ear opening covered • Supraoculars similar size • Three supraciliaries • Two anterior temporals
N. wheeleri	93 mm	• Four dark bands from nape to tail (nape and axillary bands conjoined) • Dark maculations on snout and above mouth	• Fewer and less prominent tubercles
N. cinctus	102 mm	• Five dark bands from nape to tail • Absence of dark maculations	• More numerous and prominent tubercles

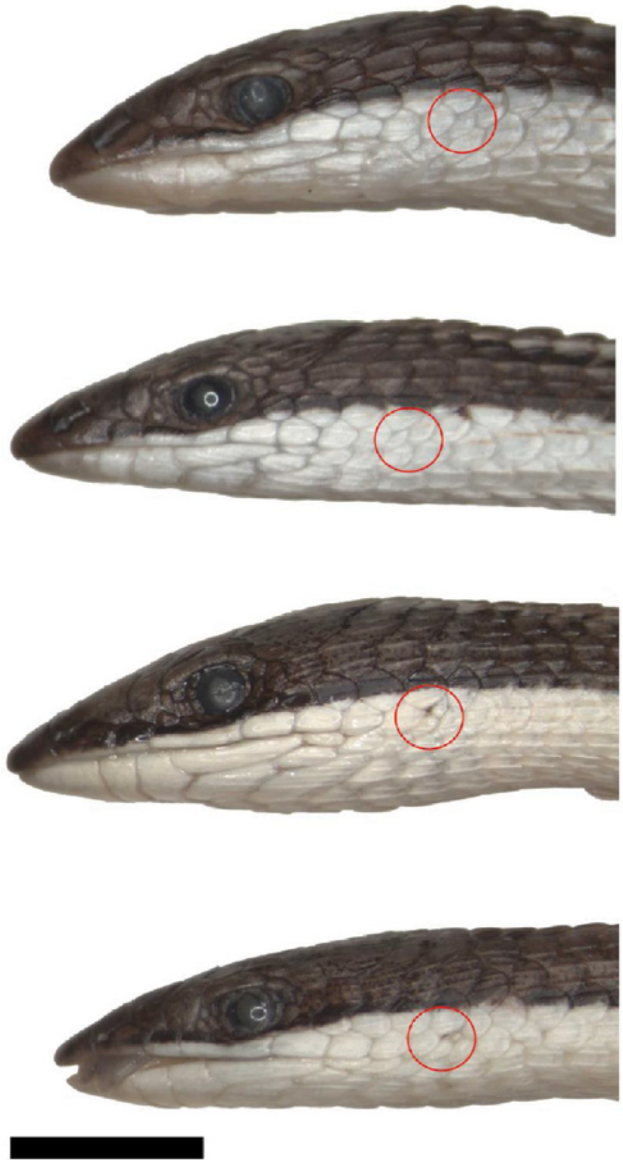


Figure 3. Ear opening comparison between *Pletholax*: upper two images: *P. gracilis*; lower two images: *P. edelensis*. Red circle indicates position of ear.

Figure 4. Chin scalation in *Nephrurus*: upper – *N. wheeleri* (WAM R97737); lower – *N. cinctus* (WAM R114268).

(Aprasia < 4 mm, some < 2 mm) generally have shorter tails, contributing to a more substantial overall appearance. Delma concinna, perhaps the most similar pygopod externally, is of similar proportions to the two Pletholax species, but is longer (both body and tail) and wider.

For *N. wheeleri*, maximum body size (Tables 1, 2) and density of tubercles were greater in *cinctus* compared to the nominate form, especially notable on the chin (Fig. 4). In addition, we also observed fewer dorsal bands (Figs. 1, 5) and darker facial maculations on the nominate form (Fig. 6), consistent with Storr's original description of subspecies.

Molecular phylogenetics

Phylogenetic analyses of multilocus datasets indicate considerable molecular distances among subspecies of both *N. wheeleri* and *P. gracilis*. *ND2* genetic distances between *P. gracilis gracilis* and *P. gracilis edelensis* (~15%) are more pronounced, and roughly equivalent to interspecific distances within *Delma* and *Aprasia*, two other pygopodid genera (9). *ND2* genetic distances between *N. wheeleri wheeleri* and *N. wheeleri cinctus* (~10%) are on par with (*N. amyae—N. asper—N. sheai*, 10%), greater than (*N. deleani—N. laevissimus*, 7.8%), or moderately less than (*N. levis—N. stellatus*, 17%) distances among other sister species pairs within *Nephrurus* (Figs. 8, 10).

Systematic conclusions

For the two subspecies of *Pletholax*, we found several morphological and genetic differences between the two widely separated populations. The genetic results indicated species-level divergences comparable to differences between other pygopod species (Fig. 7). The morphology mirrored these differences, with a difference in body size (Table 1), ear opening (Fig. 3), several scale traits and patterning. Applying the criteria of integrative taxonomy, the consistent differences in distribution, morphology and genetics all lead us to conclude that raising the subspecies to full species best reflects the evolutionary divergence and the morphological distinctiveness of the two groups (e.g., Padial et al. 2010; Hillis, 2019).

The two subspecies of *N. wheeleri* differed significantly genetically (Fig. 8, from Brennan and Oliver, 2017). In addition, we also found pronounced morphological differences in disparate characters. These included differences in body size (Table 1), scalation and patterning. For example, *N. w. wheeleri* had less pronounced tubercles on the head and dorsal surfaces than *N. w. cinctus*, and the size and number of tubercles on the chin was reduced in the nominate form (Fig. 4). Major dorsal pattern differences were conspicuous (Fig. 5), and consistent with Storr's original description, especially the separation of the wide anterior band in *N. w. wheeleri* into two narrower bands in *N. w. cinctus*. In addition, *N. w. wheeleri* specimens always possessed dark maculations on the labials, whereas in *N. w. cinctus* the dark maculations were usually absent (Fig. 6). Based on the consistent molecular genetic and morphological differences, we elevate *N. w. cinctus* to full species, *N. cinctus* which is consistent with an ethos of making integrative taxonomic decisions.

Taxonomy

Genus *Pletholax* Cope, 1864

Type species – *P. gracilis*, by monotypy.

Content: *Pletholax gracilis* (Schlegel), *Pletholax edelensis* Storr

Diagnosis. Extremely slender small pygopod species, distinguishable from all other genera by keeled scales completely encircling body and tail, including unenlarged ventral row.

Etymology. According to Storr et al. (1990): “Possibly based on Greek stem *pleth-* denoting fullness or completeness, in allusion to the strong keeling” (p. 126).

Pletholax gracilis (Schlegel, 1864)

West coast keeled legless geckos
Figures 1, 3

Type specimens. Holotype RMNH 3670 from ‘South West Australia’. No other collection details known.

Diagnosis. Distinguished from *P. edelensis* by presence of visible ear opening, smaller body size, posterior supraocular 1.5–2.0 times larger than anterior, two supraciliaries, three anterior temporals and darker dorsal pattern.

Description. A small (to 78 mm SVL), extremely narrow (~3 mm wide) species with tail 3 times as long as SVL (Table 1); masses ranged from 1.2g (~60 mm SVL; several individuals) to 2.7 g (90 mm SVL; WAM R120973) head narrow with long pointed snout; snout convex in lateral view, narrowing to a blunt tip; in dorsal view, sides of the snout straight-sided and tapering evenly to a blunt tip; brow protrudes slightly over eyes; small nostril located one-quarter along suture between supranasal and first labial; ear opening oblong and small (~0.1–0.2 mm in diameter), with posterior temporal scale (this scale with dark above and pale below) covering most of the larger ear opening, posterior to opening 3 very small scales; rostral scale large with straight to slightly concave dorsal edges; 1 pair of supranasals in contact; 1 pair of prefrontals in contact; 2 frontals; 1 pair of frontoparietals in contact; 2 parietals not in contact; 1 small interparietal; usually 5 (occasionally 4) supralabials; usually 4 (occasionally 3) infralabials; 1 supraloreal; 2 supraciliaries; 2 supraoculars; scales on the head heavily keeled, with up to 7 keels occurring over a single scale.

Neck is slightly more constricted than the widest part of the head (above the eyes); scales with 2 parallel keels; 15 or 16 scale rows at mid-body; dorsal scale counts numbering 58–62 rows from back of head to above cloaca; scales are slightly enlarged posterior to head to the nuchal region; scales similar in size along length of body until tail where they decrease in size; hind limb flaps represented by a single pointed scale; tail is long and cylindrical, tapering to a fine point.

Colouration. In life, dorsum light grey with dark dashed borders, often a darker vertebral line visible especially on tail; lateral surfaces dark grey to dark brown or rufous, extending from side of snout to tail with lower edge with dark dashed borders only on forebody; keels slightly darker than rest of scale, often forming additional fine dark lines; ventrolateral edge and ventrum pale grey; posterior supralabials, lower jaw, ventral sides of head and anterior ventrum usually bright yellow, dorsal dark and ventral yellow surfaces highly contrasting on head; top of head dark brown to grey; eyes jet black. In preservative, similar to life except yellow on anterior ventral surfaces fades to light grey and rufous colouration on sides less discernible. Some individuals varied in the thickness and solidity of the dark border between the dorsal and lateral zones, and also in the darkness of the thin line along the midline. In more recently-preserved individuals, a hint of yellow under the chin and anterior body was visible.

Habitat. White and grey sandplains vegetated with *Banksia* woodland and heath (from collector's notes and Shea and Peterson [1993]).

Ecology. Displays both burrowing or ‘sand-swimming’ behaviour, as well as possible climbing on to low vegetation (Shea and Peterson, 1993). Termites with occasional observations of nectar feeding have been reported (Ehmann [1992; Shea and Peterson [1993]; Bush et al. [2007]). Reproduction occurs in spring, with two eggs per clutch (Shea and Peterson, 1993).

Distribution. Western coast of south-western Australia (Fig. 1). The northernmost record is from Zuytdorp Nature Reserve (south-western section), then south along the coast to the Perth region. Occurrences are usually within 40 km from the coast, but occur as far inland as Martinjinni Nature Reserve near Dalwallinu (140 km inland). In the Perth region, many records from as far south as Thompsons Lake Nature Reserves, with outlying records from Gosnells, Talbot Road Reserve, Red Hill, Ellenbrook, Muchea and Joondalup.

Older records from within the Perth area may be from populations no longer extant, including Maylands, South Perth, East Victoria Park and Willetton. However, recent

Figure 5. Dorsal pattern variation in preserved specimens of *Nephrurus*: upper – *N. wheeleri*; lower – *N. cinctus*.

records from Bold Park indicate populations still can occur within the Perth urban area.

There are two historical records from south of the Perth-Fremantle area in the Australian Museum. According to OZCAM (ozcam.org.au; accessed August 2019), AMS R13815 and AMS R26628 with the localities of 'Mandurah near Pinjarra' and 'Mandurah near Pinjarrah [Pinjarra]', respectively, both collected by A. Robinson on 2 October 1950. No further specimens have been collected from this locality, indicating these populations are no longer extant or the collecting locations are possibly in error.

Conservation status. This species appears to be secure owing to its wide distribution in south-western Australia, including many reserves. See also Shea and Peterson (1993) for further comments.

Etymology. From the Latin *graci*, meaning 'slender', and *lis* for 'resembling', *gracilis* – slender-like, in allusion to its slender long body.

Pletholax edelensis Storr, 1978

Shark Bay keeled legless geckos
Figures 1, 3

Type specimens. Holotype WAM R54627, collected 4 km south of Useless Loop, Shark Bay, WA, Australia (26°10'S, 113°25'E) by G. Harold and M. Peterson on 24 August 1976. Paratypes: WAM R54755, 5 km S Useless Loop, WA, Australia; WAM R54814, WAM R54863, 4 km S Useless Loop, WA, Australia; WAM R55085, 10 km NW Useless Loop, WA, Australia.

Figure 6. Dark maculations on snout and labials of *Nephrurus*: upper – *N. wheeleri*; lower – *N. cinctus* (photos – R.J. Ellis) (uncollected specimens).

Diagnosis. Distinguished from *P. gracilis* by absence of externally visible ear opening, larger body size, supraoculars similar in size (i.e. posterior not much larger than anterior), three supraciliaries (formed by division of long anterior supraciliary), two anterior temporals and lighter dorsal pattern with greater contrast between dorsal and lateral zones.

Description. A small (to 91 mm SVL), extremely narrow (up to 4 mm wide) species with tail 3 times as long as SVL (Table 1); head narrow, long pointed snout; snout convex in lateral view, narrowing to a blunt tip; in dorsal view, snout sides straight coming to a gradual point; brow slightly protruding over eye; small nostril located one-quarter along suture between supranasal and first

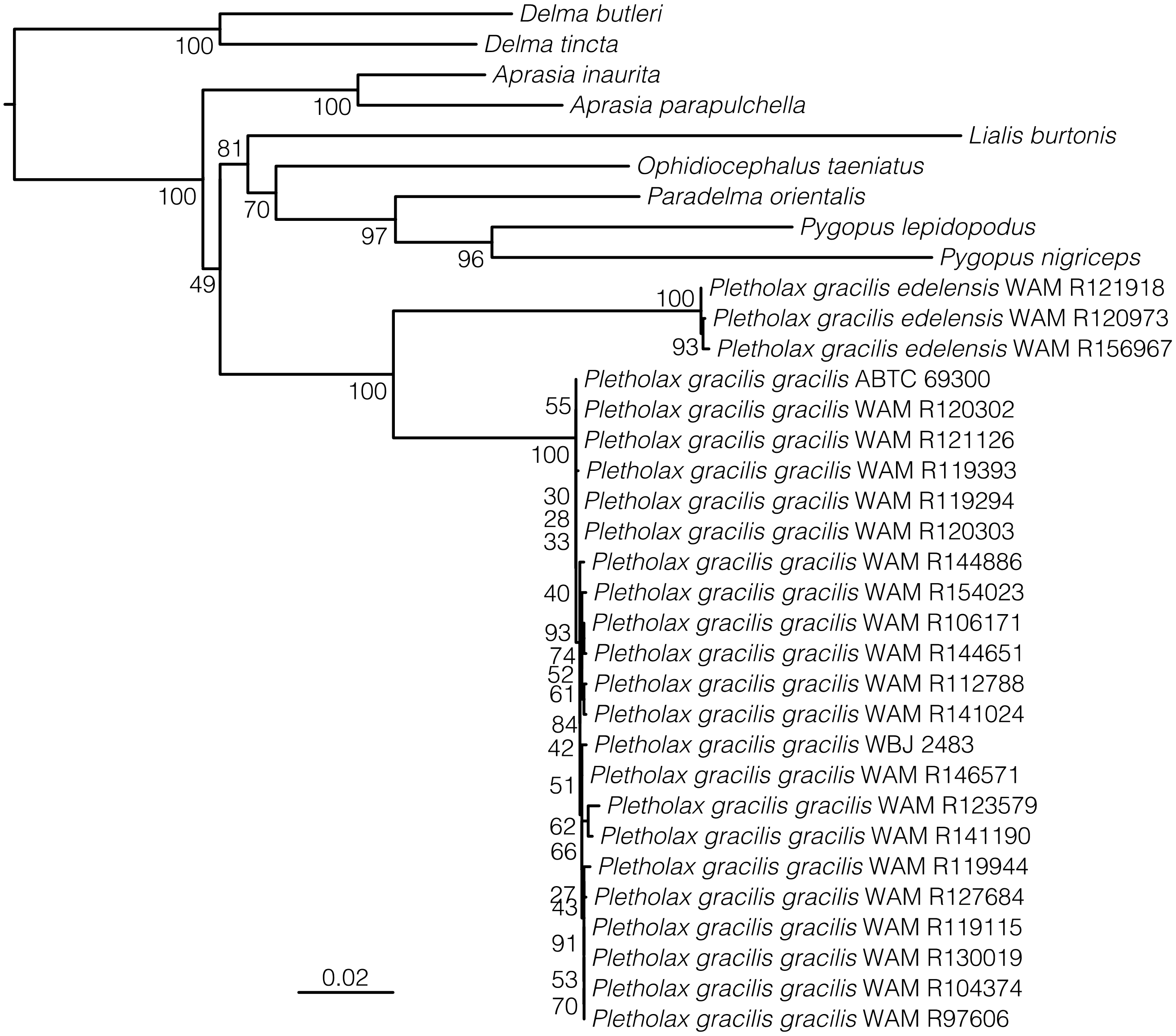


Figure 7. Multilocus phylogeny of the pygopod genus *Pletholax* indicates considerable molecular distances between *Pletholax* taxa.

labial; no ear opening; rostral scale large with slightly concave dorsal edges; 1 pair of supranasals in contact; 1 pair of prefrontals in contact; 2 frontals; 1 pair of frontoparietals in contact; 2 parietals not in contact; 1 small interparietal; 5 supralabials; 4 infralabials; 1 supraloreal; 2 supraciliaries; 2 supraoculars; scales on the head heavily keeled.

Neck slightly constricted; scales with 2 keels; 15 or 16 scale rows at mid-body; 60–65 dorsal scales from nape to above cloaca; scales increasing in size posterior to head then constant in size until decreasing along the length of the tail; hind limb flaps reduced to a single pointed scale; tail extremely long and tapering to a fine point.

Colouration. In life, dorsum pale grey to white with dark wavy borders, a dark vertebral line from head to tail; lateral surfaces dark grey or brown, extending from head to tail with lower edge with dark dashed border only on forebody; on dorsum, keels darker than rest of scale, forming fine dark lines along body; ventrolateral edge and ventrum pale grey, borders on ventral scales dark-edged forming irregular longitudinal lines on ventral surfaces, especially the tail; posterior supralabials, lower jaw, ventral sides of head and anterior ventrum dull yellow, dark dorsal and ventral yellow surfaces moderately contrasting on head; top of head brown, sides of head dark brown and extending on to lateral surfaces of forebody; eyes jet black. In preservative, similar to life except dull yellow on anterior ventral surfaces fades to medium grey. For colouration, the thickness of the dark border of the dorsal stripe was slightly variable, with most individuals with a thick border but some with thin, broken borders. The dark edges to the ventral scales resulted in either straight or wavy lines on the ventral surfaces.

Habitat. Occurring on white, grey, yellow or light brown sands or coastal dunes in the Shark Bay region. Associated vegetation includes *Acacia* shrubs, spinifex and low heaths (from collectors' notes and Shea and Peterson [1993]).

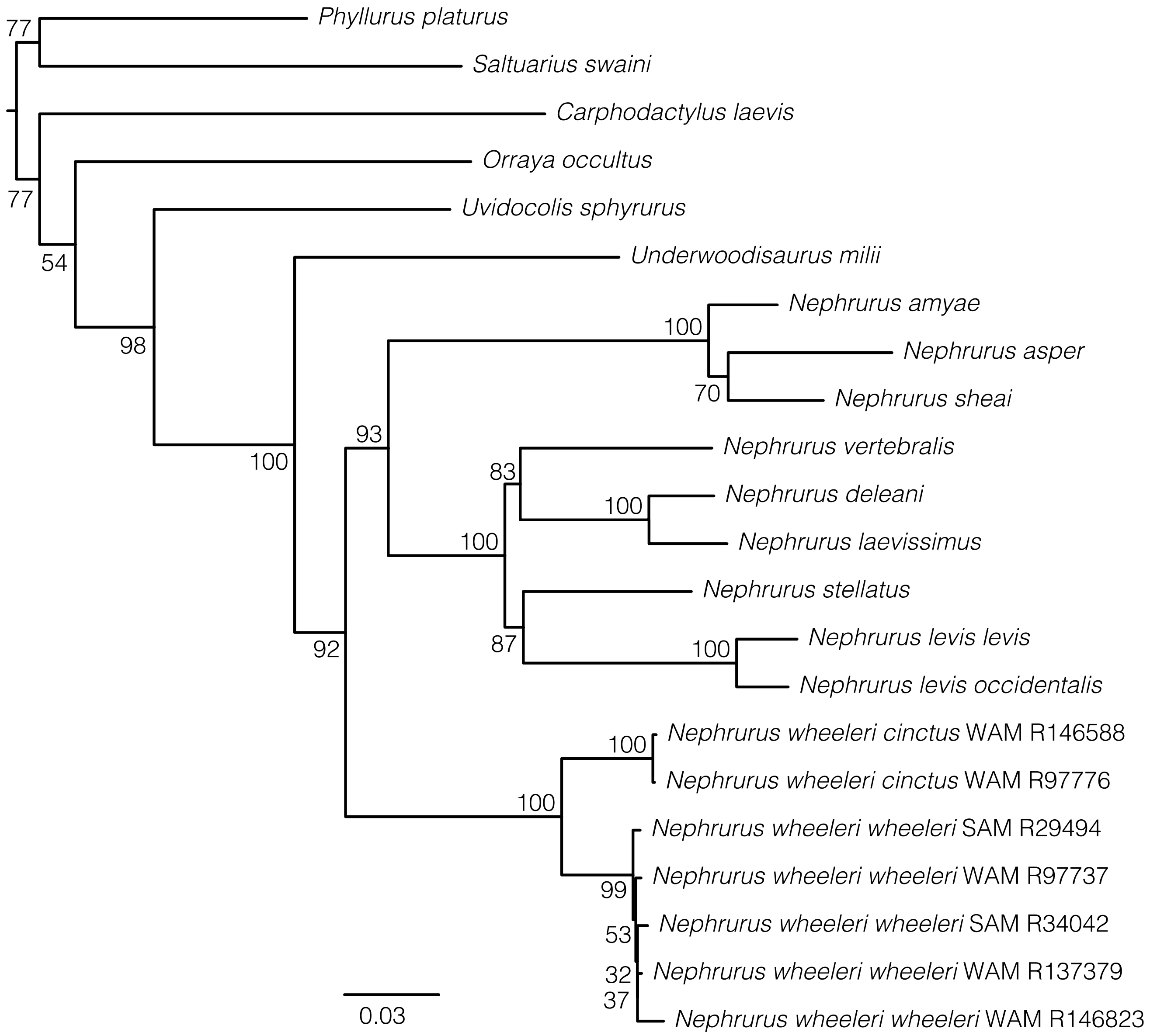


Figure 8. Multilocus phylogeny of the knob-tail gecko genus *Nephrurus* indicates considerable molecular distances between currently recognised subspecies of *Nephrurus wheeleri.*

Distribution. Restricted to the Shark Bay area on the western coast of Western Australia. Records from Edel Land, Peron Peninsula and Dirk Hartog Island (Fig. 2). The entire distribution calculated from a minimum polygon of known records is ~1500 km^2 (which also includes large areas of ocean). When *P. edelensis* was originally described, Storr reports its distribution as occurring 450 km north of Eneabba, the northernmost record of *P. gracilis* at that time. Owing to subsequent collecting in the intervening areas, this separation has been reduced to only 100 km.

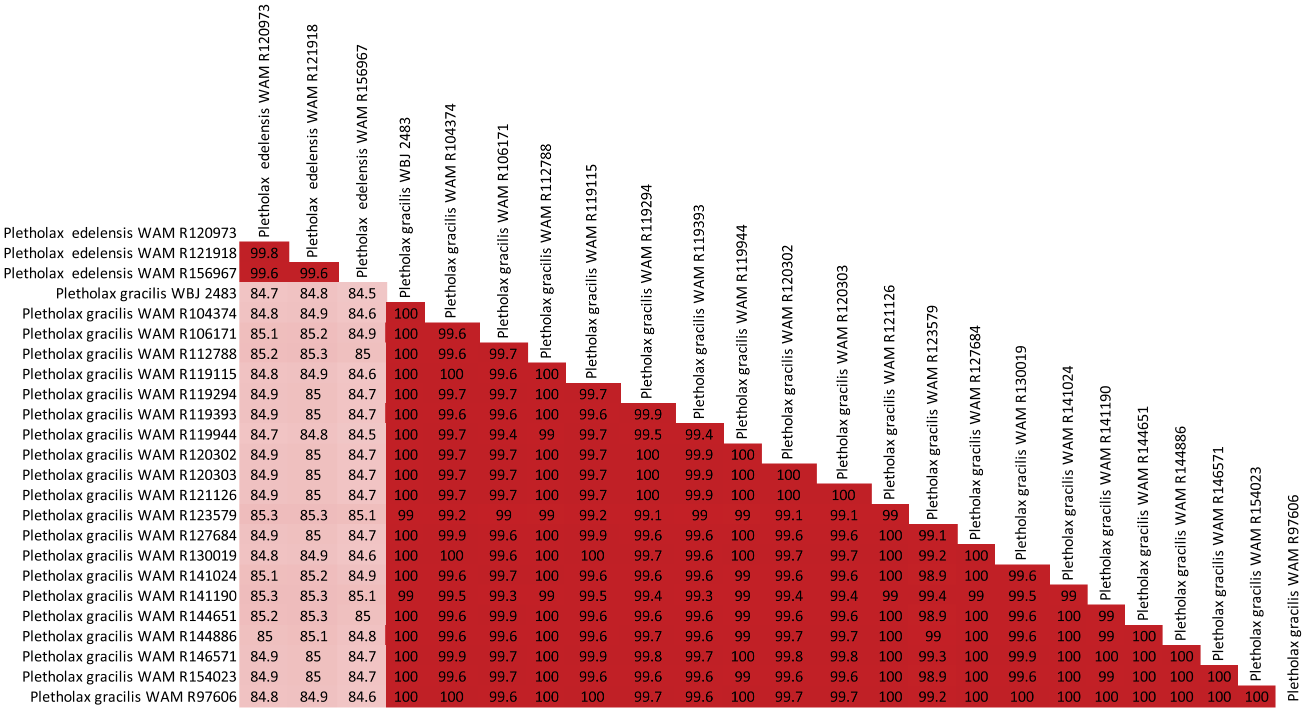
Conservation status. Although possessing a smaller distribution than *P. gracilis*, this species appears to be secure owing to lack of development in the area where it occurs. See also Shea and Peterson (1993) for further comments.

Etymology. In reference to the type locality, Edel Land, where this species occurs and where the first specimens for Storr's description were collected. The *edel-* refers to Edel Land, which means 'noble land' in Dutch (and German), and the suffix *-ensis* is Latin for 'from there'.

Genus Nephrurus Günther, 1876

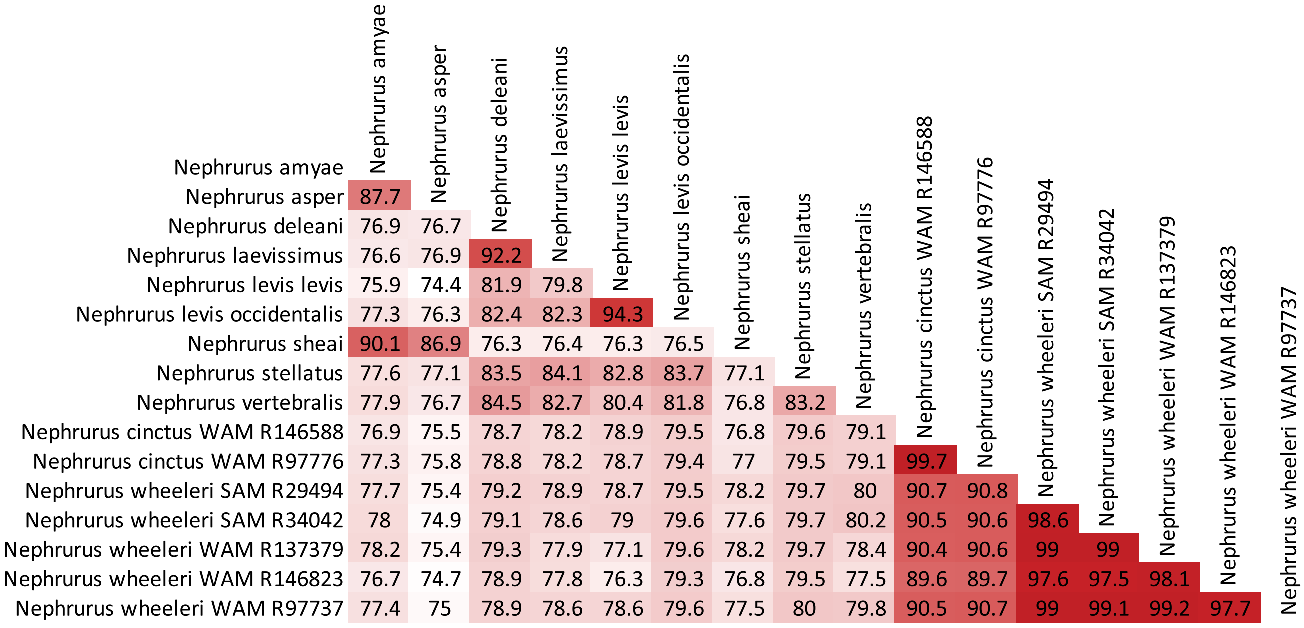
Type species – *N. asper*, by monotypy.

Diagnosis. From Oliver and Bauer (2012, p. 671): A genus of moderately to very large (adult SVL 80–137 mm) carphodactylid geckos; ventral toe scalation spinose; toes relatively short and rounded in cross section; phalangeal formula reduced (2.3.4.4.3/2.3.4.4.4 or 2.3.3.3.3/2.3.3.3.3); anterior loreals much smaller than posterior loreals, labial scales only slightly larger than neighbouring scales, 25–26 presacral vertebrae, original tail highly variable, ranging from extremely vestigal to relatively large and fat with 20–32 postsacral vertebrae, post pygal pleurapophysis absent or reduced, but always terminating in a small knob.



	Pletholax edelensis WAM R120973	Pletholax edelensis WAM R121918	Pletholax edelensis WAM R156967	Pletholax gracilis WBJ 2483	Pletholax gracilis WAM R104374	Pletholax gracilis WAM R106171	Pletholax gracilis WAM R112788	Pletholax gracilis WAM R119115	Pletholax gracilis WAM R119294	Pletholax gracilis WAM R119393	Pletholax gracilis WAM R119944	Pletholax gracilis WAM R120302	Pletholax gracilis WAM R120303	Pletholax gracilis WAM R121126	Pletholax gracilis WAM R123579	Pletholax gracilis WAM R127684	Pletholax gracilis WAM R130019	Pletholax gracilis WAM R141024	Pletholax gracilis WAM R141190	Pletholax gracilis WAM R144651	Pletholax gracilis WAM R144886	Pletholax gracilis WAM R146571	Pletholax gracilis WAM R154023	Pletholax gracilis WAM R97606
Pletholax edelensis WAM R120973																								
Pletholax edelensis WAM R121918	99.8																							
Pletholax edelensis WAM R156967	99.6	99.6																						
Pletholax gracilis WBJ 2483	84.7	84.8	84.5																					
Pletholax gracilis WAM R104374	84.8	84.9	84.6	100																				
Pletholax gracilis WAM R106171	85.1	85.2	84.9	100	99.6																			
Pletholax gracilis WAM R112788	85.2	85.3	85	100	99.6	99.7																		
Pletholax gracilis WAM R119115	84.8	84.9	84.6	100	100	99.6	100																	
Pletholax gracilis WAM R119294	84.9	85	84.7	100	99.7	99.7	100	99.7																
Pletholax gracilis WAM R119393	84.9	85	84.7	100	99.6	99.6	100	99.6	99.9															
Pletholax gracilis WAM R119944	84.7	84.8	84.5	100	99.7	99.4	99	99.7	99.5	99.4														
Pletholax gracilis WAM R120302	84.9	85	84.7	100	99.7	99.7	100	99.7	100	99.9	100													
Pletholax gracilis WAM R120303	84.9	85	84.7	100	99.7	99.7	100	99.7	100	99.9	100	100												
Pletholax gracilis WAM R121126	84.9	85	84.7	100	99.7	99.7	100	99.7	100	99.9	100	100	100											
Pletholax gracilis WAM R123579	85.3	85.3	85.1	99	99.2	99	99	99.2	99.1	99	99	99.1	99.1	99										
Pletholax gracilis WAM R127684	84.9	85	84.7	100	99.9	99.6	100	99.9	99.6	99.6	100	99.6	99.6	100	99.1									
Pletholax gracilis WAM R130019	84.8	84.9	84.6	100	100	99.6	100	100	99.7	99.6	100	99.7	99.7	100	99.2	100								
Pletholax gracilis WAM R141024	85.1	85.2	84.9	100	99.6	99.7	100	99.6	99.6	99.6	99	99.6	99.6	100	98.9	100	99.6							
Pletholax gracilis WAM R141190	85.3	85.3	85.1	99	99.5	99.3	99	99.5	99.4	99.3	99	99.4	99.4	99	99.4	99	99.5	99						
Pletholax gracilis WAM R144651	85.2	85.3	85	100	99.6	99.9	100	99.6	99.6	99.6	99	99.6	99.6	100	98.9	100	99.6	100	99					
Pletholax gracilis WAM R144886	85	85.1	84.8	100	99.6	99.6	100	99.6	99.7	99.6	99	99.7	99.7	100	99	100	99.6	100	99	100				
Pletholax gracilis WAM R146571	84.9	85	84.7	100	99.9	99.7	100	99.9	99.8	99.7	100	99.8	99.8	100	99.3	100	99.9	100	100	100	100			
Pletholax gracilis WAM R154023	84.9	85	84.7	100	99.6	99.7	100	99.6	99.6	99.6	99	99.6	99.6	100	98.9	100	99.6	100	99	100	100	100		
Pletholax gracilis WAM R97606	84.8	84.9	84.6	100	100	99.6	100	100	99.7	99.6	100	99.7	99.7	100	99.2	100	100	100	100	100	100	100	100	

Figure 9. Pairwise genetic distance matrix of the mitochondrial locus *ND2* for the genus *Pletholax*. Values indicate percent identity among samples.



	Nephrurus amyae	Nephrurus asper	Nephrurus deleani	Nephrurus laevissimus	Nephrurus levis levis	Nephrurus levis occidentalis	Nephrurus sheai	Nephrurus stellatus	Nephrurus vertebralis	Nephrurus cinctus WAM R146588	Nephrurus cinctus WAM R97776	Nephrurus wheeleri SAM R29494	Nephrurus wheeleri SAM R34042	Nephrurus wheeleri WAM R137379	Nephrurus wheeleri WAM R146823	Nephrurus wheeleri WAM R97737
Nephrurus amyae																
Nephrurus asper	87.7															
Nephrurus deleani	76.9	76.7														
Nephrurus laevissimus	76.6	76.9	92.2													
Nephrurus levis levis	75.9	74.4	81.9	79.8												
Nephrurus levis occidentalis	77.3	76.3	82.4	82.3	94.3											
Nephrurus sheai	90.1	86.9	76.3	76.4	76.3	76.5										
Nephrurus stellatus	77.6	77.1	83.5	84.1	82.8	83.7	77.1									
Nephrurus vertebralis	77.9	76.7	84.5	82.7	80.4	81.8	76.8	83.2								
Nephrurus cinctus WAM R146588	76.9	75.5	78.7	78.2	78.9	79.5	76.8	79.6	79.1							
Nephrurus cinctus WAM R97776	77.3	75.8	78.8	78.2	78.7	79.4	77	79.5	79.1	99.7						
Nephrurus wheeleri SAM R29494	77.7	75.4	79.2	78.9	78.7	79.5	78.2	79.7	80	90.7	90.8					
Nephrurus wheeleri SAM R34042	78	74.9	79.1	78.6	79	79.6	77.6	79.7	80.2	90.5	90.6	98.6				
Nephrurus wheeleri WAM R137379	78.2	75.4	79.3	77.9	77.1	79.6	78.2	79.7	78.4	90.4	90.6	99	99			
Nephrurus wheeleri WAM R146823	76.7	74.7	78.9	77.8	76.3	79.3	76.8	79.5	77.5	89.6	89.7	97.6	97.5	98.1		
Nephrurus wheeleri WAM R97737	77.4	75	78.9	78.6	78.6	79.6	77.5	80	79.8	90.5	90.7	99	99.1	99.2	97.7	

Figure 10. Pairwise genetic distance matrix of the mitochondrial locus *ND2* for the genus *Nephrurus*. Values indicate percent identity among samples.

Etymology. From the Greek word *nephros*, meaning kidney, and *ura* referring to the tail (Storr et al., 1990).

Nephrurus wheeleri (Loveridge, 1932)

Southern banded knob-tailed geckos
Figures 1, 4–6

Type specimens. Holotype MCZ 32950, from Yandil, 30 mi NE of Wiluna, WA, Australia. Paratype WAM R4459 (formerly MCZ 32955), "Yandil, thirty miles [48 km] northwest of Wiluna, WA", Australia [26°22'S, 119°49'E], A.G. Paterson, September 1931.

Diagnosis. Differs from all other *Nephrurus* by a combination of enlarged tubercles scattered over body, tubercles surrounded by enlarged scales, tail short, broad and flattened with deep ridges, narrowing to terminate in a small knob, four dark bands on the nape, dorsum and tail and background colour dull reddish brown. Further differs from *N. cinctus* by smaller body size, fewer and less prominent tubercles, especially evident on the gular region, and dark maculations on the snout and above mouth.

Description. A large (to 93.5 mm SVL) carphodactylid gecko with large head, moderately long slender limbs and digits and short wide tail terminating in a small knob (Table 1). Large and triangular head, sides slightly convex when viewed dorsally, snout convex in lateral view, head nearly as wide as body, slightly depressed, terminating in a relatively blunt snout; very large and protruding eyes with overhanging supraciliary ridge, inner edge of eye on top of head with row of ~12 enlarged tubercles, 2–4 scales separating innermost enlarged tubercles; scales on head flat and juxtaposed, reduced in size in loreal region; enlarged tubercles on canthus above nostril, eyelids, superciliary ridge and scattered across crown and post orbital area; dorsal skin on head not loose; nostrils directed dorsally and posteriorly; ear opening elongate, 4 times high as wide; supralabials and infralabials slightly enlarged relative to neighbouring scales, infralabials and supralabials have a slightly protruding transverse keel, first largest, then gradually decreasing along jaw; two adjacent rostral scales, slightly taller than first labial; mental shallow, approximately two times wider than deep; lower jaw region a mixture of small scales and enlarged tubercles, post-mental region with enlarged scales, gular region with granular scales with widely scattered slightly enlarged tubercles; narrow neck, approximately half to two-thirds the width of head. Males (max SVL – 80.2 mm) smaller than females (93.5 mm).

Dorsum covered in fine smooth scales with scattered greatly enlarged tubercles encircled by slightly enlarged scales that border the enlarged tubercles; in addition, there are also scattered moderately enlarged tubercles (not encircled by large scales) on the dorsum; on flanks, a higher density of greatly enlarged tubercles and absence or low density of moderately enlarged single tubercles; tubercles coned-shaped and striated/ridged; ventral surface covered with flat circular juxtaposed scales, scales on venter similar in size to small scales on dorsum; scales below neck and gular region small.

Slender and moderately long limbs, dorsal surface of limbs with enlarged tubercles, ventral surfaces with greatly reduced density and size of tubercles, greatest density near body; pentadactyl; moderate fingers and toes, terminating in a sharp claw, surrounded by small imbricate scales, subdigital lamellae not enlarged; claw surrounded by sheath formed by a ring of enlarged scales.

Original tail short, proximal portion flattened, twice as long as broad, sides in dorsal view slightly convex, tail with 6–8 transverse segments, segments with transverse row of enlarged tubercles, lateral edge of tail with row of enlarged protruding tubercles, distal portion narrow and cylindrical with 7–8 segments with very fine scales, terminating in a slightly enlarged knob; no pre-cloacal or femoral pores; in males, 5 or 6 enlarged cloacal spurs to either side of base of tail, reduced in females; hemipenes strongly bifid.

Colouration. Background colour light brown with reddish hues, four dark brown bands from nape to tail; above arm large dark band from nape to ¼ to ⅓ the length of between arms and legs, hiatus of dark brown pigment above arms on sides; dark brown band on posterior dorsum from mid interlimb length to anterior edge of leg, on flanks often anterior projection of band; dark brown band from posterior of limbs covering ½ to ⅔ of tail; distal portion of tail dark brown, occasionally slightly interrupted; head mottled brown with high variation; dark brown maculations on snout and labials; limbs medium brown; ventrum pale off white.

Habitat. Prefers stony soils around granite outcrops and breakaway country. Usually found active at night in rocky areas with rubble on the ground. During the day, can be found sheltering under tin or beneath pieces of iron on the soil.

Distribution. Murchison Goldfield, Western Australia (Fig. 1). Occurs from Kumarina in the north of its distribution, south-west to Weld Range, extending south to near Paynes Find. East to Kookynie, Leonara and surrounds, and extending up to Wiluna. Isolated records from near Mt Augustus, with individuals showing increased disruption to the nuchal-dorsum band (see Fig. 6, WAM R97739) and also a typical *N. cinctus* (see below).

Conservation status. This species appears to be secure and of 'Least Concern' according to IUCN criteria, owing to its broad distribution and occurrence in several reserves.

Etymology. Named after the leader of the Harvard Australian expedition that collected this species, William M. Wheeler.

***Nephrurus cinctus* (Storr, 1963)**

Northern banded knob-tailed geckos
Figure 1, 4–6

Type specimens. Holotype WAM R4284, male, "Tambrey, WA (21°38'S, 117°37'E)", Australia, collected by O. Cusack, 1931. Paratypes: WAM R1009, Jigalong, WA, Australia; R2714–16, R4285, R5271, R8099, Tambrey, WA, Australia; R12275–76, R12283*, R12284–86, Mundiwindi, WA, Australia; R13114, R14600, Mardie, WA, Australia; R13840, Roy Hill, WA, Australia; R14831–32, 14 mi. [22.5 km] SW Mundiwindi, WA, Australia. (* - lost; Ellis et al., 2018.)

Diagnosis. Differs from all other *Nephrurus* by a combination of enlarged tubercles scattered over body, tubercles surrounded by enlarged scales, tail short, broad and flattened with deep ridges, narrowing to terminate in a small knob, five dark bands on the nape, dorsum and tail and background colour dull reddish brown. Further differs from *N. wheeleri* by larger body size, larger and more numerous tubercles, especially evident on the gular region, and absence of dark maculations on the snout and above mouth.

Description. A large (to 102.1 mm SVL) carphodactylid gecko with large head, moderately long slender limbs and digits, and short wide tail terminating in a small knob (Table 1). Large and triangular head, sides slightly convex when viewed dorsally, snout convex in lateral view, head nearly as wide as body, slightly depressed, terminating in a relatively blunt snout; very large and protruding eyes with overhanging supraciliary ridge, inner edge of eye on top of head with row of ~12 enlarged tubercles, 2–4 scales separating innermost enlarged tubercles; scales on head flat and juxtaposed, reduced in size in loreal region;

enlarged tubercles on canthus above nostril and superciliary ridge, scattered across crown, eyelids and post orbital area; dorsal skin on head not loose; nostrils directed dorsally and posteriorly; ear opening elongate, 4 times high as wide; supralabials and infralabials slightly enlarged relative to neighbouring scales, infralabials and supralabials have a slightly protruding transverse keel, first largest, then gradually decreasing along jaw; two adjacent rostral scales, slightly taller than first labial; mental shallow, approximately two times wider than deep; lower jaw region a mixture of small scales and enlarged tubercles, post-mental region with enlarged scales, gular region with granular scales with densely scattered enlarged tubercles; narrow neck, approximately half to two-thirds the width of head. Males (max SVL – 87.5 mm) smaller than females (102.1 mm).

Dorsum covered in fine smooth scales with moderately densely scattered greatly enlarged tubercles encircled by slightly enlarged scales that border the enlarged tubercles, in addition there are scattered moderately enlarged tubercles (not encircled by large scales); on flanks higher density of greatly enlarged tubercles, absence or low density of moderately enlarged single tubercles; tubercles coned-shaped and striated/ridged; ventral surface covered with flat circular juxtaposed scales, scales on venter similar in size to small scales on dorsum; scales below neck and gular region small.

Slender and moderately long limbs, dorsal surface of limbs with enlarged tubercles, ventral surfaces with greatly reduced density and size of tubercles, greatest density near body; pentadactyl; moderate fingers and toes, terminating in a sharp claw, surrounded by small imbricate scales, subdigital lamellae not enlarged; claw surrounded by sheath formed by a ring of enlarged scales.

Original tail short, proximal portion flattened, less than twice as long as broad, sides in dorsal view slightly convex, tail with 6–8 transverse segments, segments with transverse row of enlarged tubercles, lateral edge of tail with row of enlarged protruding tubercles, distal portion narrow and cylindrical with 7–8 segments with very fine scales, terminating in a slightly enlarged knob; no precloacal or femoral pores; in males, 5 or 6 enlarged cloacal spurs to either side of base of tail, reduced in females; hemipenes strongly bifid.

Colouration. Background colour medium-light brown with reddish hues, five dark brown bands from nape to tail; on nape, a narrow dark band with straight edges; moderately narrow dark band posterior to arms; wide dark brown band anterior to legs; narrow to wide dark brown band on base of tail; distal portion of tail dark brown, occasionally slightly interrupted; head mottled brown with high variation with absence of dark brown maculations on snout and labials; limbs medium brown; ventrum pale off white.

Habitat. Active at night on hard soils, including stony loams. In the day, generally found by collectors under tin on hard soils, in spinifex (*Triodia* spp) clumps, and occasionally in the soil under leaf litter.

Distribution. Primarily occurs within the Pilbara region of Western Australia, with most records from the Hamersley Range (Fig. 1). Specimen records extending to Mardie in the north-west coast and south to Cane River Conservation Park, south and east to Collier Range National Park, north and east to Jigalong, Skull Springs and Mt Edgar near Marble Bar. An isolated record (WAM R157790) from south of Mt Augustus, a juvenile with five bands, is likely to be an unusual *N. wheeleri* or possibly a hybrid. Apparently largely absent from the northern Pilbara.

Conservation status. Although this species occurs in an area with active resource extraction, it should be listed as of 'Least Concern' according to IUCN criteria, owing to its broad distribution in the Pilbara region, including occurring in several reserves.

Etymology. cinctus means surrounded or encircled, possibly in allusion to the splitting of the dark nuchal band when compared with *N. wheeleri*.

Discussion

Our re-examination of the two pairs of pygopodoid subspecies considered here revealed substantial genetic and morphological evidence to support specific status of both subspecies. In both of these cases, the subspecies rank was originally used by Storr to denote morphologically divergent and geographically separate populations. But based on the genetic evidence, and also the appreciation of the relatively large morphological differences observed here compared to typical 'cryptic species', we had little hesitation in elevating each subspecies to full species.

Raising the subspecies has affected the distributions of the new full species, which in turn has implications for conservation assessment because reductions in distribution impact management and conservation planning. For example, organisations like the International Union for Conservation of Nature (IUCN) only recognise taxonomic ranks at the level of species, not subspecies. Maintaining subspecies as such when their evolutionary times of divergences are similar to that observed between other species within the same genus can result in uneven efforts to conserve these evolutionary significant units.

In the case of *Pletholax*, the species *P. edelensis* is now known to be restricted to the Shark Bay region. This area is much smaller than the former '*P. gracilis*' that would have included both subspecies. Alternate management strategies may be required for *P. edelensis*, as separate from *P. gracilis*, although recent IUCN workshops on this species concluded it was reasonably secure and would likely merit a listing of Least Concern (P. Doughty, pers. obs.). For *P. gracilis* (currently Least Concern), the elevation of *P. edelensis* reduces its distribution in areas least impacted by development. Southern portions of the distribution of *P. gracilis* show population declines and extinction associated with human development (How, 1998; How and Dell, 2000) and both *Pletholax* species may be impacted by sea level changes associated with human-induced climate change. Owing to the extremely large distributions of both *Nephrurus* species, they should be regarded as Least Concern.

Recently, when integrative taxonomy has been applied to groups of reptiles, many subspecies have been elevated to full species, often with several additional species described (e.g. *Crenadactylus* – Doughty et al., 2016; the *Gehyra koira* species complexes – Oliver et al., 2019). In other cases, subspecies have been synonomised owing to very recent divergence with any morphological differences among populations viewed as recent phenomena (e.g. tiger snakes – Keogh et al., 2005) and lack of additional morphological support (*Ctenophorus caudicinctus* – Melville et al., 2016; northern *Diporiphora* – Melville et al., 2019). Several other obvious species groups that contain subspecies could benefit from a similarly rigorous analysis of morphology and genetics, such as the skinks *Lerista macropisthophis* and *L. planiventralis* and eastern banjo frogs (*Limnodynastes*). Australian geckos are an interesting test case, as there still exist a number of subspecies, including several newly erected subspecies in the eastern leaf-tailed geckos (Couper and Hoskin, 2013). Three species of spiny-tailed *Strophurus* have subspecies: *ciliaris*, *spinigerus* and *taenicauda*. The latter species had subspecies recently erected by Brown et al. (2012), with conservation consequences owing to their occurrence in the highly degraded Brigalow Belt of Queensland.

Within the southern portion of Western Australia, where this study was focussed, several subspecies exist within pygopodoid geckos. For the two subspecies of *Diplodactylus granariensis*, the nominate form and *D. g. rex*, Hutchinson et al. (2009) elected not to synonomise *D. g. rex* despite no genetic support (Oliver et al., 2007). The dilemma was that of all the southern stone geckos, *D. g. rex* taxon was one of the most divergent in size and pattern thus showing signs of incipient speciation, so a conservative approach was adopted in maintaining recognition of the subspecies. As the speciation process can take a long time to complete, the subspecies category for *D. g. rex* is a convenient label to designate this divergent population of *D. granariensis*. Viewed from an evolutionary perspective, however, continued recognition of *D. g. rex* renders the remaining *D. g. granariensis* a paraphyletic taxon. If the taxonomic category of ‘subspecies’ does not require monophyly, and instead denotes a morphologically divergent lineage within a larger species group, then there is no conflict when there are paraphyletic subspecies. In a discussion of whether to use the taxonomic categories of species or subspecies, Grismer et al. (1994) caution against using any taxonomic arrangement that renders a taxon paraphyletic as it obscures known evolutionary history. Thus, according to this criterion, *D. g. rex* would be subsumed into a wider monophyletic *D. granariensis*.

The only other described pygopodid subspecies belongs to *Delma concinna*. We had originally intended to test the two subspecies of *D. concinna* (Kluge) in this study as well, but were limited by genetic material. Only a single tissue is available for *D. concinna major*, which was previously analysed in Maryan et al. (2015). Those results showed very little difference between the two subspecies, but no firm conclusions could be drawn on three samples that were chosen as outgroups for the *Delma australis* group. Morphologically, the Shark Bay individuals (*D. c. major*) are larger than the largest nominate form. These size differences and separated geographic distributions were the reasons Storr erected subspecies, to accommodate this variation. Preliminary morphological analyses indicated that many characters used by Storr to distinguish these subspecies actually showed wide overlap, especially in recently-collected specimens (unpublished data). This left only size differences and geographic separation to support continued recognition of subspecies. Future survey work, however, may result in sufficient specimens collected to resolve the subspecific status of *D. concinna major*.

Descriptions of subspecies have precipitously declined relative to species descriptions in recent years. This is because the continued reassessment of species with subspecies with integrative taxonomic approaches (i.e. testing for genetic differences and re-examination of specimens for consistent morphological differences), and is likely to lead to either elevation of subspecies to full species or synonomy with the nominate form. Furthermore, most new descriptions do not generally include the description of subtle variation between lineages. In certain cases, however, subspecies may capture subtle morphological and genetic differences among lineages and be useful contributions to taxonomy (e.g. Brown et al., 2012; Couper and Hoskin, 2013). Because taxonomic ranks are ultimately matters of human convention with which to communicate biological patterns, semantic discussions of the utility of subspecies will remain an ongoing debate.

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Appendix 1

Geographical data of specimens used in this study. Morphology only is denoted by "m", genotyping only is denoted by "g", and where specimens were both genotyped and morphologically detailed is was denoted with "m+g". Abbreviations: SA – South Australia; AMS – Australian Museum, Sydney; SAMA – SA Museum, Adelaide; NTM – Northern Territory Museum, Darwin.

Pletholax edelensis

WAM R54755^{m}, 5 km south of Useless Loop (26°10'S, 113°25'E); WAM R54863^{m}, 4 km south of Useless Loop (26°10'S, 113°25'E); WAM R55085^{m}, 10 km north-west of Useless Loop (26°04'S, 113°20'E); WAM R103978^{m}, Edel Land (26°17'S, 113°19'E); WAM R104259^{m} and WAM R104260^{m}, Eden Land (26°16'S, 113°19'E); WAM R120973^{m+g}, 4 km south of Peron Homestead (25°53'S, 113°33'E); WAM R121918^{g}, Carrarang Station (26°32'S, 113°30'E); WAM R124890^{m}, No Data; WAM R156967^{m+g}, Dirk Hartog Island (26°00'S, 113°12'E).

Pletholax gracilis

WAM R97606 ^{g}, Perth Airport (-31.9233°S, 115.9778°E); WAM R64723^{m}, WAM R64725^{m} and WAM R64726^{m}, Jandakot (32°07'S, 115°51'E); WAM R80935^{m} and WAM R80938^{m}, Murdoch (32°04'S, 115°49'E); WAM R82856^{m}, Wireless Hill Perth (32°01'S, 115°50'E); WAM R82912^{m}, Mooliabeenee (31°20'S, 116°02'E); WAM R97606^{m+g}, Perth Airport (31°55'S, 115°59'E); WAM R104374^{m+g}, Victoria Park, Baron-Hay Court (31°59'S, 115°53'E); WAM R106171^{g}, Marangaroo (31°48'S, 115°50'E); WAM R112788^{g}, Bold Park (31°57'S, 115°46'E); WAM R113159^{m}, Cooljarloo, 10 km west-north-west of Walyering Hill (30°37'S, 115°25'E); WAM R119115^{m+g}, Talbot Road Reserve, Swan View (31°52'S, 116°03'E); WAM R119294^{g} and WAM R119393^{g}, Wicherina Dam (28°44'S, 115°00'E); WAM R119944^{g}, Perth Airport (31°56'S, 115°58'E); WAM R120302^{m+g}, WAMR120303^{m+g}, WAM R121126^{g}, Wicherina Dam (28°44'S, 115°00'E); WAM R123579^{g}, 55 km north-north-west of Kalbarri (27°16'S, 114°02'E); WAM R127684^{g}, Hartfield Park, Perth (32°00'S, 116°00'E); WAM R130019^{m+g}, Rushton Road, Martin (32°04'S, 116°01'E); WAM R130206^{m}, Burma Road Nature Reserve (28°59'S, 115°02'E); WAM R130434^{m}, Bella Vista Nature Reserve (28°32'S, 114°40'E); WAM R138140^{m}, Mount Lesueur National Park (30°18'S, 115°13'E); WAM R141024^{g}, Ellenbrook (31°45'S, 115°59'E); WAM R141190^{g}, CA 15 km north-north-east of Lancelin (30°48'S, 115°16'E); WAM R142313^{m}, Martinjinni Nature Reserve (30°18'S, 116°27'E); WAM R143925^{m}, Watheroo National Park (30°08'S, 115°48'E); WAM R144651^{m+g}, Lot 52, Burns Beach Road (31°43'S, 115°46'E); WAM R144886^{m+g}, Marchagee Area (30°03'S, 115°14'E); WAM R146571^{g}, 7 km south of Dongara (29°19'S, 114°57'E); WAM R154023^{g}, Muchea Air Weapons Range (31°39'S, 115°55'E); ABTC69300, No Data; WBJ2483, Lesueur National Park.

Nephrurus cinctus

WAM R26532^{m}, Mount Newman (23°21'S, 119°41'E); WAM R69785^{m}, Marandoo Minesite (22°38'S, 118°09'E); WAM R74883^{m} and WAMR74884^{m}, 3 km east of Marandoo (22°37'S, 118°07'E); WAM R97776^{g}, Coolawanyah (21°49'S, 117°48'E); WAM R114268^{m}, Wittenoom Racecourse (22°14'S, 118°19'E); WAM R135435^{m}, Mount Brockman (22°19'S, 117°19'E); WAM R138194^{m}, Hamersley Range National Park (23°01'S, 118°43'E); WAM R146588^{m+g}, 231 km south-south-west of Port Headland (22°22'S, 119°59'E); WAM R156300^{m}, Chichester Range (22°14'S, 118°01'E); WAM R157588^{m}, Robe River (21°45'S, 116°05'E); WAM R162078^{m} and WAM R162111^{m}, 26 km west-north-west of Mount Berry (22°26'S, 116°13'E).

Nephrurus wheeleri

WAM R4719^{m}, Wiluna (26°35'S, 120°14'E); WAM R19092^{m}, Wilgie Mia (26°56'S, 117°42'E); WAM R22628^{m}, Poona (27°08'S, 117°28'E); SAMA R29494^{g}, 47 km north-north-east of Leonora (28°31'S, 121°33'E); SAMA R34040^{g}, Yoothapinna Homestead, Meekatharra (26°31'S, 118°30'E); WAMR69787^{m}, Marandoo Campsite (22°38'S, 118°07'E); WAM R74723^{m}, 8.7 km east-north-east Yuinmery (28°32'S, 119°05'E); WAM R84113^{m} and WAM R84115^{m}, Bilyuin, Murchison River (25°54'S, 118°40'E); WAM R97017^{m}, Wanmulla Outcamp (27°15'S, 118°20'E); WAM R97736^{m}, Ned's Creek Station (25°29'S, 119°39'E); WAM R97737^{m+g}, Cunyu Station (26°01'S, 120°07'E); WAM R97739^{m}, Ned's Creek Station (25°29'S, 119°39'E); WAM R127592^{m}, 8 km east of Leonora (28°53'S, 121°25'E); WAM R137379^{g}, Yuinmery Homestead rubbish tip (28°34'S, 119°01'E); WAM R146823^{g}, Wydgee Station (28°51'S, 117°50'E); WAM R156166^{m}, Doolgunna Homestead (25°41'S, 119°13'E); SAMA R29494^{g}, 47 KM NNE Leonora (28°31'S, 121°33'E); SAMA R34042^{g}, Yoothapinna HS (26°31'S, 118°30'E).