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Spots before the eyes: revision of the saxicoline geckos of the *Gehyra punctata* (Squamata: Gekkonidae) species complex in the Pilbara region of Western Australia

Paul Doughty[1,*], Aaron M. Bauer[2], Mitzy Pepper[3] and J. Scott Keogh[3]

[1] Department of Terrestrial Zoology, Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia.

[2] Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, U.S.A.

[3] Division of Evolution, Ecology & Genetics, Australian National University, Canberra, ACT 0200, Australia.

[*] Corresponding author: paul.doughty@museum.wa.gov.au

ABSTRACT – The *Gehyra punctata* species complex in the Pilbara and surrounding regions of Western Australia has long been known for its confused taxonomy. Recent collections in the region have enabled a reassessment of specimens currently referable to *G. punctata*. We assessed populations genetically using newly generated mitochondrial DNA data in conjunction with recently published phylogenomic data and an unpublished allozyme analysis. In addition, we carried out a detailed morphological examination involving hundreds of specimens across this taxon's range. Many possible candidate species were recovered from these analyses, and the re-examination of morphology indicated two major clades: one small-bodied and one large-bodied, each comprising multiple divergent lineages within them. A syntype of *Peropus variegatus punctatus* Fry, 1914, believed to have been lost at the time of Mitchell's revision in 1965, was recently found in the Western Australian Museum collections, and is here designated as the lectotype of *G. punctata sensu stricto*.

In addition to *G. punctata* from the Pilbara craton, the large-bodied clade comprises several species: *G. macra* sp. nov. – sister to *G. punctata* and confined to the northern Pilbara, and two more southerly distributed species, *G. punctulata* sp. nov. and *G. polka* sp. nov.; and a small-bodied species restricted to the south-western Pilbara region in the Hamersley Range, *G. fenestrula* sp. nov. Within the small-bodied clade a slightly larger-sized species is described as *G. media* sp. nov. For the other highly structured small-bodied lineage, one of the groups diverged morphologically and was recovered as the basal group in the phylogenomic data, despite being nested within the small-bodied lineage in the mitochondrial dataset. As this population is also geographically restricted to the Burrup Peninsula, we describe it as *G. peninsularis* sp. nov., based on the combined evidence. The remaining very small-bodied lineages we describe as *G. micra* sp. nov.

The new species are diagnosable on the basis of morphology, colour and patterns of pale and dark spots. The revision of the *G. punctata* species complex adds seven new species to the western arid zone, and further establishes the Pilbara as the region with the highest gecko diversity and endemism in Australia.

KEYWORDS: *Gehyra fenestra*, *Gehyra fenestrula* sp. nov., *Gehyra macra* sp. nov., *Gehyra media* sp. nov., *Gehyra micra* sp. nov., *Gehyra peninsularis* sp. nov., *Gehyra polka* sp. nov., *Gehyra punctulata* sp. nov., mtDNA, *ND2*.

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INTRODUCTION

The rock-dwelling spotted forms have proved as difficult to classify as the variegated tree-dwelling species.

– F.J. Mitchell on *Gehyra* (1965, p. 302)

Gehyra is a 'taxonomist's nightmare'…

– M. King (1979, p. 376)

Geckos of the genus *Gehyra* are among the most taxonomically confusing within the Australian herpetofauna owing to their conservative body form, widely varying characters within taxa, remote locations for many species complexes and poor preservation of colour patterns in museum specimens (King 1983; Sistrom et al. 2009, 2014; Doughty et al. 2012, 2018; Kealley et al. 2018). Recently, progress has been made resolving the affinities of *Gehyra* to other gekkonine geckos (Heineke et al. 2011; Gamble et al. 2012; Sistrom et al. 2014) and delimiting species boundaries (Horner 2005; Sistrom et al. 2009, 2013; Oliver et al. 2010, 2016; Doughty et al. 2012, 2018; Hutchinson et al. 2014). As King (1983) pointed out 35 years ago, taxonomic progress on *Gehyra* has been particularly hindered by the loss of colour patterns in preservative and that 'too few specimens from too few localities have been examined' (p. 739).

The wide variation within recognised forms has characterised work on *Gehyra* throughout its history. In a taxonomic treatment of the genus in Australia over 50 years ago, Bustard (1965a) noted the wide range of variation within *G. australis* Gray, 1845 and *G. variegata* (Duméril & Bibron, 1836), concluding that, despite this variation, the two taxa were indeed full species and not mere subspecies as asserted by Mitchell (1955) (n.b. no mention was made of *G. dubia* [Macleay, 1877], indicating Bustard was unaware of this name). In the late 1970s and early 1980s, work on documenting the karyotypes of widely distributed *Gehyra* taxa in Australia by King and Moritz began to reveal the true confusion in the genus and resulted in many species descriptions (reviewed in King 1979, 1983; Moritz 1986; Sistrom et al. 2009, 2013). Based on widely varying karyotypes across the region, new species were erected to accommodate several chromosomally and morphologically divergent populations, i.e. *G. nana* Storr, 1978, *G. montium* Storr, 1982, *G. purpurascens* Storr, 1982, *G. pamela* King, 1982a, *G. minuta* King, 1982b, *G. borroloola* King, 1984a, *G. robusta*, King, 1984a and *G. occidentalis* King, 1984b, including the resurrection of *G. dubia*. In addition, other distinctive forms were also described based on morphology, i.e. *G. catenata* Low, 1978 and *G. xenopus* Storr, 1978. After this active period in *Gehyra* systematics, no further species were recognised for over 20 years until the description of *G. koira* Horner, 2005 (with two subspecies, *koira* and *ipsa*) based on morphology. Recent work drawing from combined genetic and morphological data has resulted in many new species descriptions from the Australian Monsoonal Tropics (Doughty et al. 2012, 2018; Oliver et al. 2016; Bourke et al. 2017) and Central Ranges (Hutchinson et al. 2014), and the first proper descriptions of *G. lazelli* Wells & Wellington, 1983 (Sistrom et al. 2009) and *G. kimberleyi* Börner & Schüttler, 1983 (Oliver et al. 2016).

One of the most recalcitrant groups within *Gehyra* is the *G. punctata* (Fry, 1914) species complex from the Pilbara, Gascoyne and eastern Murchison regions of Western Australia (WA), and sometimes reported from the southern Kimberley (Storr et al. 1990; Wilson & Swan 2008; but see King 1981; Doughty et al. 2018). In his assessment in the 1910s of collections from the Western Australian Museum (WAM), Fry originally described this taxon as a 'variety' of *G. variegata* based on a small female from the 'Strelley River, Pilbara' that corresponded with Central Ranges specimens from the Horn Expedition (see Ellis et al. 2018) stating that: 'In all structural characters it agrees with the variable *P.* [*Peropus*] *variegatus*, but the color pattern is so different that I propose to distinguish it under the varietal name of *punctatus*' (p. 178). He then went on to describe in a few sentences the 'russet brown' colouration marked with many spots to distinguish it from *Peropus variegatus variegatus* (i.e. *G. variegata* and the eastern *G. versicolor* Hutchinson, Sistrom, Donnellan & Hutchinson, 2014). Zietz (1920) later synonymised *punctata* with *variegata*, only for this to be reversed by Loveridge (1934), who retained *punctata* as a subspecies of *G. variegata*, and also considered its distribution to be restricted to Western Australia (excluding the Central Ranges). In a comment on a nomenclatural note on *Gehyra*, including *G. punctata*, by Chrapliwy et al. (1961), Bustard (1965b) raised this taxon to full species status based on his collections of sympatric *G.* '*variegata*' (= *G. versicolor* or *G. montium*) on trees and *G.* '*punctata*' (= *G. minuta*, *G. moritzi* Hutchinson, Sistrom, Donnellan & Hutchinson, 2014 or *G. pulingka* Hutchinson, Sistrom, Donnellan & Hutchinson, 2014) on rocks in central Australia, believing *G. punctata* occurred as far as northern Queensland (n.b. his detailed treatment of *Gehyra* mentioned in Bustard [1965a, b] was never published, possibly owing to the appearance of Mitchell's own detailed revision published later that year).

In a review of the genus that emphasised osteological differences, Mitchell (1965) redescribed all Australian forms recognised at that time, including *G. punctata*. Unfortunately, he could not examine the type specimen as it could not be located by the staff of the WAM or the Australian Museum, Sydney (AMS) when searching through material that Fry likely consulted (Mitchell 1965, pp. 301–302; n.b. Fry died in World War I shortly after the publication of his 1914 work; Adler 2007). When focussing on material from the Pilbara region in WA, Mitchell found evidence for four species: *G. variegata*, *G. punctata*, *G. fenestra* Mitchell, 1965 and *G. pilbara* Mitchell, 1965, the latter two of which

he described as new species in his review. Key to Mitchell's concept of Fry's *G. punctata* was that it was a small-bodied species, based on Fry's statement that 'in all structural characters it agrees with the variable *P. variegatus*' (p. 178, and also quoted by Mitchell 1965, p. 303). Despite presenting data that *G. fenestra* was larger than *G. punctata* (mean snout-vent length [SVL] of 61 vs. 46 mm, respectively) and had a more strongly depressed head and body, Mitchell found that many characters overlapped between the two taxa, stating '…the present study clearly indicates that no characters can be employed as absolute criteria for species identification…' (p. 308). Based on the material listed for *G. punctata* and also the map shown in his fig. 10, it is clear that this taxon included other species from the Shark Bay area in WA and also the Northern Territory. He also cited ecological differences from collectors' notes indicating that *G.* '*punctata*' had been collected from under rocks adjacent to rocky pools whereas *G. fenestra* had been collected from boulders and crevices (p. 303). Thus, although acknowledging outstanding issues in the delimitation of species boundaries between the two taxa, he stood by the osteological differences he found, particularly a single fenestra in the pubis of his small-bodied '*punctata*' and two in *fenestra* (hence the specific name), and differences in the mesosternal ribs.

After Mitchell's (1965) revision, most small-bodied *Gehyra* with a reddish background colour, spots and an association with rocks had been referred to as *G. punctata*, including those from the northern tropics from the Kimberley to Queensland, and also the Central Ranges. Workers in the 1970s and 1980s left the Pilbara region and its reddish, spotted forms of *Gehyra* relatively uninvestigated, and instead focussed on describing forms elsewhere (see above). However, the two species of reddish-brown spotted *Gehyra* from the Pilbara were synonymised by Storr (1982) in his description of *G. purpurascens* and *G. montium* from the Central Ranges. The reddish, spotted *G. montium* presumably had been previously referred to *G. punctata* as early as Fry's 1914 publication and so necessitated a redescription (although recent work has found the Central Ranges to contain several more *Gehyra* species, as well as discovering that *G. montium* extends across the western deserts and is widespread in the Pilbara [Sistrom et al. 2013; Hutchinson et al. 2014; Kealley et al. 2018]). Without commenting on the type specimens of either taxa, Storr (1982) synonymised *G. fenestra* with *G. punctata* based on an overlap of characters, concluding his characteristically brief paper with: 'I suspect that Mitchell's concept of *G. punctata* was partly based on Pilbara specimens of *G. variegata* and/or *G. pilbara*. At any rate I believe that only three species of *Gehyra* occur in the Pilbara' (p. 59).

Recently, however, R.J. Ellis reidentified the specimens in the WAM collections that were loaned to Fry in the 1910s, including the female specimen that Fry (1914) referred to as the 'type' (see detailed account in Ellis et al. 2018). As Fry also referred to an illustration of a spotted gecko from the Horn Expedition to the Central Ranges in his description, this necessitates a lectotype designation as the specimen upon which the illustration is based constitutes a second syntype in addition to the rediscovered female in the WAM collection. Although the sub-adult female syntype is in quite poor condition, it is recognisable as the large-bodied form of *G. punctata* from the Pilbara (Ellis et al. 2018). Coupled with examination of the *G. fenestra* types, which are in reasonable condition, this has greatly facilitated assignment of names to the *G. punctata* species complex. See the Taxonomy section below and Ellis et al. (2018) for resolution of the type specimens of *G. punctata* and *G. fenestra*.

Despite the confusion in the past, new collections of *Gehyra* from the western rocky areas of the Pilbara and regions to the south have resulted in an increase in material to assess *Gehyra* diversity from this area. In particular, environmental impact assessments carried out by biological consultants required for mining proposals and the WA Department of Environment & Conservation's (now Department of Biodiversity, Conservation & Attractions) Pilbara Biodiversity Survey (PBS) (McKenzie et al. 2009; Doughty et al. 2011) resulted in the collection of a large series of *G. punctata sensu lato* specimens, most of which had tissue samples taken for genetic analysis. Therefore it is timely to reassess the status of the many forms of *G. punctata* from the region using evidence from morphology, mtDNA, distribution and habitat preferences. We also draw on a recent phylogenomic analysis of *Gehyra* (Ashman et al. 2018) and an unpublished pilot study using allozyme electrophoresis (M. Adams and P. Doughty, unpublished data). The combined genetic and morphological evidence indicates that *G. punctata* as currently conceived is paraphyletic, with two major clades: one with four larger-bodied species and one small-bodied species, and a second clade with three smaller-bodied species, resulting in the description of seven new species from the Pilbara region herein.

METHODS

APPROACH AND MATERIAL EXAMINED

We undertook an integrated approach and used both morphological and genetic data to determine species boundaries within the *G. punctata* species complex based on recently collected specimens from the Pilbara and rocky regions to the south, including the eastern Gascoyne, eastern Murchison and Yalgoo bioregions (Thackway and Cresswell 1995). We initially grouped specimens into several different morphologies, then ran select specimens for allozyme profiles in the mid-2000s (M. Adams and P. Doughty, unpublished data). The resulting groups recovered from the allozyme analysis then guided further mtDNA sequencing and morphological examinations. New specimens and tissues for genetic analyses were integrated into the revision, and recently the missing type of Fry was located to help

resolve the application of names. Preliminary mtDNA phylograms generated by Sistrom et al. (2013) and for this study informed the study of Ashman et al. (2018), who drew samples from within mtDNA lineages and used exon capture techniques to carry out a detailed phylogenomic assessment of nearly all *Gehyra* species that firmly established independently-evolving lineages. Similar to Kealley et al. (2018), we use the findings of Ashman et al. (2018) based on few individuals per lineage and coupled them with our expanded mtDNA sampling to provide sufficient genotyped specimens for morphological analyses and for mapping distributions.

Almost all specimens examined had tissue samples taken and some were photographed during specimen preparation to document the dorsal colours and patterns that typically fade in preservative. Most specimens are from the WAM collections, supplemented by tissues from the South Australian Museum, Adelaide (SAMA) and the Museum and Art Gallery of the Northern Territory (NTM). Appendix 1 lists specimens examined, and whether their mtDNA, allozymes, nDNA and/or morphology were analysed.

MITOCHONDRIAL DNA

Taxonomic sampling, DNA extraction and PCR

We sampled from within the groups identified through the allozyme analysis, and sequenced 178 samples variously identified as *G. punctata* and *G. pilbara* for the mtDNA NADH-hydrogenase subunit 2 gene (*ND2*). In addition, we supplemented these samples with 83 mtDNA data from other studies (Sistrom et al. 2009; Pepper et al. 2013; J. Huey and P. Doughty, unpublished data).

DNA was obtained from the allozyme homogenates for new samples in this study using the EDNA HiSpEx tissue kit (Chaga) following the manufacturers protocol. The *ND2* region was amplified and sequenced in three overlapping fragments, using the forward primer L4437 (5'-AAGCTTTCGGGGCCCATACC-3'; Macey et al. 1998) and the reverse primer $tRNA^{Asn}$ (5'-CTAAAATRTTRCGGGATCGAGGCC-3'; Read et al. 2001). A modified version of L4882 (5'-CAACCTGACAAAAAHTHGCMC-3'; Macey et al. 2000) was used as an internal sequencing primer.

PCR amplification was performed in a 25 µl reaction mix consisting of 12.5 µl GoTaq (Promega), 10.5 µl double distilled water, 1.0 µl of both forward and reverse primers (10 pmol) and 1.0 µl of template DNA. Amplification of the fragment was conducted using a Corbett PC-960C cooled thermal cycler with an activation step at 94°C for 3 min, followed by 37 cycles of denaturation at 94°C for 30 s, annealing at 60°C for 30 s, and extension at 72°C for 60 s followed by a final extension step at 72°C for 10 min. Approximate concentration and size of amplification products was determined by electrophoresis in a 2% agarose gel stained with 5.0 ul SYBR Safe (Invitrogen) and visualised under ultra-violet light. Target products were purified using 0.4 µl Exonuclease I, and 1.6 µl shrimp alkaline phosphatase (exo/SAP).

Cycle-sequencing reactions were performed in reaction volumes of 20 µl, consisting of 1.0 µl BigDye (Applied Bio-systems), 4.5 µl of 5X sequencing buffer, 0.32 µl Primer (10 pmol), 12.5 µl double distilled water and 1.0 µl purified PCR product. To precipitate sequence products and to remove all unincorporated nucleotides, 40 µl of cold 100% ethanol and 3µl of NaOAc was added to each sample and left for 15 min at room temperature. Precipitated DNA was pelleted by centrifuging for 30 mins and washed three times in 150 µl of 70% ethanol with a 10 min centrifuge step. Pellets were dried before being dissolved in 20 µl of HiDi formamide and run on an ABI 3100 auto-sequencer. All genes were sequenced from both 3' and 5' ends separately. Sequences were edited and assembled using Sequencher 3.0 (Genes Codes Corporation). Alignment of sequences was first performed automatically using the software MUSCLE (Edgar 2004), then refined by eye in Se-Al (Rambaut 1996). Protein-coding regions were translated into amino acid sequences using the vertebrate mitochondrial genetic code or universal nuclear genetic code and were checked for internal stop codons and frame-shift mutations.

Phylogenetic analyses

Each edited alignment comprised 1,044 characters for 261 individuals. We used PartitionFinder (Lanfear et al. 2012) to determine the best partitioning strategy for the mtDNA locus, whereby codon positions one and two were considered together, and codon three was partitioned separately. Maximum likelihood (ML) estimation of the phylogeny of the dataset was performed in RAxML, v.7.0.4 (Stamatakis 2006). The data were analysed under the Generalized Time Reversible model of sequence evolution (variable base frequencies, and a symmetrical substitution matrix) (Rodríguez et al. 1990), and with an across site rate variation modelled to a Gamma distribution (GTR+Γ). The best ML tree was determined using 20 distinct randomised Maximum Parsimony (MP) starting trees. Support values were estimated from 1,000 bootstrap replicates, with bootstrap values above 80 considered as strong support. In our summary phylogram (Figure 1) we present a reduced subset of specimens for legibility. Appendix 1 provides details of all specimens sequenced that we used to generate distribution maps and to identify individuals for morphological analyses.

MORPHOLOGY

Individuals for which we had allozyme profiles were initially chosen as the core group of samples with which to establish morphological boundaries among taxa and to choose further samples for mtDNA analysis. Specimens examined are in the type lists under species accounts and Appendix 1.

Morphological characters (Table 1) were measured with digital calipers to the nearest 0.1 mm, except SVL and TailL that were measured with a rule to the nearest 0.5 and 1.0 mm, respectively. Scale counts (e.g. labial scales, subdigital lamellae) were also scored and we

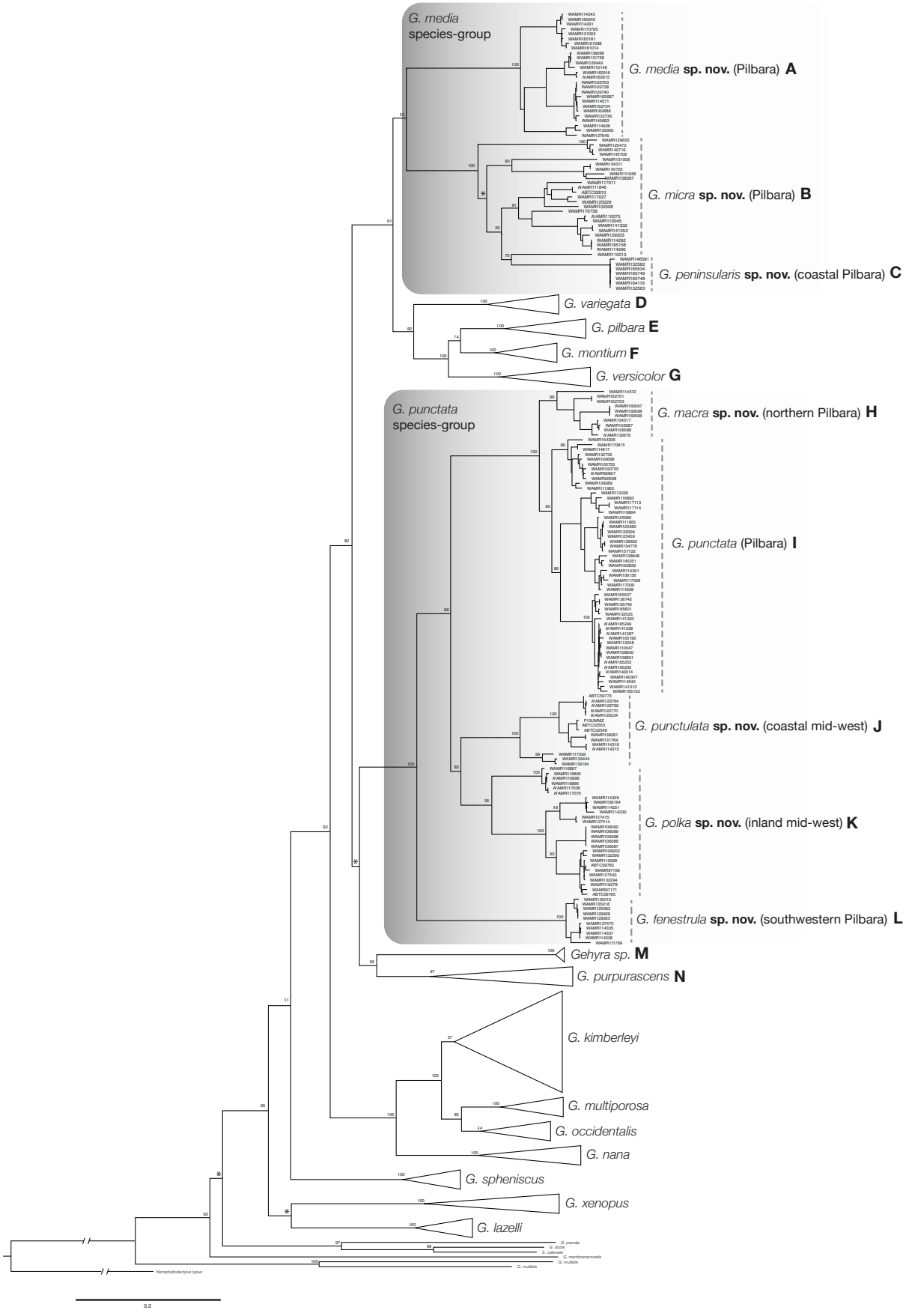

FIGURE 1 Phylogram of the *Gehyra variegata* group and related species focussed on the *G. punctata* species complex based on the mitochondrial gene *ND2*. Numbers above or on the left of nodes on the tree refer to ML bootstrap support values from the RAxML analysis; "*" indicates values < 50.

followed the terminology for scales around the tip of the snout in Sistrom et al. (2009; fig. 6, p. 24), except for modification of Hutchinson et al. (2014) to refer to the 'postmentals' as inner chin shields, and to the 'sublabials' as parinfralabials as suggested by King (1982b). Notes on reproduction for males and females were also made, but few females were gravid. Live or moribund photographs of vouchered specimens (or unvouchered based on geography) were used for the description of colour and patterns.

SPECIES CONCEPT EMPLOYED

Australian *Gehyra* pose a taxonomic challenge in that intraspecific morphological variation is often high and interspecific differences subtle. The availability of large samples across the Pilbara and adjacent regions has allowed us to identify putative phylogenetic signal from widely overlapping phenotypic differences. However, recognition of species-level taxonomic units was also guided by the unpublished allozyme data set and mtDNA phylograms. In addition, we drew from an extensive phylogenomic analysis of Australian *Gehyra* (Ashman et al. 2018), which recovered with high support all the lineages described as new species here. Thus we have employed an integrative taxonomic approach (Padial et al. 2010), whereby we base taxonomic decisions on multiple lines of evidence.

We here employ a general lineage-based species concept (Frost and Hillis 1990; Frost et al. 1992; Mayden 1997; de Queiroz 1998, 2007) and treat as species those entities that clearly represent independent historical lineages based on two or more lines of evidence. In practical terms, we have focussed on the operational criteria that permit us to infer independently-evolving lineages (Wiens and Penkrot 2002; Sites and Marshall 2003, 2004; Bauer et al. 2006; Camargo and Sites 2013). Such criteria may be either tree-based or character-based and we employ both approaches in this paper, basing our taxonomic decisions on the conjunction of data from mtDNA phylograms, the phylogenomic analysis of Ashman et al. (2018), the unpublished pilot allozyme analysis and diagnostic morphological traits. Although distribution patterns alone should not be used in erecting initial hypotheses of species boundaries, geographic concordance with other evidence of lineage independence may be corroborative of taxonomic decisions based on tree- and character-based delimitations (Bergmann and Russell 2007). When there was conflict among datasets, we weighed up the total evidence to arrive at a taxonomic conclusion. Owing to the difficult nature of working with the *G. punctata* species complex, we have taken a conservative approach in naming species, electing to recognise species for which there was strong support from multiple lines of evidence, despite some conflict between datasets. The most difficult choice was the recognition of *G. peninsularis* sp. nov. (lineage C on Figure 1), as this was recovered inside *G. micra* sp. nov. (lineage B) in the mtDNA data, yet in the nDNA analysis of Ashman et al. (2018) it was recovered as the sister of *G. media* sp. nov. (lineage A) + *G. micra* sp. nov. However, owing to consistent morphological differences and geographic isolation, the balance of evidence indicated this was a species.

This revision greatly stabilises the taxonomy of this species complex by applying names to lineages recovered from the robust genetic and morphological analyses. Future work will be able to further analyse diversity within some of our species units such as *G. micra* sp. nov., as this taxon possesses complex phylogenetic structure but for which there are few morphological characters to distinguish them from other species at present.

TABLE 1 Morphological characters measured on *Gehyra punctata* species complex specimens.

Abbreviation	Definition
SVL	Snout-vent length: from tip of snout to anterior edge of cloaca.
TailL	Tail length: from cloaca to tail tip; original or regenerated tails noted.
HeadL	Head length: from tip of snout to edge of retroarticular process of upper jaw; caliper held at oblique angle.
HeadW	Head width: widest part of head, measured behind eyes.
HeadD	Head depth: deepest part of head behind eyes, with caliper on lower jaw bones.
LegL	Leg length: length of lower leg measured from heel to knee with leg at right angle.
SupLab	Number of supralabial scales, defined as being larger than surrounding scales on head.
InfLab	Number of infralabial scales, defined as being larger than surrounding scales on head.
SupNas	Suprnasal scales: scored whether in contact or separated by internasal scales.
Notched infralabial	Scored which InfLab (2nd or 3rd) if posterior edge of InfLab was notched when contacted by parinfralabial scale.
4TLam	Fourth toe lamellae: number of expanded lamellae, excluding triangular-shaped wedge at tip.
PCP	Pre-cloacal pores: counted if pore perforated, usually yellowish (dimpled scales not counted).

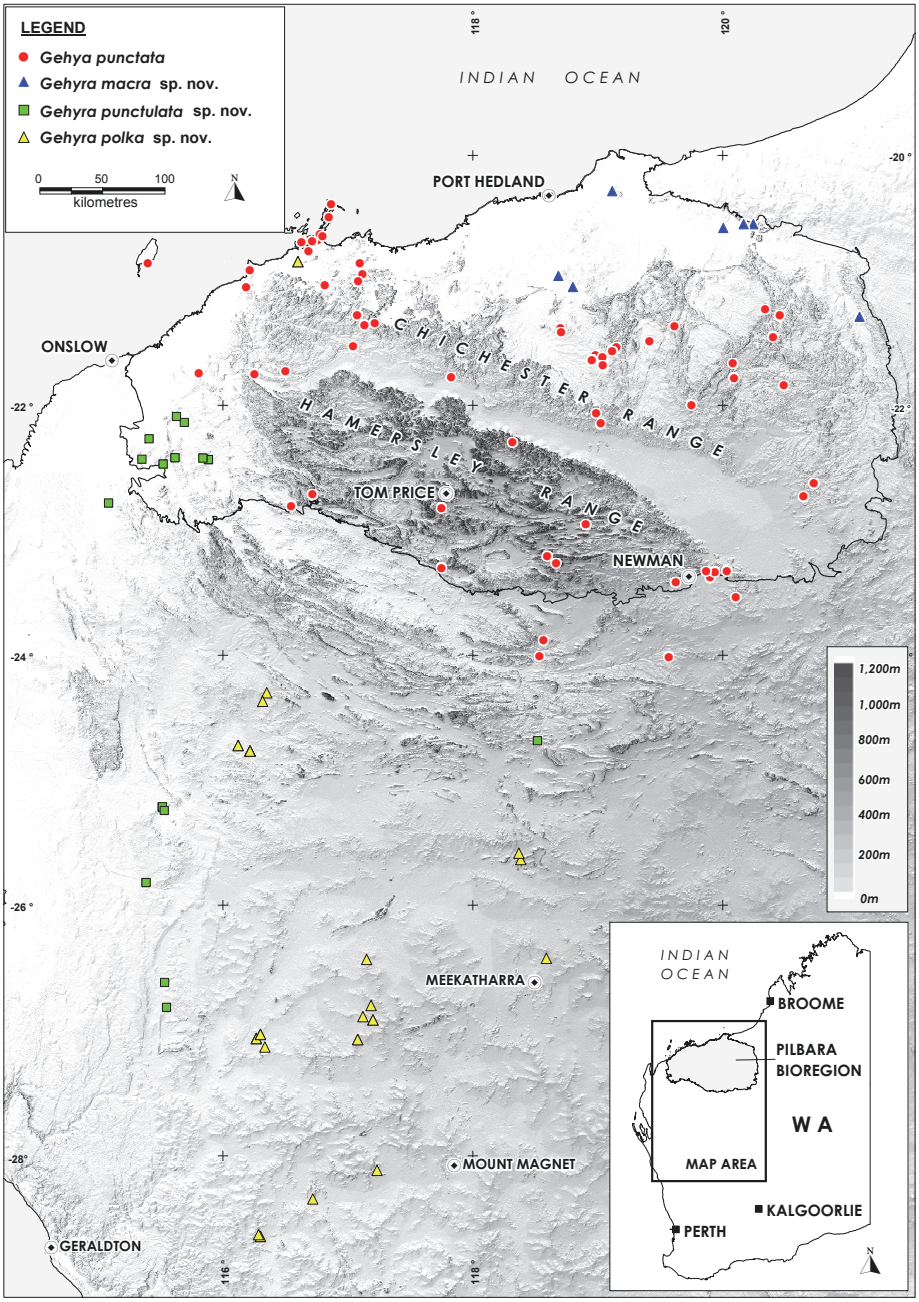

FIGURE 2 Distribution of the large-bodied members of the *Gehyra punctata* species-group in the Pilbara and regions to the south in Western Australia based on individuals with mtDNA genotyping or allozymes: *G. punctata*, *G. macra* sp. nov., *G. punctulata* sp. nov. and *G. polka* sp. nov.

RESULTS

MITOCHONDRIAL DNA

Our analysis of mtDNA recovered many groups that corresponded to the allozyme groups from the initial pilot study, as well as many other described taxa, including those in other recent *Gehyra* studies (Figure 1; Ashman et al. 2018; Kealley et al. 2018; Moritz et al. 2018). A conspicuous feature of the phylogram was the recovery of two major clades that roughly consisted of small and large-bodied forms of *G. punctata s.l.* and other closely allied taxa, confirming that *G. punctata* as presently conceived is paraphyletic with several cryptic lineages within each clade.

The larger-bodied *G. punctata* clade, henceforth the '*G. punctata* species-group' had three major clades within it: a Pilbara craton clade (lineages H + I), a clade south of the Pilbara (lineages J + K) and another with a small body size and restricted distribution in the southeast Pilbara near Newman (lineage L) (Figures 2–3). The Pilbara craton clade had specimens that corresponded to the type of Fry's *G. punctata*,

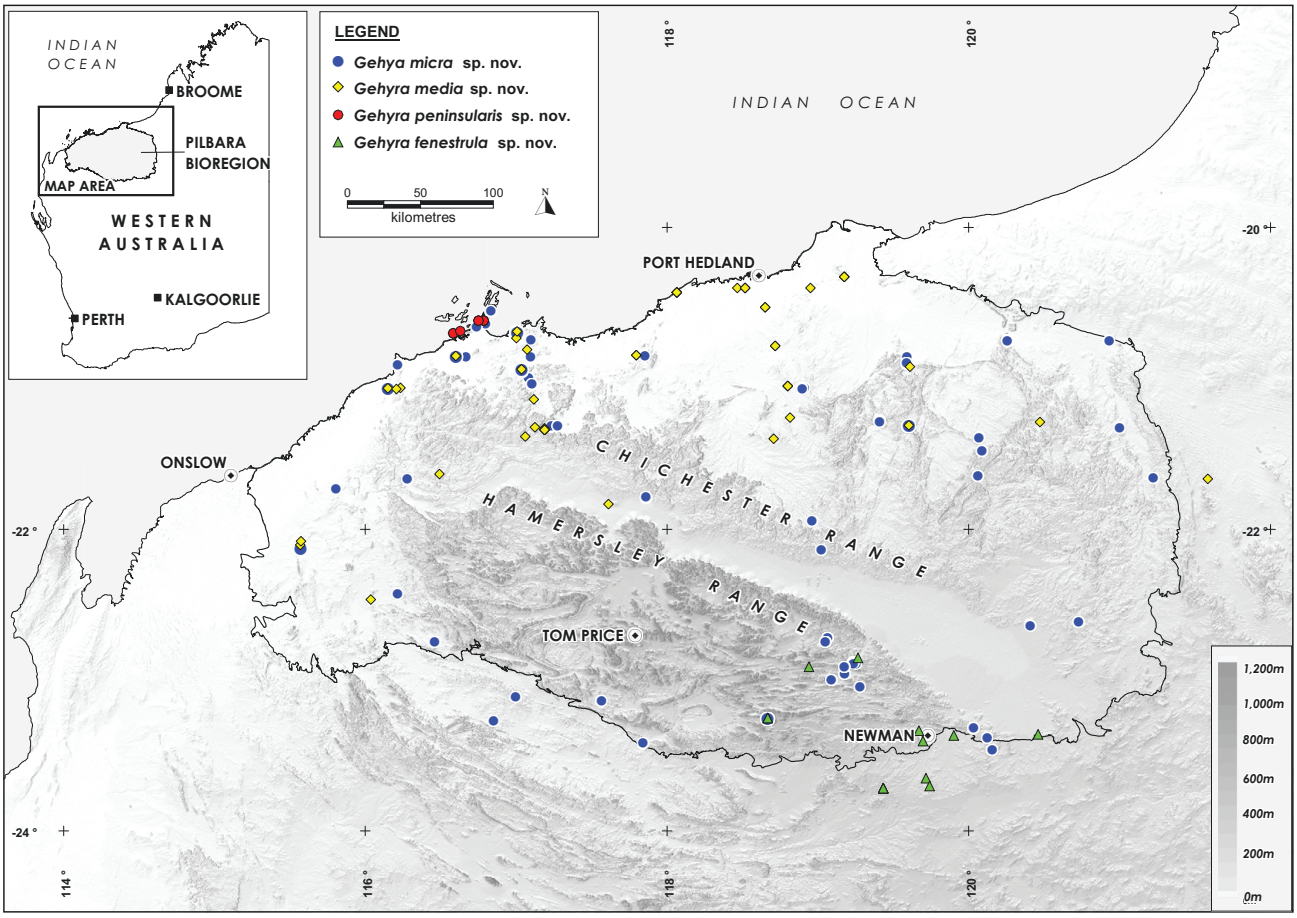

FIGURE 3 Distribution of the small-bodied members of the *Gehyra punctata* species complex in the Pilbara in Western Australia based on individuals with mtDNA genotyping or allozymes: *G. media* sp. nov., *G. micra* sp. nov., *G. peninsularis* sp. nov. (the *G. media* species-group) and *G. fenestrula* sp. nov. (part of the *G. punctata* species-group).

i.e. lineage I, to which we refer that species name. In addition, there was an even larger-bodied form within this clade that was restricted to the northern Pilbara (lineage H). This large-bodied form was the sister lineage to *G. punctata*. The southernmost clade (lineages J + K) ranged as far south as Yalgoo at ~28°S latitude and approximately 200 km inland from Geraldton on the west coast, and this clade showed significant genetic structuring among some populations. However, two major monophyletic groupings within the southern clade corresponded with geography and dorsal patterning (see below). The Newman lineage (lineage L) is sister to all other large-bodied lineages, with individuals from this clade reaching only small to moderate sizes.

A weakly divergent small-bodied clade, henceforth the '*G. media* species-group', comprises two major groups and is sister to a different group of small-bodied species in the arid clade of the *G. variegata* group that included *G. variegata*, *G. pilbara*, *G. montium* and *G. versicolor* (Figure 1; Kealley et al. 2018). The two major groups within this lineage showed different levels of genetic structure within them, with one (*G. media* sp. nov., lineage A) being fairly uniform (corresponding to a lineage with moderate-sized individuals) and one (*G. micra* sp. nov., lineage B + *G. peninsularis* sp. nov., lineage C) with significant structure (with mostly small body sizes), including a geographically restricted form from the Burrup Peninsula on the northern Pilbara coast (Figure 3).

Both the *G. punctata* and *G. media* species-groups, plus the *G. variegata* species-group (Hutchinson et al. 2014; Kealley et al. 2018) were sister to the *nana* clade, i.e. saxicoline species from the Australian monsoonal tropics (Moritz et al. 2018).

MORPHOLOGICAL ANALYSES

Examination of specimens assigned to the various groups based on the mtDNA data presented here, along with the unpublished allozyme and the recently published tree based on large numbers of nDNA exon captures (Ashman et al. 2018), resulted in the recognition of several morphological characters such as the configuration of scales on the underside of the chin and various pattern elements that could be used to diagnose taxa (Table 2 and species accounts in the Taxonomy section, below). As the two available names

TABLE 2 Summary of key morphological features that differ among members of the *Gehyra punctata* species complex. Figures or text in bold denotes groups with the more extreme character state within the species complex. Sample size was 12 per species, except *G. fenestrula* sp. nov. with 11 and *G. polka* sp. nov. with 13. See Table 1 for explanation of measurements. Brackets for "Notched infralabial" indicates this state was occasionally observed.

Character	*G. punctata* Fry	*G. macra* sp. nov.	*G. punctulata* sp. nov.	*G. polka* sp. nov.	*G. fenestrula* sp. nov.	*G. media* sp. nov.	*G. micra* sp. nov.	*G. peninsularis* sp. nov.
SVL (mm)	**59.3**	**66.0**	51.8	53.8	41.3	43.2	**37.4**	42.2
Mean (range)	**(55.5–65.0)**	**(59.0–73.5)**	(48.0–56.0)	(49.0–61.0)	(36.0–48.0)	(36.5–50.0)	**(34.0–46.5)**	(36.0–48.5)
Supralabials	**10.0**	9.4	9.4	9.3	9.3	**8.0**	**8.3**	**8.4**
Mean (range)	**(9–12)**	(9–10)	(9–10)	(9–10)	(8–10)	**(7–9)**	**(8–9)**	**(7–10)**
Snout shape	Broad	Broad	Moderate	Moderate	Narrow	Narrow	**Very narrow**	**Very narrow**
Mental	**Short mental; concave sides where infralabial contacts.**	**Short mental; concave sides where infralabial contacts.**	Long mental with straight or slightly concave sides.	Long mental with straight or slightly concave sides.	Long mental with straight sides.	Long mental with straight sides.	Long mental with straight sides.	Long mental with straight sides.
Notched infralabial	**3rd**	**3rd**	2nd	2nd	2nd (3rd)	2nd	2nd (3rd)	2nd (3rd)
4TLam	7.8	**9.2**	7.3	7.2	6.3	**5.9**	**5.8**	6.6
Mean (range)	(7–8)	**(7–10)**	(7–8)	(7–8)	(6–7)	**(5–6)**	**(5–6)**	(6–7)
Pre-cloacal pores	13.3	**17.0**	10.8	11.3	10.8	10.8	14.5	12.1
Mean (range)	(9–15)	**(14–21)**	(8–13)	(10–13)	(9–12)	(8–15)	(10–19)	(7–15)
N males	27	9	9	11	4	18	22	9
Pattern	Rich reddish-brown; bars or spots with dark (anterior) and pale (posterior) elements in contact; bands around tail.	Light reddish-brown; large diffuse or irregular-shaped dark and pale spots tending to not be in contact; pale vertebral zone.	Reddish-brown and lightly stippled background; small dark and pale spots separated.	Brownish-red on relatively plain background; large dark and pale spots separated.	Rich reddish-brown; small widely-separated spots; spots with dark (anterior) and pale (posterior) elements.	Reddish-brown; dark and pale spots not in contact.	Reddish-brown; small dark and pale spots not in contact, or joining to form alternating transverse bars.	Reddish-brown; moderate-sized dark and pale spots in rows.
Head stripes	Canthal, loreal and upper post-orbital moderate and variable; temporal short; no lower post-orbitals or a spot.	Canthal and loreal diffuse to strong; temporal short or a spot; no post-orbitals.	Canthal weak; loreal and temporal variable; no post-orbitals.	Canthal weak and loreal variable; temporal absent to weak; no post-orbitals.	Canthal weak; loreal and temporal present; no post-orbitals.	Canthal and loreal weak; temporal variably expressed; no post-orbitals.	Canthal, loreal and temporal; no post-orbitals.	Canthal, loreal and temporal; no post-orbitals.

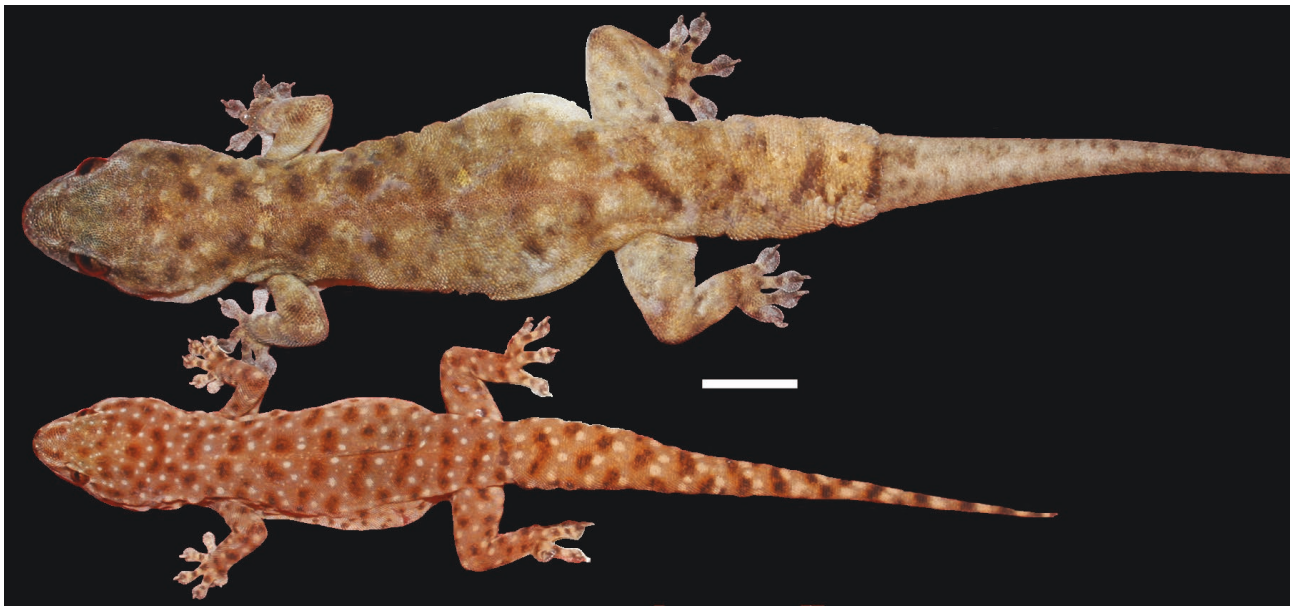

FIGURE 4 Image of *Gehyra macra* sp. nov. (WAM R162688) (upper) and *G. media* sp. nov. (holotype, WAM R162687) (lower), collected from the same outcrop in the northern Pilbara (Photo: P. Doughty).

(i.e. *punctata* and *fenestra*) refer to the same taxon, here we review the morphological characters that differ among *G. punctata s.l.* taxa described here.

Based on the rediscovery of Fry's syntype of *Peropus variegatus punctatus* and its resemblance to the large-bodied common form in the Pilbara (see Ellis et al. 2018 for a detailed treatment), we interpret this name to apply to the widespread large-bodied form on the Pilbara craton, i.e. lineage I of Figure 2. Mitchell (1965) proposed the name *G. fenestra* for this species and provided a detailed diagnosis and description in his revision. This form is morphologically distinctive owing to its large body size, pattern elements made up of a solid dark bar or spot (anterior) joined to a solid or broken pale bar or spot (posterior) scattered on the dorsum and its crevice-dwelling habits, usually being found around boulders and on vertical rock faces.

Within the *G. punctata* species-group, there were four other lineages. The northern lineage (*G. macra* sp. nov., lineage H) had very large body size (up to 73.5 mm SVL – the largest of any species within the arid clade of the *G. variegata* group) and more numerous subdigital lamellae (up to 10) than all other taxa. This lineage was confined to the northern Chichester subregion of the Pilbara and was parapatric with respect to *G. punctata* and syntopic with the smaller-sized species from the *G. media* species-group (Figures 2–3), even occurring on the same rock outcrops (Figure 4). Although evidence from mtDNA show this large-bodied form has only recently diverged from *G. punctata*, the differences in allozymes (unpublished data) and morphology, coupled with the observations of parapatry or sympatry, indicate it is an independently evolving lineage. The study of Ashman et al. (2018) also identified this lineage as a distinct species.

The two southern lineages of the *G. punctata* species-group were similar to *G. punctata* but differed in their dorsal patterns by having clearly separated dark and pale spots vs. a pattern with the dark (anterior) and pale (posterior) bars or spots in contact. The two southern species were further separable on the relative size of the spots, with the eastern inland lineage (lineage K) having large spots, whereas the lineage to the west and north (lineage J) had smaller spots. These two species tended to be smaller than *G. punctata* and possessed differences in scalation as well (Table 2, Appendix 2). We describe these forms as *G. punctulata* sp. nov. for the fine-spotted form and *G. polka* sp. nov. for the form with larger spots.

In the mtDNA phylogram of the *G. punctata* species-group was a distinct basal lineage (lineage L) with small body size with most specimens from the Hamersley Range near the town of Newman in the southwest Pilbara (Figure 3). This form was morphologically similar to several other species in the *G. punctata* species complex but differed subtly in pattern and was clearly genetically distinctive based on the mtDNA presented here, the allozyme pilot study data (where it constituted a unique group) and the study of Ashman et al. (2018). We also describe this lineage as a new species, *G. fenestrula* sp. nov.

The mtDNA analyses also found two lineages of the *G. media* species-group that were more closely related to common and widely distributed members of the arid zone *G. variegata* group such as *G. variegata*, *G. pilbara* and *G. montium*, which also occur in the Pilbara. Similar to the *G. punctata* species-group, individuals of the two mtDNA lineages possessed a reddish-brown background colour overlain with dark and pale spots or bars but tended to have smaller body sizes and narrower snouts. In addition, these forms were usually collected

among small rocks or scree and were rarely found on boulders or vertical rock faces, supporting Mitchell's (1965) observations of the small-bodied form (his *G. punctata*) on the ground among small rocks and the large-bodied form (his *G. fenestra*) preferring vertical crevices among boulders and outcrops.

Within the *G. media* species-group, the lineage (lineage A) with moderate body size was relatively uniform genetically in the mtDNA data (Figure 1) and had a dorsal pattern of discrete dark and pale spots that tended to not be in contact, and regularly spaced. We describe this form largely from the northern Pilbara as *G. media* sp. nov. The other group was even smaller in size with the background pattern featuring more bars in alternating rows and contact among dark and pale elements. There was considerable structure within this group in the mtDNA data and nDNA data of Ashman et al. (2018). One lineage (lineage C) within this clade was restricted to the Burrup Peninsula area near Karratha and possessed a more elongate body than other lineages. In addition, Ashman et al. (2018) recovered the Burrup Peninsula lineage as basal to all other *G. media* species-group lineages, supporting its distinctiveness. Therefore, we describe this lineage as *G. peninsularis* sp. nov., with the remaining lineages described as *G. micra* sp. nov. (lineage B).

TAXONOMY

Genus *Gehyra* Gray, 1834

TYPE SPECIES

Gehyra pacifica Gray, 1834 (= *Gehyra oceanicus* [Lesson, 1830]), by monotypy.

Gehyra punctata (Fry, 1914)

Spotted Pilbara Rock Gehyra

Figures 5, 7

Peropus variegatus punctatus Fry, 1914: 178.

MATERIAL EXAMINED

Lectotype

Australia: ***Western Australia:*** WAM R176100 (formerly 9879; subadult female), 'Strelley River, Pilbara' WA 20°33'S, 119°00'E], J.B. Cleland, collection date unknown, presumably 1907, here designated. As noted in the introduction of this paper and in Ellis et al. (2018), there has been confusion regarding the identity of *Gehyra punctata* virtually since its description. A century of subsequent research has led to the recognition that spotted *Gehyra* from the Pilbara and other rocky regions from the Australian arid zone represent many different species that share a superficially similar phenotype, especially with respect to colouration and the presence of dark and pale spots on the dorsum. This has been exacerbated by the inability of several recent workers to locate the Strelley River specimen cited by Fry (1914), and by oversight of the fact that a specimen illustrated in Lucas and Frost (1896, p. 124, pl. IX, figure 3) also constitutes part of the type series. The latter specimen, collected on the Horn Expedition, appears to represent the taxon presently recognised as *G. moritzi* Hutchinson, Sistrom, Donnellan and Hutchinson, 2014, and may correspond to NMV D268, although the illustration appears to be a somewhat idealised representation if it, is indeed based on this specimen (see Ellis et al. 2018). In order to stabilise the application of the name *G. punctata* and permit its comparison with the many other spotted congeners from the Pilbara, including many named as new in this paper, we hereby select WAM R176100 as the lectotype of *G. punctata*. This results in the application of the name to the specimen actually examined by Fry. Ellis et al. (2018) provide a detailed explanation of the history of the specimens that have been associated with this taxon, and include photographs of the lectotype, now in a poor state of preservation.

Paralectotype

Australia: ***Northern Territory:*** Specimen illustrated in figure 3 on pl. IX, p. 124, Lucas and Frost (1896); possibly corresponding to NMV D268 in the herpetological collection of Museum Victoria. Collected from the Central Ranges on the Horn Scientific Expedition. See explanation above for lectotype designation.

Synonymy, Storr (1982):

Gehyra fenestra Mitchell, 1965

Holotype

Australia: ***Western Australia:*** WAM R20199, 'adult male, rock crevice near summit of Mt. Herbert' (p. 307) (estimate: ~21.33°S, 117.22°E), by F.J. Mitchell and W.H. Butler on 25 July 1958.

Paratypes

Australia: ***Western Australia:*** WAM R20198, 'roof of cave near Tambrey Homestead'; WAM R20200, 'under rock, Big Hill Pool'; WAM R20201, 'rocks on table-land behind Tambrey Homestead'; WAM R20202, 'under rocks on the side of Mt. Herbert'; SAMA R496, 'under rocks on the side of Mt. Herbert'; SAMA R4597, R4601–2, '3 specimens from table-land behind Tambrey Homestead'; SAMA R4600, 'summit of Mt. Herbert'.

DIAGNOSIS

Differs from non-Australian *Gehyra* by lack of extensive webbing between toes III and IV, a cutaneous fold along the posterior margin of the hindlimb and the

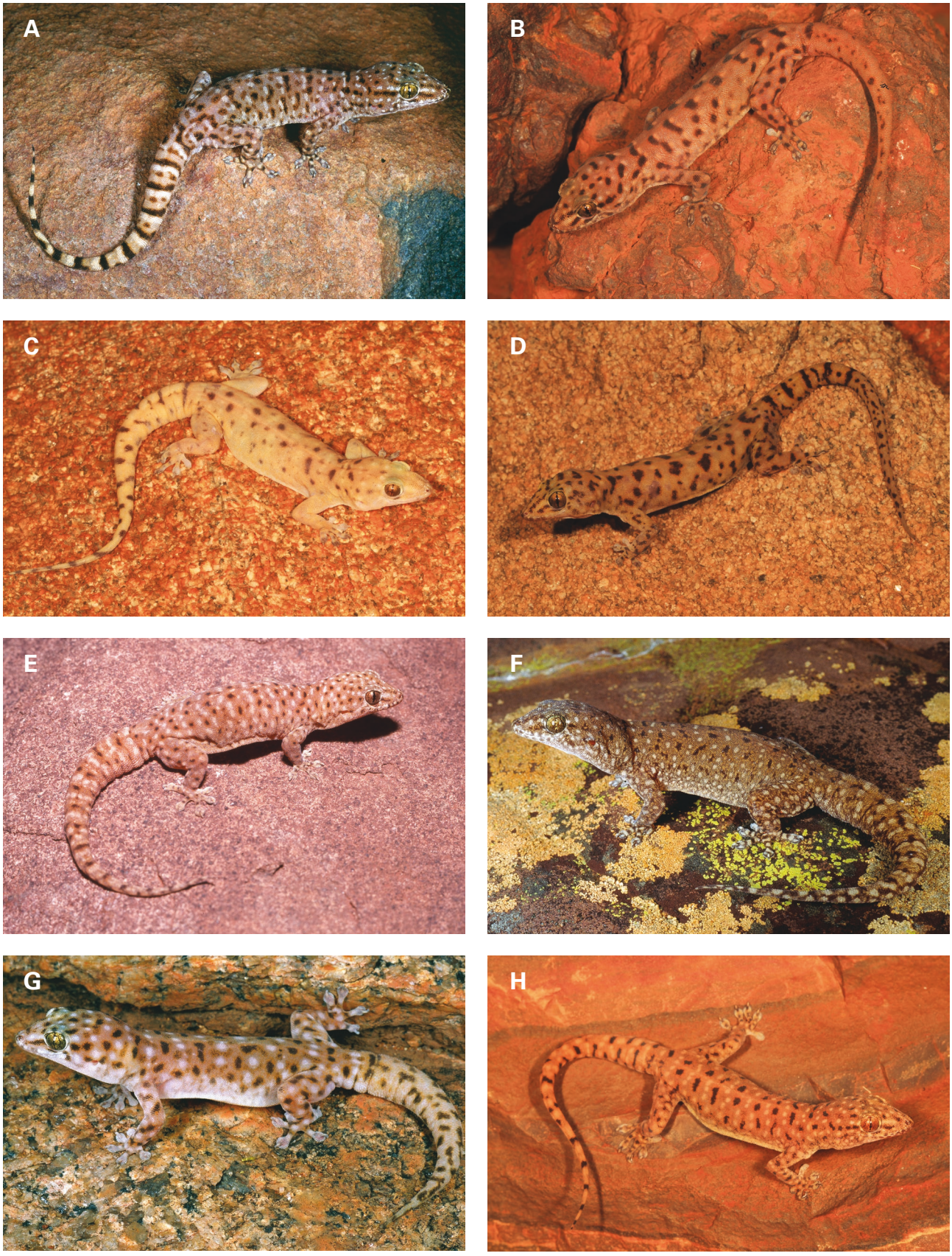

FIGURE 5 Images in life of the large-bodied members of the *Gehyra punctata* species-group: A) *G. punctata* – Burrup Peninsula, Western Australia (Photo: B. Maryan); B) *G. punctata* – Red Hill Station, Western Australia (Photo: R.J. Ellis); C–D) *G. macra* sp. nov. – Indee Station, Western Australia (Photo: R.J. Ellis); E) *G. punctulata* sp. nov. – Callytharra Springs, Western Australia (Photo: G.M Shea); F) *G. punctulata* sp. nov. – Butcher's Track, Muggon Station, Western Australia (Photo: B. Maryan); G) *G. polka* sp. nov. – Walga Rock, Western Australia (Photo: B. Maryan); H) *G. polka* sp. nov. – Mt Augustus, Western Australia (Photo: R.J. Ellis).

presence of transversely widened subcaudal scales. Distinguished from other Australian *Gehyra* by possession of moderate body size (up to 65 mm SVL), gabled rostral, upper postnasal 1/3 the size of lower, 9–12 supralabials, first supralabial narrower and taller than second, mental length short often with concave sides where in contact with first infralabial, two pairs of chin shields, inner chin shield in contact with second infralabial, first parinfralabial encroaching on posterior edge of third infralabial; subdigital lamellae on fourth toe 7–8, lamellae divided and without basal wedge of granules; background colour reddish-brown with markings consisting of dark (anterior) and pale (posterior) bars or spots usually in contact (or narrowly separated), occasionally forming transverse bars; canthal, loreal, temporal and upper post-orbital stripes usually present, post-orbital stripe variably expressed, often reduced to a spot, pale patch between canthal and loreal stripes near eye; original tails ringed by dark (anterior) and pale (posterior) bands; typically 11–15 pre-cloacal pores in males.

Further distinguished from other reddish-brown *Gehyra* from the region as follows. From *G. fenestrula* sp. nov., *G. media* sp. nov., *G. micra* sp. nov. and *G. peninsularis* sp. nov. by larger body size, broader snout, more pronounced jaw adductor muscles and first parinfralabial in contact with third (not second) infralabial; from *G. macra* sp. nov. by smaller body size, fewer subdigital lamellae and pre-cloacal pores, more reddish dorsum, and clearly demarcated markings comprised of dark (anterior) and pale (posterior) elements; from *G. punctulata* sp. nov. and *G. polka* sp. nov. by larger body size, first parinfralabial usually encroaching on posterior edge of third (not second) infralabial, and pale and dark elements of markings on dorsum in contact; from *G. pilbara* by larger body size, longer and broader snout, and larger markings on dorsum; and from *G. montium* by larger body size, absence of reticulations on dorsum and larger, more pronounced dark and pale markings.

DESCRIPTION

From series of recently collected specimens listed in Appendix 1. Body size medium (mean 59.3 mm SVL), habitus slightly robust, depressed dorsally, flat ventrally with defined ventro-lateral fold. Head depressed (HeadD = 38% HeadL), in profile snout long and eye over half the length of the snout, snout (interorbital/frontal region) almost straight (a slight convexity), canthus rounded and slightly raised forming shallow concavity in between canthal ridges, nostril region swollen; jaw adductor musculature robust and protruding laterally; in dorsal view, head widest behind eyes narrowing anteriorly to triangular snout with rounded tip; neck constricted to approximately 4/5 maximum head width. Scales on top and sides of snout >3 times larger than crown and rest of body; scales in contact with nostril – rostral, supranasal, 2 postnasals (upper one third the size of lower) and first supralabial; supralabials 9–12; infralabials 8–10; rostral strongly gabled dorsally, deeply furrowed medially, rostral crease 50–70% of height of rostral; internasals 0–1; nostrils circular and directed dorsally and slightly posteriorly. Mental triangular, penetrating 1/3 between inner chin shields, sides of mental in contact with first infralabial usually concave; inner chin shields in contact with second infralabial; outer chin shield ~60% of height of inner chin shield with straight to rounded outer edge, in contact with second (occasionally third) infralabial, first parinfralabial and granules below parinfralabials; eye moderate, pupil oval with crenulated edges (3 scallops on each side); above and anterior to eye a projecting ridge and posterior-dorsal edge slightly covered by layer of skin; ear opening oval and oriented vertically.

Dorsal scales small and homogeneous, juxtaposed, moderately rounded with apex slightly posterior; ventral scales 2–3 times larger than dorsal scales, flat and slightly imbricate. In males, pre-cloacal pores usually 11–15, arranged in a chevron with the apex pointing anteriorly; cloacal spurs 2–4 slightly enlarged, rounded and projecting scales on both sides of cloacal opening.

Limbs short, moderately developed; projecting narrow claws present on all digits except digit I, claw projects above and beyond expanded toe pads, dorsal edge of toe pad with elongate row of scales forming a fringe; below digit a single row of 6–8 enlarged round to oval tubercles increasing in size towards toe pads, distal 2–3 divided; no conspicuous webbing between digits; subdigital lamellae divided, no wedge of granules at base, number on fourth finger 6 or 7, fourth toe 7 or 8.

Tail long and thin, ovoid at body, tapering to a fine point; scales on dorsal surface of original tail ~2 x size of scales on body, flattened and arranged in regular rows; ventral scales of original tails enlarged and oriented transversely, scales on regenerated portion as for original but forming less regular rows on dorsal surface.

Colouration. In life, rich reddish-brown background colour on dorsum; approximately eight rows of markings (from neck to hindlimbs), markings consisting of a dark (anterior) spot or short bar in contact with a pale spot or bar, occasionally markings connect forming transverse rows (Figure 7). Head as for body but dark spots smaller, canthal, loreal and temporal stripes moderately marked but variable in expression, usually a dark upper post-orbital stripe but lower absent or reduced to a spot; labials, rostral and lower sides of snout dark brown, hiatus of pigment on labial sutures; dorsal surface of limbs with smaller or more diffuse markings; tail ringed by dark (anterior)

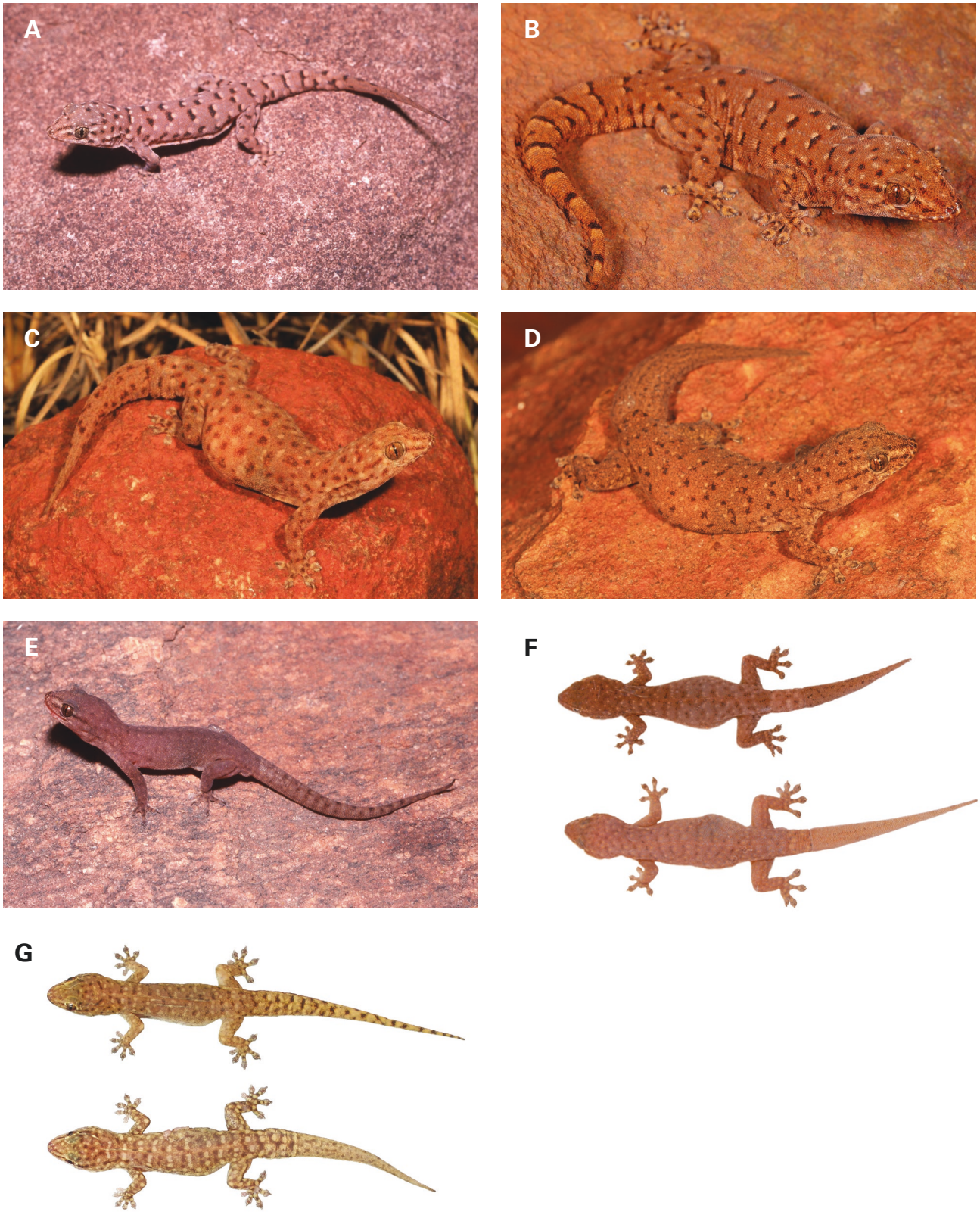

FIGURE 6 Images in life of small-bodied species of the *Gehyra punctata* species complex – *G. fenestrula* sp. nov. from the *G. punctata* species-group, and the three members of the *G. media* species-group: A) *G. fenestrula* sp. nov. – 31.3 km east of Prarie Downs, Western Australia (Photo: G.M. Shea); B) *G. fenestrula* sp. nov. – 28 km east of Newman, Western Australia (Photo: B. Maryan); C) *G. media* sp. nov. – 67 km south of Port Hedland, Western Australia (Photo: R.J. Ellis); D) *G. media* sp. nov. – Nanutarra Roadhouse, Western Australia (Photo: R.J. Ellis); E) *G. micra* sp. nov. – Ashburton Downs, Western Australia (Photo: G.M. Shea); F) *G. micra* sp. nov. – Wheelarra Hill, Western Australia (top – WAM R111845, bottom – WAM R11846) (Photos: P. Doughty); G) *G. peninsularis* sp. nov. – Burrup Peninsula, Western Australia (top – WAM R165748, bottom – WAM R165749) (Photos: P. Doughty).

and pale (posterior) bands; venter pale with diffuse pigmentation; infralabials, palmar and plantar surfaces and ventral surface of tail slightly darker; eye orange with dark pupil. In preservative, the reddish hues tend to be lost, and the markings less distinct.

VARIATION

Table 2 and Appendix 2 present variation in size and meristic characters, and Figure 7 shows a range of variation in dorsal patterns. The smallest male with fully expressed pre-cloacal pores was 52.0 mm SVL with 11 pores, with a likely subadult at 47.0 mm SVL with only 7 pores. Of 27 males, the lowest count was one individual with 9, otherwise the lowest was 11 (several males). Females with conspicuous eggs or enlarged follicles ranged from 48.0 mm to 58.5 mm SVL. Females lack pre-cloacal pores and enlarged cloacal spurs, but otherwise resemble males.

Colouration varied from a rich reddish-brown to a more subdued brown, the spots on the dorsum occasionally connected to form transverse bars, and the dark and pale elements were sometimes not in contact – usually narrow but occasionally evenly spaced. Juveniles and subadults possessed darker and more contrasting markings to background colour. Coastal Pilbara and Barrow Island individuals had prominent bars as well as small spots. Canthal, loreal and temporal head stripes were somewhat variably expressed, with wider and darker parts and thinner and lighter parts within the same stripe. Post-orbital stripes were more variable: the lower post-orbital stripe was occasionally present, and connected to ear opening in some specimens; upper post-orbital stripe was occasionally absent, although spots sometimes joined above eye to form an irregular stripe.

HABITAT AND ECOLOGY

Gehyra punctata is commonly encountered on the vertical faces of large boulders on rocky outcrops in the Pilbara region. Figure 8 shows a typical rock face on which *G. punctata* commonly occurs. Collectors' notes on the WAM database mention vertical rock faces, rock platforms, ironstone and granite outcrops, gorges, scree slopes, crevices and 'under rock on rock'. Occasional entries mention creek banks and rarely on trees or shrubs. PBS site descriptions mention the following attributes: boulder slope to range, massive outcrop, scree slope under scarp, stone valley floor and skeletal clay and stones over massive duricrust on top of mesa.

In the PBS, a large number of pitfall traps were deployed across the region to capture terrestrial vertebrates (McKenzie et al. 2009), and opportunistic searching at night for herpetofauna was also undertaken. It is interesting to note that very few *G. punctata* were captured in pitfall traps, whereas small-bodied members

FIGURE 7 Variation among *Gehyra punctata* specimens. Scale bar = 10 mm.

FIGURE 8 Typical habitat of *G. punctata* in the Pilbara: vertical rock face with deep crevices near Pannawonica (Photo: R.J. Ellis).

of the complex were trapped at much higher frequency in pitfall traps (Doughty et al. 2011). In contrast, searching for lizards with head torches at night on rocky ridges almost invariably resulted in large numbers of *G. punctata* seen and collected, with very few of the small-bodied *G. punctata* species complex members seen. This recent result mirrors the observations reported by Mitchell (1965) and reflect the preference of *G. punctata* to shelter in deep crevices on vertical rocks on cliff faces and boulder fields.

DISTRIBUTION

Generally confined to the Pilbara craton, except the northern portion of the Pilbara where it is replaced by *G. macra* sp. nov., with isolated populations in the western edge of the Little Sandy Desert. Also on Barrow Island (Figure 2).

REMARKS

In hindsight, Storr's decision to synonymise *G. fenestra* (Mitchell's large-bodied taxon) with *G. punctata* (believed by Mitchell to be the small-bodied form described by Fry) seems to be a case where wide variation in morphology resulted in a conservative application of a single name. However, previous workers could not have suspected the high numbers of *Gehyra* that occur in the Pilbara region at the time. Indeed, at the initiation of this project, we did not envisage so many species present in such a relatively small area, including the occurrence of *G. montium* as well as the species resembling *G. vareigata* described in Kealley et al. (2018). A problem in recognising the great diversity is the similar appearance of many of the species to each other, relative to *G. variegata*-like species – that is, reddish, spotted *Gehyra* associated with rocks. *Gehyra* can also be very variable in appearance within species (e.g. Sistrom et al. 2012; Hutchinson et al. 2014; Doughty et al. 2018). The presence of so many similar-looking species in one area resulted in Storr taking a conservative stance, viewing *G. 'punctata'* as a variable species, ultimately deciding to collapse them in to a single taxon. In addition, further collections from the Pilbara have uncovered more specimens of the newer species, although almost all were represented in collections that Storr examined.

As *G. punctata* is widespread throughout the Pilbara craton, including several national parks and nature reserves, and is abundant where it occurs, we regard it as being of least conservation concern.

ETYMOLOGY

Punctata means 'small spots'. Fry would have been using this name in reference to the spotted pattern in *G. punctata* as opposed to the network of irregular lines in *G. variegata* and other arboreal species.

***Gehyra macra* sp. nov.**

Large Pilbara Rock Gehyra

Figures 4, 5, 9

urn:lsid:zoobank.org:act:01D323B0-89A4-4008-AC0F-D4E702D3A6CA

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** WAM R162703, an adult male collected from Baldy Rock (21.05°S, 118.80°E), by P. Doughty, C.A. Stevenson, and P.G. Kendrick on 17 May 2006.

Paratypes

Australia: ***Western Australia:*** WAM R154517 (male), Yarrie Mining Camp (20.533°S, 120.233°E); WAM R156587 (male), (20.5488°S, 120.1681°E); R160096–7 (males), WAM R160098 (female), 13 km southeast of Braeside (21.280°S; 121.096°E); WAM R162688 (female), WARM R162701 (female), WAM R162702 (male), as for holotype; WAM R173363 (males), Roy Hill Rail chainage 76, 65 km south of Port Hedland (20.9658°S, 118.6844°E); WAM R173364 (female) and WAM R173366 (male), Roy Hill Rail chainage 75, 67 km south of Port Hedland (20.9618°S, 118.6846°E).

DIAGNOSIS

Differs from non-Australian *Gehyra* by lack of extensive webbing between toes III and IV and a cutaneous fold along the posterior margin of the hindlimb, and the presence of transversely widened subcaudal scales. Distinguished from Australian *G. variegata* group members by very large body size (to 73.5 mm SVL), depressed body and head, relatively slender tail, moderately long and broad snout with swollen nostril region, robust jaw adductor musculature, strongly gabled rostral, upper postnasal half the size of lower, 0–1 internasals, first supralabial slightly taller and narrower than second, 9–10 supralabials, inner chin shields in contact with second infralabial, first parinfralabial encroaching on third infralabial, fourth finger lamellae 8–9, fourth toe lamellae 8–10, lamellae divided and lacking wedge of granules at base of toe, pre-cloacal pores in adult males 14–21; reddish to greyish-brown background colour, dorsal pattern variable, with scattered pale and dark spots, short transverse bars or blotches usually not in contact, slightly paler vertebral zone, canthal and loreal head stripes present but variable expressed, temporal head stripe short or reduced to a spot, post-orbital stripes absent.

DESCRIPTION OF HOLOTYPE

Body size moderately large (69.0 mm SVL) with robust habitus, depressed dorsally, flat ventrally with defined ventro-lateral fold. Head depressed (HeadD = 35% HeadL), in profile snout moderately long and almost half as long as eye, snout (interorbital/frontal region) straight, canthus broadly rounded and slightly raised forming shallow depression in between canthal ridges, nostril region swollen; in dorsal view, head widest behind eyes narrowing anteriorly to broadly rounded snout; robust laterally protruding jaw adductor musculature, neck only slightly constricted. Scales on top and sides of snout >3 times larger than crown and rest of body; scales in contact with nostril – rostral, supranasal, 2 postnasals (upper half the size of lower) and first supralabial; first supralabial slightly taller and narrower than second; supralabials 10, infralabials 8; rostral height 1.9 mm, width 2.7 mm, strongly gabled dorsally, deeply furrowed medially, rostral crease ~45% of height of rostral; internasal 1; nostrils circular and directed dorsolaterally. Mental length 2.9 mm, width 2.8 mm, triangular with straight sides except concave where in contact with first infralabial, penetrating 1/3 in to inner chin shields; inner chin shields in short contact with second infralabial; chin shields ~60% of height of inner chin shield with rounded outer edge in contact with granules, first parinfralabial encroaching on posterior edge of third infralabial, an elongate granule between chin shield and third infralabial and in contact with posterior edge of second infralabial; eye relatively small, pupil oval with crenelated edges; above eye a projecting anterior ridge; ear opening moderately large, oval, and oriented at a 30° angle (anterior edge lower).

Dorsal scales small and homogeneous, juxtaposed, moderately rounded with apex slightly posterior; ventral scales 2–3 times larger than dorsal scales, flat and slightly imbricate; scales on limbs as for body. Pre-cloacal pores 17, arranged in a chevron with the apex pointing anteriorly; cloacal spurs 1 (right side) or 5 (left), slightly enlarged, rounded and projecting scales to either side of cloaca.

Limbs short, moderately developed; projecting narrow claws present on all digits except digit I, claw projects above and beyond expanded toe pads, dorsal edge of toe pad with elongate row of scales forming a fringe; below digit a row of 4–6 enlarged round to oval tubercles increasing in size towards toe pads, last 2–3 divided; no conspicuous webbing between digits; subdigital lamellae divided, number on fourth finger 9, fourth toe 10.

Tail ovoid at body, original portion swollen, regenerated portion gradually narrowing to a fine point; proximal original tail 25 mm from cloaca, distal regenerated portion 58 mm; scales on dorsal surface of original tail ~2 x size of scales on body, slightly imbricate and rounded with posterior apex, arranged in regular rows; ventral scales of original tails enlarged (3.9 x 1.6 mm at base) and oriented transversely, scales on regenerated portion as for original but forming less ordered rows.

Colouration (in preservative). Light brown pinkish-grey background colour on dorsum; scattered small to large dark brown and pale spots not in contact; head as for body but snout dark brown, canthal, loreal, temporal

FIGURE 9 Variation among *Gehyra macra* sp. nov. specimens. Holotype specimen is on the left. Scale bar = 20 mm (white and dark both 10 mm each).

FIGURE 10 Habitat of *G. macra* sp. nov. and *G. media* sp. nov. in the northern Pilbara (Indee Station): granitic outcrops with domes and boulder piles (Photo: R.J. Ellis).

stripes present, a poorly-defined upper post-orbital stripe, no lower post-orbital stripe; vertebral zone noticeably lighter in shade compared to surrounding areas on dorsum; dorsal surface of limbs with diffuse markings; venter pale with diffuse pigmentation (especially near ventrolateral edge), infralabials, and ventral surface of tail darker near edges, digits, palmar and plantar surfaces dark grey.

VARIATION

Table 2 and Appendix 2 show variation in meristic characters. Females lacked pores and the enlarged cloacal spurs of males. Pre-cloacal pores of males varied from 14–21, and there was no association with body size and number of pores (the largest male had the fewest pores).

Colouration varied from a light greyish-brown background to a dark reddish-brown. Dark and pale spots were scattered and usually not in contact. One specimen (WAM R160096, Figure 10) had dark bars with longitudinal extensions towards the midline, whereas another specimen (WAM R173366, Figures 5 and 9) had highly irregular-shaped dark blotches. A juvenile (WAM R132679) also showed a similar pattern, and the markings are more vibrant than in larger individuals. Figure 9 shows variation across several specimens.

HABITAT AND ECOLOGY

From collector's notes and personal observations, individuals have been collected from beneath exfoliating rocks on granite rock outcrops (Figure 10), with observations of individuals running across the tops of domes towards shelter (P. Doughty, M. Pepper, R.J. Ellis, pers. obs.).

DISTRIBUTION

Confined to the northern edge of the Pilbara, including south and east of Port Hedland, Shay Gap, Cundaline Gap and near Braeside on the eastern edge of the Pilbara (Figure 2).

REMARKS

Although only weakly divergent from *G. punctata* in the mtDNA phylogram shown in Figure 1, *G. macra* sp. nov. differed in the nDNA data set of Ashman et al. (2018) and differed strikingly in morphology across several characters as well. The more subdued greyish-brown colouration with more poorly-defined spots compared to *G. punctata* may be an adaptation to the relatively low and browner granite outcrops of the northern Pilbara where this species occurs (Pepper et al. 2013).

In addition to the large body size, this species is extremely robust, with a large deep head and well-developed jaw adductor musculature. This is the largest species of the entire arid zone radiation of the *G. variegata* group, and with only *G. occidentalis* from the northern Kimberley in the *G. nana* clade reaching similar sizes (~75 mm maximum SVL).

Owing to its remote location, relatively large distribution and occurrence on less lucrative granitic geology (vs ironstones to the south), we regard this species as of least conservation concern. However, more information on its ecology and habitat preferences are warranted, including the extent of its true distribution in the Pilbara.

ETYMOLOGY

Macra is derived from the Greek *makros* meaning large or long. It is used as an adjective here.

***Gehyra punctulata* sp. nov.**

Small-spotted Mid-west Rock Gehyra

Figures 5, 11

urn:lsid:zoobank.org:act:9D5BF909-B245-4235-9680-4F7828D3DED2

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** WAM R139194, an adult male collected at Mount Minnie (22.2650°S, 115.4072°E) by P.G. Kendrick on 26 June 2000.

Paratypes

Australia: ***Western Australia:*** WAM R113599 and WAM R113633 (males), 30 km east-north-east of Nanutarra (22.4166°S, 115.6167°E); WAM R117038 (female) and WAM R117040 (male), 18 km west of Mt Stuart Homestead (22.4333°S, 115.8833°E); WAM R131769 (female), Muggon Station (26.6166°S, 115.5333°E); WAM R163106 (female), 19.5 km south-south-west of Mt Amy (22.4193°S, 115.8380°E).

DIAGNOSIS

Differs from non-Australian *Gehyra* by lack of extensive webbing between toes III and IV and a cutaneous fold along the posterior margin of the hindlimb and transversely widened subcaudal scales. Distinguished from other Australian *Gehyra* by possession of moderate body size (up to 56 mm SVL) and broad snout, dorsal edge of rostral flat to gabled and moderately furrowed, upper postnasal 1/3 the size of lower, 9–10 supralabials, first supralabial slightly taller and narrower than second, inner chin shields in contact with second infralabial, first parinfralabial in contact with posterior edge of second infralabial, mental scale penetrates along half the length of the inner chin shields with straight sides or slight concavity in contact with first infralabial, subdigital lamellae on fourth finger 6–7, fourth toe 7–8, lamellae divided and without basal wedge of granules; background colour light reddish to

greyish-brown with small dark and pale spots not in contact and evenly spaced, canthal stripe weak, loreal and temporal stripe variable, post-orbital stripes absent, tail with alternating dark and pale rows of spots, dark spots forming bands distally.

Further distinguished from other reddish-brown *Gehyra* in the mid-west and Pilbara regions as follows. It resembles *G. polka* sp. nov. most closely but differs by possessing a darker and more stippled background with smaller spots. From *G. media* sp. nov., *G. micra* sp. nov. and *G. peninsularis* sp. nov. by larger body size, longer and more depressed snout and more numerous supralabials and subdigital lamellae; from *G. punctata* by slightly smaller body size, first parinfralabial encroaching on posterior edge of second (not third) infralabial and dark and pale spots on dorsum not in contact; from *G. macra* sp. nov. by smaller body size, fewer subdigital lamellae and pre-cloacal pores, more reddish dorsum, clearly demarcated spots and lack of a pale, narrow vertebral stripe; from *G. pilbara* and *G. montium* by larger body size, longer snout, and distinct markings on dorsum without background reticulations.

DESCRIPTION OF HOLOTYPE

Body size medium (54.0 mm SVL), depressed dorsally, flat ventrally with defined ventro-lateral fold (Figure 11). Head moderately depressed (HeadD = 38% HeadL), in profile snout moderately long and less than twice the length of the eye, snout (interorbital/frontal region) straight, canthus broadly rounded and slightly raised forming shallow depression in between canthal ridges, nostril region slightly swollen; moderately developed jaw adductor musculature protruding laterally posterior to mouth; in dorsal view head widest behind eyes narrowing anteriorly to triangular snout with rounded tip; neck constricted to approximately 4/5 maximum head width. Scales on top and sides of snout >3 times larger than crown and rest of body; scales in contact with nostril – rostral, supranasal, 2 postnasals (upper 40% the size of lower) and first supralabial; supralabials 9, infralabials 9; rostral height 1.3 mm, width 2.2 mm, rostral flat dorsally, furrowed medially, rostral crease 40% of height of rostral, then angling to right for another 20% of rostral length; internasals 1; nostrils circular and directed dorsolaterally. Mental triangular, length 2.6 mm, width 2.0 mm, penetrating 55% in to inner chin shields, sides slightly concave where in contact with first infralabial; inner chin shields in broad contact with second infralabial; outer chin shield 2/3 the height of inner chin shield with rounded outer edge in contact with second infralabial, first parinfralabial and enlarged granule below parinfralabial row; pupil oval with crenulated edges (3 scallops on each side); above and anterior to eye a projecting ridge and posterior-dorsal edge slightly covered by layer of skin; ear openings oval and oriented horizontally with anterior end more dorsal than posterior.

Dorsal scales small and homogeneous, juxtaposed, moderately rounded with apex slightly posterior; ventral scales ~2 times larger than dorsal scales, flat and slightly imbricate; scales on limbs as for body. Pre-cloacal pores 10, arranged in a chevron with the apex pointing anteriorly; cloacal spurs in a single row with 3 (right) and 2 (left) enlarged and projecting scales on both sides of cloacal opening.

Limbs short and moderately developed; projecting narrow claws present on all digits except digit I, claw projects above and beyond expanded toe pads, dorsal edge of toe pad with elongate row of scales forming a fringe; below digit a single row of 6–8 enlarged round to oval tubercles increasing in size towards toe pads, distal tubercle divided; no conspicuous webbing between digits; subdigital lamellae divided, no wedge of granules at base, number on fourth finger 7, fourth toe 8.

Tail long and thin, somewhat depressed basally, becoming cylindrical distally, tapering to a fine point; original portion 6 mm, regenerated portion 43 mm with irregular longitudinal folds along dorsal surface (an artefact of preservation) and irregular rows of scales dorsally and transversely elongated subcaudals.

Colouration. In preservative, light brown background colour on dorsum; small dark brown and pale spots from snout to end of original portion of tail; pale spots rounded with thin dark brown border, dark markings rounded with some more irregularly shaped; dark and pale markings not in contact and evenly spaced on dorsum. Head as for body but dark spots smaller; canthal and loreal stripes weak, weak temporal stripe posterior to eye on right side, pale patch between canthal and loreal stripes, left temporal and post-orbital stripes absent reduced to a spot; supralabials, rostral and lower sides of snout moderately stippled with dark brown; dorsal surface of limbs with diffuse alternating light and dark spots; venter pale yellowy-cream.

VARIATION

Table 2 and Appendix 2 presents variation in size and meristic characters, and Figure 11 illustrates the range of variation found in dorsal patterns. Females lack pre-cloacal pores and cloacal spurs, but otherwise resemble males. A male with a SVL of 43 mm had 10 pores that were only weakly expressed, indicating an approximate size at maturity. There were no gravid females or any with noticeable follicular development in the sample.

On original tails scales on the dorsal surface were arranged in regular transverse rows, with transversely widened subcaudal scales, with the proximal 1–5 scales potentially divided.

Background colouration varies from a light reddish-brown to dark greyish-brown. The spots on the dorsum were usually small, with a few individuals having somewhat larger spots. Most spots circular, but some irregular and tending to elongate transversely. In the

FIGURE 11 Variation among *Gehyra punctulata* sp. nov. specimens. Holotype specimen is on the left. Scale bar = 10 mm. (Photo: R.J. Ellis).

majority of individuals spots were scattered evenly, with others having the spots form alternating rows of dark and pale spots. Original tails had alternating rows of dark and pale spots, with the dark spots tending to coalesce to form solid bands, especially distally.

HABITAT AND ECOLOGY

Very little is known of this species. Collector's notes mention granite outcrops and ridges, a dry stream bed and undulating stony ground. Specimens collected from rock crevices, under exfoliating granite slabs, rocks or under rubbish.

DISTRIBUTION

Occurs inland of the mid-west coast of Western Australia. In the south, from Toolonga Nature Reserve near Murchison, north to Callythara Springs, 40 km east of Gascoyne Junction. A separate population from genotyped individuals occurs in the western Pilbara area, from approximately 100 km south-east of Onslow in the Cane River area (Figure 2).

We include one subadult specimen with atypically large spots for this species (WAM R114320) from near Collier Range National Park based on an allozyme profile that placed it within *G. punctulata* sp. nov. This indicates that this species could also occur to the east in the Ashburton region south of the Pilbara and *G. punctata* and north of *G. polka* sp. nov. Further collecting from this area could better resolve species boundaries and evaluate the possibility of introgression.

REMARKS

As for *G. polka* sp. nov., this species was recovered from the Ashman et al. (2018) exon capture analysis as an independent evolving lineage, and we also found support for its distinctiveness from the mtDNA data (Figure 1). Within this lineage, the two geographically separated populations of genotyped individuals are also distinct in the mtDNA phylogram. It is likely there are intervening populations in between these two known ones, and there were no obvious phenotypic differences between them. The elongate north-south distribution inland along the coast appears to follow granitic outcrops, with *G. polka* sp. nov. replacing this species to the east. Resolving where precisely the two species come together is an area for future research, as they are similar in body size and appearance. Owing to this species' broad distribution and abundance where it occurs, we regard it as being of least conservation concern.

ETYMOLOGY

Punctulata is the diminutive of *punctata*, referring to this species' smaller spots relative to those of *G. punctata* and *G. polka* sp. nov.

Gehyra polka sp. nov.

Large-spotted Mid-west Rock Gehyra

Figures 5, 12

urn:lsid:zoobank.org:act:E74FB1B1-B463-4762-B537-9DA0A79C7F4F

HOLOTYPE

Australia: ***Western Australia:*** WAM R132290, an adult male collected 6 km north-west of Noondie Outstation (27.0744°S, 117.0789°E) by B. Maryan on 11 April 1998.

PARATYPES

Australia: ***Western Australia:*** WAM R119368–9 (males), 50 km south-west of Yalgoo (28.65°S, 116.30°E); WAM R127414–5 (males), 10.3 km south of Yinnietharra Homestead (24.7202°S, 116.1197°E); WAM R127543 (female), Barnong Homestead (28.6333°S, 116.2833°E); WAM R132291 (male), as for holotype; WAM R132294 (male), Marlandy Hill (28.1216°S, 117.2331°E).

DIAGNOSIS

Differs from non-Australian *Gehyra* by lack of extensive webbing between toes III and IV and a cutaneous fold along the posterior margin of the hindlimb, and the presence of transversely widened subcaudal scales. Distinguished from other Australian *Gehyra* by possession of moderate body size (up to 61 mm SVL) and widened snout, well-developed jaw adductor musculature, moderately gabled rostral, upper postnasal 1/3 the size of lower, 9–10 supralabials, first supralabial slightly taller and narrower than second, inner chin shields in contact with second infralabial, first parinfralabial in contact with posterior edge of second infralabial, mental scale long, penetrating along half the length of the inner chin shields with straight sides or slight concavity when in contact with first infralabial, subdigital lamellae on fourth finger 6–7, fourth toe 7–8, lamellae divided and without basal wedge of granules; background colour reddish-brown with large dark and pale spots not in contact, canthal stripe weak, loreal and temporal stripes variably expressed, no post-orbital stripes, tail with alternating dark and pale bands.

Further distinguished from other reddish-brown *Gehyra* in the mid-west and Pilbara regions as follows. It resembles *G. punctulata* sp. nov. most closely, but differs by possessing a more plain and reddish background with larger spots. From *G. media* sp. nov., *G. micra* sp. nov. and *G. peninsularis* sp. nov. by larger body size, longer and more depressed snout and more numerous supralabials and subdigital lamellae; from *G. punctata* by slightly smaller body size, first parinfralabial encroaching on posterior edge of second (vs third) infralabial and dark and pale spots on dorsum not in contact; from *G. macra* sp. nov. by smaller body size, fewer subdigital lamellae and pre-cloacal pores, more reddish dorsum, clearly demarcated spots and lack of a pale, narrow vertebral stripe; from *G. pilbara* and *G. montium* by larger body size, longer snout, and distinct markings on dorsum without background reticulations.

DESCRIPTION OF HOLOTYPE

Body size medium (56.0 mm SVL), depressed dorsally, flat ventrally with defined ventro-lateral fold (Figure 12). Head moderately depressed (HeadD = 40% HeadL), in profile snout moderately long and less than twice the length of the eye, snout (interorbital/frontal region) straight, canthus broadly rounded and slightly raised forming shallow depression in between canthal ridges, nostril region swollen; in dorsal view snout moderately wide, jaw adductor musculature well-developed and laterally protruding behind jaw, head widest behind eyes narrowing anteriorly to triangular snout with rounded tip; neck constricted to approximately 3/4 maximum head width. Scales on top and sides of snout >3 times larger than crown and rest of body; scales in contact with nostril – rostral, supranasal, 2 postnasals (upper one third the size of lower), and first supralabial; supralabials 9, infralabials 7; rostral height 1.5 mm, width 2.2 mm, rostral gabled dorsally, deeply furrowed medially, rostral crease 40% of height of rostral; internasals 1; nostrils circular and directed dorsolaterally. Mental triangular, length 2.8 mm, width 1.9 mm, penetrating 2/3 in to inner chin shields, sides slightly concave where in contact with first infralabial; inner chin shields in broad contact with second infralabial; outer chin shield half the height of inner chin shield with straight to rounded outer edge in contact with second infralabial, first parinfralabial, and granules below parinfralabials; pupil oval with crenulated edges (3 scallops on each side); above and anterior to eye a projecting ridge and posterior-dorsal edge slightly covered by layer of skin; ear opening round (right) or slightly oval and oriented horizontally (left).

Dorsal scales small and homogeneous, juxtaposed, moderately rounded with apex slightly posterior; scales on flanks slightly smaller and arranged more irregularly; ventral scales ~2 times larger than dorsal scales, flat and slightly imbricate; scales on limbs as for body. Pre-cloacal pores 12, arranged in a chevron with the apex pointing anteriorly; cloacal spurs 3 enlarged and projecting scales on both sides of cloacal opening.

Limbs short and moderately developed; projecting narrow claws present on all digits except digit I, claw projects above and beyond expanded toe pads, dorsal edge of toe pad with elongate row of scales forming a fringe; below digit a single row of 6–8 enlarged round to oval tubercles increasing in size towards toe pads, distal tubercle divided; no conspicuous webbing between digits; subdigital lamellae divided, no wedge of granules at base, number on fourth finger 6, fourth toe 7.

Tail original, long and thin, somewhat depressed basally, becoming cylindrical distally, tapering to a

fine point; scales on dorsal surface of original tail ~2 x size of scales on body, flattened and arranged in regular rows; ventral scales of original tails enlarged (2.5 x 1.4 mm at base) and oriented transversely.

Colouration. In preservative, light brown background colour on dorsum; alternating rows of predominantly transversely-oriented dark brown and pale markings from snout to end of original portion of tail; whitish markings rounded to oval spots, dark markings more variable in shape, some asymmetrical and/or fused to form larger blotches; dark and pale markings not touching on dorsum. Head as for body but dark spots smaller; canthal stripes weak, loreal stripe present and continuing as weak temporal stripe posterior to eye, pale patch between canthal and loreal stripes, a short dark post-orbital stripe on right side, less distinct on left; supralabials, rostral and lower sides of snout lightly stippled with dark brown; inner chin shields pale white; dorsal surface of limbs with diffuse alternating light and dark markings; venter pale cream; ventral surface of tail slightly darker, with dorsal pattern extending onto lateral subcaudal surfaces.

VARIATION

Table 2 and Appendix 2 presents variation in size and meristic characters, and Figure 12 illustrates the range of variation found in dorsal patterns. Females lack pre-cloacal pores and enlarged cloacal spurs, but otherwise resemble males. Background colouration varies from a rich to light reddish-brown. The spots on the dorsum exhibit a range of size variation from fine to quite large, with most pale white spots being large and circular but with some individuals having more irregular spots (Figure 12); dark spots tending to be more irregularly shaped. Rows of spots generally evenly spaced, with 6–9 rows of dark markings between nape and sacrum; pale spots often with diffuse edges, especially on flanks, and poorly defined anterior to orbits. Dark markings on tail sometimes forming complete narrow transverse bands proximally; dark and light markings may contact one another on tail. In life, anteriormost granular throat scales and medial portion of tail venter with an orangey-brown suffusion; dark dorsal and hindlimb markings surrounded by 2–3 rows of taupe to orange-tinged granules; iris coppery. As for the other species, juveniles tend to have darker and more contrasting markings.

HABITAT AND ECOLOGY

Rocky outcrops, including sandstone, granite and metamorphosed rocks. Notes from collectors indicate specimens were often encountered under slabs of rocks at the top of outcrops, and active individuals are seen on vertical rock faces as well as horizontal surfaces. Figure 13 shows a typical boulder pile where *G. polka* sp. nov. occur in the Weld Range.

DISTRIBUTION

Occurs in the mid-west of Western Australia, as far south and west approximately 150 km east of Geraldton near Yalgoo, then inland north through Mt Magnet, Meekatharra and Kumarina, and as far north and west as Mt Augustus (Figure 2). Outlying records were found near Karratha at Mardie Pool. This may have resulted from an error handling the tissue sample in the field or in the lab. Alternatively, this is a popular camping area for the Pilbara region (P. Kendrick, pers. comm.) and the specimens may have been inadvertently transported here.

FIGURE 12 Variation among *Gehyra polka* sp. nov. specimens. Holotype specimen is on the left. Scale bar = 10 mm.

FIGURE 13 Habitat of *G. polka* sp. nov.: dark granitic jumbled rock in Weld Range (Photo: R.J. Ellis).

REMARKS

It is interesting to note the clear genetic separation of *G. punctulata* sp. nov. and *G. polka* sp. nov. in Ashman et al. (2018), although the sample sizes were small (4 and 2, respectively). Our mtDNA analysis also recovered these taxa as monophyletic lineages, but with some geographic structure evident. The similarity between the two species indicates a moderate-large body size in the regions south of the Pilbara may be adaptive in the absence of both larger-bodied rock-dwelling *Gehyra* species (*G. punctata* and *G. macra* sp. nov.) and the smaller saxicoline species (*G. fenestrula* sp. nov., *G. media* sp. nov., *G. micra* sp. nov. and *G. peninsularis* sp. nov.).

Owing to its southern occurrence, many photographs of '*G. punctata*' are of this species (e.g. Storr et al. 1990, plate 10, Figure 1; Bush et al. 2007). This species is widespread and locally abundant in rocky areas that are unsuitable for agriculture, although they may be locally affected by mining activity. It occurs in protected areas at Mt Augustus National Park and other reserves from ex-pastoral leases (e.g., Waldburg and Mt Phillip). We therefore regard it as of least conservation concern.

ETYMOLOGY

Polka is an allusion to the polka dot patterns on the dorsum of this species. The Bohemian 'polka dance' was fashionable in the mid-19th century, and *polka* was appended to the names of many goods and objects, but only 'polka dot' is in use today. The word may have been a modification of the Czech *pulka*, meaning 'half', in reference to the quick steps employed in the dance. Used as a noun in apposition.

***Gehyra fenestrula* sp. nov.**

Hamersley Range Spotted Gehyra

Figures 6, 14

urn:lsid:zoobank.org:act:6E92943F-8CB1-4DA2-B10D-381FBB7850C9

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** WAM R111769, male collected from Wheelarra Hill (PBS site BDRS03; 23.3586°S, 120.4590°E) by Pearson, D., Morris, K. and Pepper, M. on 2 October 2005.

Paratypes

Australia: ***Western Australia:*** WAM R71633 (male), 21 km west-south-west Marillana homestead (22.67°S, 119.22°E); WAM R114337 (male), 35 km southeast of Prarie Downs (23.7166°S, 119.4333°E); WAM R125083

(female), 15 km east of Newman (23.37°S, 119.90°E); WAM R127475 (female), 32 km south of Newman (23.65°S, 119.72°E); WAM R129925 (female), West Angelas, 100 km west-north-west from Newman (23.25°S, 118.67°E); WAM R135018 (female), Mt Whaleback (23.3347°S; 119.6694°E).

DIAGNOSIS

Differs from non-Australian *Gehyra* by lack of extensive webbing between toes III and IV and a cutaneous fold along the posterior margin of the hindlimb, and the presence of transversely widened subcaudal scales. Distinguished from other Australian *Gehyra* by moderately small body size (to 48.0 mm SVL), depressed body and head, moderately long and narrow snout with swollen nostril region, gabled rostral, upper postnasal slightly smaller than lower, 0–2 internasals, 8–10 supralabials, first supralabial narrower and taller than second, inner chin shields usually in contact with second infralabial, or if not, narrowly excluded, first parinfralabial encroaching on second or rarely third infralabial, fourth finger lamellae 5–6, fourth toe lamellae 6–7, lamellae divided and lacking wedge of granules at base of toe, pre-cloacal pores in adult males 9–12; in preservative, light to dark brown background colour, dorsal pattern with small widely scattered spots, spots formed by dark (anterior) and pale (posterior) elements in contact, spots sometimes forming irregular transverse rows; loreal and temporal head stripes moderately developed, canthal stripe weak, post-orbital stripes absent or reduced to a spot; white patch above and below loreal and occasionally temporal stripe.

Further distinguished from other *Gehyra* from the region with reddish-brown colouration as follows: from *G. punctata*, *G. macra* sp. nov., *G. punctulata* sp. nov. and *G. polka* sp. nov. by smaller body size and fewer subdigital lamellae; further distinguished from *G. macra* sp. nov. by adult males possessing fewer pre-cloacal pores (9–12 vs. 14–21); from *G. media* sp. nov., *G. micra* sp. nov. and *G. peninsularis* sp. nov. by more numerous supralabials; from *G. pilbara* by longer and more depressed head, longer inner chin shields in contact with second infralabial and spots on dorsum more clearly demarcated from background colour; and from *G. montium* by fewer subdigital lamellae and lacking short bars (vs spots) or network of irregular dark lines.

DESCRIPTION OF HOLOTYPE

Body size moderately small (44.5 mm SVL), depressed dorsally, flat ventrally with defined ventro-lateral edge. Head depressed (HeadD = 39% HeadL), in profile snout moderately long, snout (interorbital/frontal region) straight with angle just anterior to eyes, canthus broadly rounded and slightly raised forming shallow depression in between canthal ridges, nostril region swollen; in dorsal view head widest behind eyes narrowing anteriorly to rounded snout; neck only slightly constricted. Scales on top and sides of snout ~3 times larger than crown and rest of body; scales in contact with nostril – rostral, supranasal, 2 postnasals (upper slightly smaller than lower) and first supralabial; first supralabial slightly taller than second; supralabials 9, infralabials 7; rostral height 1.1 mm, width 1.8 mm, deeply furrowed medially, rostral crease ~55% of height of rostral; internasal 1; nostrils circular and directed dorsolaterally. Mental length 2.0 mm, width 1.6 mm, triangular, straight sides shared with first infralabial, penetrating 50% along inner chin shields; inner chin shields in moderate contact with second infralabial; chin shields ~55% of height of inner chin shield with rounded outer edge in contact with 1st parinfralabial and surrounding granules, first parinfralabial encroaching on posterior edge of second infralabial; pupil oval with crenelated edges (spectacle opaque); above and anterior to eye a projecting ridge; ear opening moderately large, oval, and oriented at a 30° angle (anterior edge lower).

Dorsal scales small and homogeneous, juxtaposed, moderately rounded with apex slightly posterior; ventral scales 2–3 times larger than dorsal scales, flat and slightly imbricate; scales on limbs as for body. Pre-cloacal pores 9, arranged in a shallow chevron with the apex pointing anteriorly; cloacal spurs 3 on each side, slightly enlarged, rounded and projecting scales to either side of cloaca.

Limbs short and moderately developed; projecting narrow claws present on all digits except digit I, claw projects above and beyond expanded toe pads, dorsal edge of toe pad with elongate row of scales forming a fringe; below digit a row of 6–9 enlarged round to oval tubercles increasing in size towards toe pads, last 2–3 divided; no conspicuous webbing between digits; subdigital lamellae divided, number on fourth finger 5, fourth toe 6.

Tail ovoid at body, original portion swollen, regenerated portion gradually narrowing to a fine point, but with a 5 mm regenerated portion coming off the tip of the tail at nearly a right angle; proximal original tail 15 mm from cloaca, distal regenerated portion 19 mm; scales on dorsal surface of original tail ~2 x size of scales on body, slightly imbricate and rounded with posterior apex, arranged in regular rows; ventral scales of original tails enlarged (2.1 x 0.9 mm at base) and oriented transversely (proximal 3–4 scales divided), scales on regenerated portion as for original but forming less ordered rows on dorsal surfaces, ventral surfaces with enlarged transverse scales as for original portion.

Colouration (in preservative). Light brown background colour on dorsum; widely scattered small dark brown and pale spots in contact or slightly separated, with dark anterior element and pale posterior element; dark elements above shoulders forming short bars; head as for body, canthal, loreal, temporal stripes present, weak lower post-orbital stripe; dorsal surface of limbs with fine dark and pale spots; venter pale with diffuse pigmentation (especially near ventrolateral edge), infralabials, and ventral surface of tail darker near edges, digits, palmar and plantar surfaces grey.

VARIATION

Table 2 and Appendix 2 present variation in quantitative characters, Figure 6 shows two individuals in life and Figure 14 shows variation in dorsal patterning in preserved specimens. Body size of measured specimens varied between 36.0–48.0 mm SVL, with the smallest male possessing pre-cloacal pores at 43.5 mm SVL. Despite a female-biased sample, only one large female (48.0 mm SVL) was conspicuously gravid. Other specimens were generally <30 mm SVL. There were only four adult males, and pre-cloacal pore counts were 9, 11, 11 and 12.

Other specimens had similar colouration and patterning to the holotype, a light sandy brown to dark reddish-brown background colour. Spotting showed more variation, with a typical pattern of dark (anterior) and pale (posterior) elements in contact, spots overall quite small and widely spaced. A variation in several specimens was the pale element of the spot being circular and somewhat large, resulting in the dark anterior element having a 'U'-shape. In one individual (WAM R125083) the spots formed transverse rows, especially posteriorly.

HABITAT AND ECOLOGY

Very little known, as the description is based on relatively few specimens. Collectors' notes mention occurrence on banded ironstone outcrops, under granite caprock, edge of river gorge and shrubland and spinifex steppe on Mt Whaleback. PBS sites where specimens were pit-trapped occurred on rocky outcrops with large boulders and scree.

DISTRIBUTION

Restricted to a relatively small area in the south-east Pilbara region of Western Australia, including Packsaddle Range, Mt Whaleback and other locations near the mining town of Newman (Figure 3).

REMARKS

Gehyra fenestrula sp. nov. is an unusual species, as it has a body size typical of many other species of the arid clade of the *G. variegata* group (mean ~41 mm SVL), yet appears to be a basal lineage of the large-bodied *G. punctata* complex members (Figure 1). Coupled with its restricted range in the south-eastern Pilbara and unique dorsal pattern of small widely-spaced spots with dark and pale elements together, *G. fenestrula* sp. nov. seems to be more of a relictual species that persists in the Hamersley Range despite the evolution and expansion of more recent and widespread species such as *G. punctata* and *G. micra* sp. nov.

Despite its relatively restricted distribution compared to other species treated here, *G. fenestrula* sp. nov. occurs over a wide enough area in the Pilbara such that its conservation status would seem to be secure, i.e. least

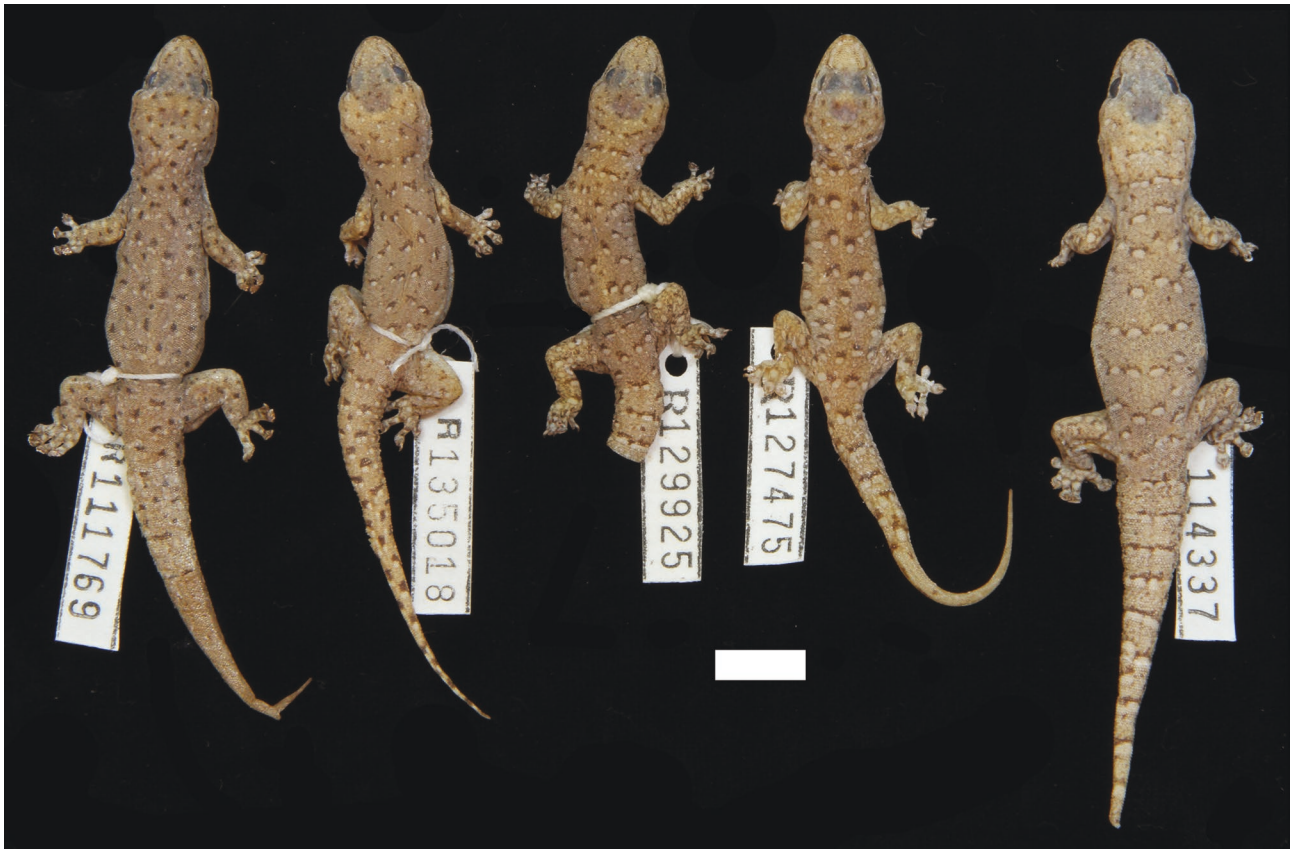

FIGURE 14 Variation among *Gehyra fenestrula* sp. nov. specimens. Holotype specimen is on the left. Scale bar = 10 mm.

concern. Nevertheless, further studies on its behaviour and habitats would be of interest, especially how it interacts ecologically with other similar and related rock-dwelling forms where it occurs.

ETYMOLOGY

Fenestrula is the diminutive of *fenestra* and refers to the fact that this species is the smallest member of the large-bodied *G. punctata* complex lineage, to which the junior synonym *G. fenestra* Mitchell belongs. The name thereby acknowledges Mitchell's contributions to Pilbara *Gehyra* systematics despite having his name of *fenestra* being a junior synonym of *punctata* owing to the inability of WAM staff to locate Fry's *punctata* type in the 1960s.

***Gehyra media* sp. nov.**

Medium Pilbara Spotted Rock Gehyra

Figures 4, 6, 15

urn:lsid:zoobank.org:act:665D3755-5CD0-44F0-B03F-A568C0FC4686

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** WAM R162687, adult male, collected from Baldy Rock, Pilbara region (21.05°S, 118.80°E), by P. Doughty, C.A. Stevenson and P.G. Kendrick on 15 May 2006.

Paratypes

Australia: ***Western Australia:*** WAM R160940, male, 9 km northwest of Lake Poongkaliyarra (20.9399°S, 118.0640°E); WAM R161014, female, 3.5 km south of Marda Pool (21.065°S, 116.150°E); WAM R162686, male, as for holotype; WAM R162704, female, as for holotype; WAM R174289, female, Nanutarra Roadhouse (22.46434°S, 116.03714°E).

DIAGNOSIS

Differs from non-Australian *Gehyra* by lack of extensive webbing between toes III and IV, a cutaneous fold along the posterior margin of the hindlimb, and the presence of transversely widened subcaudal scales. Differs from other Australian *Gehyra* by possessing small body size, moderately narrow snout, weakly gabled rostral, upper postnasal half to 1/3 the size of lower, 7–9 supralabials, first supralabial taller and usually narrower than second, mental long with straight sides, inner chin shields in contact or narrowly excluded with second infralabial, second infralabial notched by encroachment of first parinfralabial, 5 or 6 divided lamellae on the fourth toe (without basal wedge of granules), in adult males 8–15 pre-cloacal pores arranged in a chevron. Dorsal pattern with dark brown and pale spots on light reddish-brown background, spots usually not in contact; canthal and loreal stripes weak, temporal stripe variable expressed, post-orbital stripes reduced to at most a spot, pale zone between canthal and loreal stripes.

Further distinguished from other *Gehyra* from the region with reddish-brown colouration as follows: from *G. punctata*, *G. macra* sp. nov., *G. punctulata* sp. nov. and *G. polka* sp. nov. by smaller body size, shorter and more convex snout and fewer subdigital lamellae; further distinguished from *G. macra* sp. nov. by adult males possessing fewer pre-cloacal pores (8–15 vs 14–21); from *G. fenestrula* sp. nov. by dark and pale spots separated (vs joined); from *G. micra* sp. nov. by slightly larger body size, broader snout and dorsal pattern consisting of scattered spots (vs rows of short bars) and pale spots with dark border; from *G. peninsularis* sp. nov. by fewer subdigital lamellae (5–6 vs 6–7) and pattern consisting of small spots not in contact (vs large spots tending to form transverse rows); from *G. pilbara* by longer and more depressed head, longer inner chin shields in contact with first infralabial and spots on dorsum more clearly demarcated from background colour; and from *G. montium* by fewer subdigital lamellae and lacking short bars (vs spots) or network of irregular dark lines.

DESCRIPTION OF HOLOTYPE

Body size small (48.0 mm SVL), depressed dorsally, flat ventrally with defined ventro-lateral edge. Head depressed (HeadD = 33% HeadL), snout short and narrow with orbit length over half the length of the snout; snout shape (interorbital/frontal region) convex, a fold of skin on snout (an artefact of preservation), canthus broadly rounded and poorly defined, nostril region only slightly swollen at tip; in dorsal view head widest behind eyes narrowing anteriorly to triangular snout with rounded tip; neck constricted to 3/4 maximum head width. Scales on top and sides of snout >3 times larger than crown and rest of body; scales in contact with nostril – rostral, supranasal, 2 postnasals (lower twice the size of upper) and first supralabial; supralabials 8, first taller and narrower than second, infralabials 7; rostral width 2.1 mm, height 1.2 mm, weakly gabled dorsally, furrowed medially, rostral crease ~50% of height of rostral; internasal 1; nostrils circular and directed laterodorsally. Mental 1.7 mm long, 1.5 mm wide, triangular with straight sides, penetrating 1/3 in to inner chin shields; elongate inner chin shields in contact with second infralabial; outer chin shields 2/3 the height of inner chin shield, in contact with second infralabial and first parinfralabial; third chin shield 1/3 height of outer. Eye large, pupil oval with crenulated edges (3 scallops on each side); above and anterior to eye a projecting ridge with posterior-dorsal edge slightly covered by superficial layer of skin; ear opening small and circular.

FIGURE 15 Variation among *Gehyra media* sp. nov. specimens. Holotype specimen is on the left. Scale bar = 10 mm.

Dorsal scales small and homogeneous, juxtaposed, moderately rounded with apex slightly posterior; ventral scales 2–3 times larger than dorsal scales, flat and slightly imbricate; scales on limbs as for body. Pre-cloacal pores 9, arranged in a short chevron with the apex pointing anteriorly; cloacal spurs – 3 slightly enlarged, rounded and projecting scales on each side of cloaca.

Limbs short and moderately developed; projecting narrow claws present on all digits except digit I, claws project above and beyond expanded toe pads, dorsal edge of toe pad with elongate row of scales forming a fringe; below digit a row of enlarged round to oval tubercles increasing in size towards toe pads, distal 2–3 tubercles divided; no conspicuous webbing between digits; subdigital lamellae divided, no wedge of granules at base, number of subdigital lamellae on fourth finger and toe 6.

Tail long and thin, slightly ovoid at body, tapering to a fine point; original tail 55 mm; scales on dorsal surface of original tail ~2 x size of scales on body, squarish, flattened and arranged in regular rows; ventral scales of tail enlarged (up to 1.6 x 1.1 mm near base) and oriented transversely or divided and squarish with rounded posterior edges.

Colouration. In life, a light brown background colour with loosely formed rows of rich reddish-brown blotches and small pale spots; reddish-brown blotches occasionally joining to form short transverse bars; canthal, loreal and temporal stripes present, with pale area between canthal and loreal stripes, post-orbital stripes reduced to a spot at most; pale spots finer on top of head and snout and larger on tail; tail without well-defined bands except near tip; eye reddish-orange with dark pupil. In preservative, as for life except as follows: light brown background colour on dorsum; pale spots with dark brown border; supralabials, rostral and lower sides of snout dark brown; dorsal surface of limbs as for head; venter pale, infralabials slightly darker.

VARIATION

Table 2 and Appendix 2 present variation in quantitative characters, and Figures 6 and 15 show a range of dorsal patterns. Body size ranged up to 50.0 mm SVL. To increase sample sizes, we scored 13 additional males not measured for Table 2 and Appendix 2 for the presence and number of pre-cloacal pores, and the average of 18 males was 10.8, range of 8–15. The smallest male with pores was 32.5 mm SVL. Females lack pre-cloacal pores and enlarged cloacal

spurs, instead having slightly raised analogous scales bordering the cloaca. Several females possessed eggs or large follicles (always only one), with the smallest reproductively active female being 38.0 mm SVL. This indicates a large range in adult body sizes for both males and females of this species.

For patterning, the spots in juveniles often had the dark and pale markings in contact, but with an increase in size the spots tended to spread apart more conspicuously representing a possible age shift in this character. The well-defined border of the small pale spots is usually visible in preserved specimens, but in some individuals it is not apparent. Some individuals (e.g. WAM R159912) had very fine spots covering the dorsum. Regenerated tails had some spotting with highly variable and irregular patterns.

HABITAT AND ECOLOGY

Collection notes mention under small rocks near roadsides, *Triodia* plain on stony sandy soil, granite rocks, rocky drainage lines, sandplain and dune slope. Human habitats include under sheets of tin and 'old airstrip'. Of the PBS sites where specimens were pit-trapped, notes on habitat included low stony hills, bedrock debris, rock fragments, scree and gravel on the lower slopes of hills, thin layer of rock pebbles and clay over massive stone, broken rocks and stones on outcrop surface and a low ridge on slope of basalt outcrop. These site descriptions are of low-lying rocks rather than large boulders on outcrops that the *G. punctata* species-group members typically inhabit.

DISTRIBUTION

Pilbara region of Western Australia (Figure 3). *Gehyra media* sp. nov. occurs throughout the Pilbara, except in the Hamersley Range.

REMARKS

Within the Pilbara region, *G. media* sp. nov. occurs in the northern portion and also extends to the western area south-west of Pannawonica. Although *G. micra* sp. nov. also has a small body size, *G. media* sp. nov. is slightly larger, suggesting some habitat partitioning between the two species. Interestingly, it is absent from the Hamersley Range, although the small-bodied species *G. fenestrula* sp. nov. and *G. micra* sp. nov. occur in the eastern portion.

Owing to its widespread distribution in the Pilbara and apparent abundance, we regard this species as of least conservation concern.

ETYMOLOGY

Media is derived from the neuter of *medius*, meaning middle, in reference to this species' intermediate size between *G. micra* sp. nov. and *G. macra* sp. nov.

***Gehyra micra* sp. nov.**

Small Pilbara Spotted Rock Gehyra

Figures 6, 16

urn:lsid:zoobank.org:act:535AB2F7-FDF7-4388-8035-0DFE5A8595F6

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** WAM R165158, adult male, collected from 3.5 km north of Karratha Station (PBS site DRW05) (20.8539°S, 116.669°E), by P. Doughty and L. Gibson on 17 May 2005.

Paratypes

Australia: ***Western Australia:*** WAM R110011 (female), 6 km north-west of Roebourne (20.7364°S, 117.099°E); WAM R110013 (male), 5 km south of Lake Poongkaliyarra (21.0364°S, 117.106°E); WAM R110045 (female) and WAM R110073 (female), 13.5 km west of Wickam (PBS site DRC11) (20.6884°S, 117.007°E); WAM R125029 (male), Yandicoogina (22.7125°S, 119.0672°E); R160879 (female), 3.5 km south of Marda Pool (PBS site DRW11) (21.0655°S; 116.15°E).

DIAGNOSIS

Differs from non-Australian *Gehyra* by lack of extensive webbing between toes III and IV and a cutaneous fold along the posterior margin of the hindlimb, and the presence of transversely widened subcaudal scales. Distinguished from other Australian *Gehyra* by small body size (mean 37.4 mm, maximum 46.5 mm SVL), depressed body and head, snout short and narrow with slightly swollen nostril region, top of rostral weakly curved, upper postnasal smaller than lower postnasal; postnasals ~half the size of supranasals; 0–1 small internasals; nostril surrounded by rostral, supranasal, 2 postnasals and first supralabial; 8 or 9 supralabials, first supralabial slightly taller and narrower than second; mental elongate with straight sides and penetrating to half the length of the inner chin shield, inner chin shields in contact with second infralabial, first parinfralabial encroaching on second (usually) or third (occasionally) infralabial, fourth finger and toe lamellae 5–6, lamellae divided and lacking wedge of granules at base of toe, pre-cloacal pores in adult males 10–19; reddish-brown background colour, dorsal pattern with short transverse pale and dark bars or spots not in contact; canthal, loreal and temporal stripes present, white patch between canthal and loreal stripes and pale bar above temporal stripe usually present.

Further distinguished from other reddish-brown *Gehyra* in the Pilbara as follows. From *G. peninsularis* sp. nov. by less elongate body shape, spots on dorsum smaller with pale spots tending to form transverse bars, canthal stripe darker, and scales on chin more pigmented; from *G. media* sp. nov. by smaller body

FIGURE 16 Variation among *Gehyra micra* sp. nov. specimens. Holotype specimen is on the left. Scale bar = 10 mm.

size, narrower snout and spots tending to be ordered in rows with pale spots lacking dark edging and often forming transverse bars; from *G. fenestrula* sp. nov. by smaller body size, narrower snout, fewer supralabials and subdigital lamellae, and pale spots tending to form transverse bars with dark and pale elements not in contact; from *G. punctata* by smaller body size, deeper head, fewer supralabials and subdigital lamellae and pale dark and pale elements of markings not in contact; from *G. macra* sp. nov. by much smaller body size, fewer supralabials and subdigital lamellae, more reddish dorsum and clearly demarcated spots; from *G. pilbara* by longer and narrower snout, chin shields not very reduced in length and lacking a diffuse reticulum as a dorsal background pattern; from *G. montium* by smaller body size, narrower snout, fewer subdigital lamellae, more numerous pre-cloacal pores and lacking dark reticulum on dorsum.

DESCRIPTION OF HOLOTYPE

Body size small (35.0 mm SVL), depressed dorsally, flat ventrally with defined ventro-lateral fold. Head moderately depressed (HeadD = 39% HeadL), in profile snout moderately long and longer than eye, snout (interorbital/frontal region) straight, canthus broadly rounded and slightly raised forming shallow depression in between canthal ridges, nostril region only slightly swollen; in dorsal view head widest behind eyes narrowing anteriorly to relatively narrow snout; neck constricted to 2/3 of the widest part of the head. Scales on top and sides of snout >3 times larger than crown and rest of body; scales in contact with nostril – rostral, supranasal, 2 postnasals (upper half the size of lower), and first supralabial; first supralabial slightly taller and narrower than second; supralabials 8, infralabials 7; rostral height 0.9 mm, width 1.4 mm, slightly rounded dorsally, weakly furrowed medially, rostral crease ~55% of height of rostral; internasals 0; nostrils circular and directed dorsolaterally and slightly anteriorly. Mental length 1.6 mm, width 1.4 mm, triangular, penetrating just over half the length of the inner chin shields; inner chin shields in short contact with second infralabial; outer chin shields 2/3 the height of inner chin shield with rounded outer edge (right) or more acute edge (left) in contact with granules, first parinfralabial encroaching on posterior edge of second infralabial, followed by 2 (right) or 3 (left) parinfralabials; eye relatively small, pupil oval with crenelated edges; above and anterior to eye a projecting ridge; ear opening moderate size, oval, and lower edge angled forward ~10°.

Dorsal scales small and homogeneous, juxtaposed, moderately rounded with apex slightly posterior; ventral scales 2–3 times larger than dorsal scales, flat and slightly imbricate; scales on limbs as for body. Pre-cloacal pores 17, arranged in a chevron with the apex pointing anteriorly; cloacal spurs 1 (right side) or 5 (left), slightly enlarged, rounded and projecting scales to either side of cloaca.

Limbs short, arms slender, legs more robust; projecting narrow claws present on all digits except digit I, claw projects above and beyond expanded toe pads, dorsal edge of toe pad with elongate row of scales forming a fringe; below digit a row of 3–6 enlarged round to oval tubercles increasing in size towards toe pads, last 2–3 divided; no conspicuous webbing between digits; subdigital lamellae divided, number on fourth finger 5, fourth toe 6. Tail ovoid at body, but broken near body; regenerated portion 48 mm, narrowing to a point.

Colouration (in preservative). Light greyish-brown background colour on dorsum and upper surfaces; rows of alternating pale or brown transverse bars (or spots on nape and crown) not in contact; canthal, loreal and temporal stripes present, pale patch between canthal and loreal stripes, pale bar posterior to eye above temporal stripe; labial scales stippled with hiatus near sutures; dorsal surface of limbs with scattered pale spots; venter dull cream; infralabials, upper limbs, posterior edge of thigh, digits, and palmar and plantar surfaces dark grey.

VARIATION

Table 2 and Appendix 2 presents variation in quantitative characters, and Figure 16 shows a range of dorsal patterns. The smallest male with fully expressed pre-cloacal pores was 33.5 mm SVL, with another male that was 30.0 mm SVL having 13 pores that were only weakly perforated. The smallest female with an enlarged follicle or egg was 34.5 mm SVL. Most adult body sizes were in the 35–40 mm SVL range, but with an exceptionally large individual reaching a maximum of 46.5 mm SVL.

Pattern was somewhat variable, with usually short dark and pale bars across the dorsum, often forming transverse rows but many individuals had isolated spots. The head stripes were variably expressed as well, but the loreal and temporal stripe were prominent, canthal stripe usually present but variably expressed and post-orbital stripes absent or reduced to a spot at best.

HABITAT AND ECOLOGY

Encountered among low rocks on horizontal surfaces, only rarely observed on vertical rocks or trees. Typical habitats are like the scree at the base of the vertical rock face to the left in Figure 8. Collectors' notes indicate its occurrence on *Triodia* plains on stony sandy soil, rocky hills and gorges, schist and granite outcrops, under rocks, with one specimen on a rock face and one 1.5 m on a small tree in a creek line.

During the PBS survey, as for *G. media* sp. nov., this species was captured in high numbers in pitfall traps (Doughty et al. 2011). PBS sites where *G. micra* sp. nov. was captured include rocky hillsides, scree and gibber below massive outcrops and breakaway, sides of basalt hills with rock fragments, *Triodia* hilltop with bedrock debris, valley floor plain with pebbles, duricrust on top of mesa and rock-sheets below outcrops (McKenzie et al. 2009).

DISTRIBUTION

Occurs widely across the Pilbara craton, but absent from the central and western portions of the Hamersley Range and also the Burrup Peninsula near Karratha where it is replaced by *G. peninsularis* sp. nov. (Figure 3).

REMARKS

This species is one of the smallest within the arid clade of the *Gehyra variegata* group at typically less than 40 mm SVL. This small body size with narrower snout and preference for low rocks indicates a decided shift away from the climbing habits of other species from the *G. punctata* species-group. However, it is similar in body size and habits to *G. media* sp. nov., and the two species overlap over most of the Pilbara, suggesting they may differ subtly in habitat preferences and feeding ecology that are yet to be discerned. However, these two species do slightly displace each other geographically with *G. micra* sp. nov. absent from the northern edge of the Pilbara, and *G. media* sp. nov. absent from the Hamersley Range and areas to the east where records of *G. micra* sp. nov. occur (Figure 3).

Owing to this species' abundance and widespread distribution in the Pilbara, we regard its conservation status as of least concern.

ETYMOLOGY

Micra is derived from the Greek *mikros* meaning small. Used as an adjective.

***Gehyra peninsularis* sp. nov.**

Burrup Peninsula Rock Gehyra

Figures 6, 17

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MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** WAM R165749, an adult male collected from Dampier Port, Burrup Peninsula (20.6166°S, 116.7500°E) by G. Harold and L. Beesley on 26 April 2006.

Paratypes

Australia: ***Western Australia:*** WAM R132562 (female), WAM R146581 (male), Burrup Peninsula (20.6161°S, 116.7850°E); WAM R165748 (female), as for holotype; WAM R165239 (female), 2.4 km west of Hearson Cove, Burrup Peninsula (20.617°S, 116.772°E); WAM R165240 (male), 3.4 km north-east of Dampier, Burrup Peninsula (20.658°S, 116.741°E).

DIAGNOSIS

Differs from non-Australian *Gehyra* by lack of extensive webbing between toes III and IV and a cutaneous fold along the posterior margin of the hindlimb, and the presence of transversely widened subcaudal scales. Distinguished from other Australian *Gehyra* by small body size (mean 42.2 mm, maximum 48.5 mm SVL), depressed body and head, snout short and narrow with slightly swollen nostril region, top of rostral weakly curved, furrowed medially, upper postnasal half the size of lower; 0–1 small internasals (supranasals usually in contact); nostril surrounded by rostral, supranasal, 2 postnasals and first supralabial; 7–10 supralabials, first supralabial slightly taller and narrower than second, mental elongate with straight sides and penetrating to approximately half the length of the inner chin shield, inner chin shields in contact with second infralabial, first parinfralabial encroaching on second (usually) or third (occasionally) infralabial; fourth finger and toe lamellae 5–6, lamellae divided and lacking wedge of granules at base of toe, pre-cloacal pores in adult males 7–15; light reddish-brown background colour, dorsal pattern comprised of rows of alternating moderately large pale and dark spots, often forming transverse bars; canthal, loreal and temporal stripes present, pale white patch between canthal and loreal stripes and pale bar above temporal stripe usually present.

Further distinguished from other reddish-brown *Gehyra* in the Pilbara as follows. From *G. media* sp. nov. by larger spots tending to be in contact and forming transverse bars, and pale spots lacking dark edging; from *G. micra* sp. nov. by more elongate body shape and spots on dorsum larger, forming thicker transverse bars; from *G. fenestrula* sp. nov. by deeper head, fewer supralabials, and pale spots tending to form transverse bars with dark and pale elements not in contact; from *G. punctata* by smaller body size, deeper head, fewer supralabials and subdigital lamellae and pale dark and pale elements of markings not usually in contact; from *G. macra* sp. nov. by much smaller body size, fewer supralabials and subdigital lamellae, more reddish dorsum and clearly demarcated spots; from *G. pilbara* by longer and narrower snout, chin shields not very reduced in length and lacking a diffuse reticulum as a dorsal background pattern; from *G. montium* by narrower snout, inner chin shield in contact with second infralabial and different dorsal pattern: lacking short dark and pale bars and/or dark reticulum on dorsum.

DESCRIPTION OF HOLOTYPE

Body size small (41.0 mm SVL), depressed dorsally, flat ventrally with defined ventro-lateral fold. Head moderately depressed (HeadD = 37% HeadL), in profile snout moderately long and longer than eye, snout (interorbital/frontal region) straight, canthus broadly rounded and slightly raised forming shallow depression in between canthal ridges, nostril region only slightly swollen; in dorsal view head widest behind eyes narrowing anteriorly to triangular snout with rounded tip; neck constricted to approximately ¾ maximum head width; scales on top and sides of snout >3 times larger than crown and rest of body; scales in contact with nostril – rostral, supranasal, 2 postnasals (upper half the size of lower), and first supralabial; first supralabial slightly taller and narrower than second; supralabials 8, infralabials 7; rostral height 0.9 mm, width 1.8 mm, flat dorsally, furrowed medially, rostral crease ~50% of height of rostral; no internasals; nostrils circular and directed dorsolaterally and slightly anteriorly. Mental length 1.8 mm, width 1.9 mm, narrow and triangular, penetrating half the length of the inner chin shields; inner chin shields in narrow contact with first infralabial; outer chin shields 2/3 the height of inner chin shield, first parinfralabial encroaching on posterior edge of second infralabial; pupil oval with crenelated edges; above and anterior to eye a projecting ridge; ear opening moderate size, oval, and lower edge angled forward ~30°.

Dorsal scales small and homogeneous, juxtaposed, moderately rounded with apex slightly posterior; ventral scales 2–3 times larger than dorsal scales, flat and slightly imbricate; scales on limbs as for body; pre-cloacal pores 14, arranged in a chevron with the apex pointing anteriorly; cloacal spurs 3 on each side, slightly enlarged, rounded and projecting scales to either side of cloaca.

Limbs short, arms slender, legs more robust; projecting narrow claws present on all digits except digit I, claw projects above and beyond expanded toe pads, dorsal edge of toe pad with elongate row of scales forming a fringe; below digit a row of 3–5 enlarged round to oval tubercles increasing in size towards toe pads, last 1–3 divided; no conspicuous webbing between digits; subdigital lamellae divided, number on fourth finger 5, fourth toe 6. Tail ovoid at body, original portion 10 mm and swollen, regenerated portion ~34 mm and gradually narrowing to a fine point; scales on dorsal surface of original tail ~2 x size of scales on body, slightly imbricate and rounded with posterior apex, arranged in regular rows; ventral scales of original tails enlarged and oriented transversely, scales on regenerated portion as for original but forming less ordered rows.

Colouration. In preservative, light brown background colour on dorsum; alternating regular rows of moderately large pale or dark spots on dorsum. Head as for body but dark spots smaller; canthal stripe weak, loreal and temporal stripes present, post-orbital stripes absent, white patch between canthal and loreal stripes; labial scales near tip of snout lightly pigmented, hiatus of pigment near sutures; dorsal surface of limbs with pale scattered spots; venter pale cream.

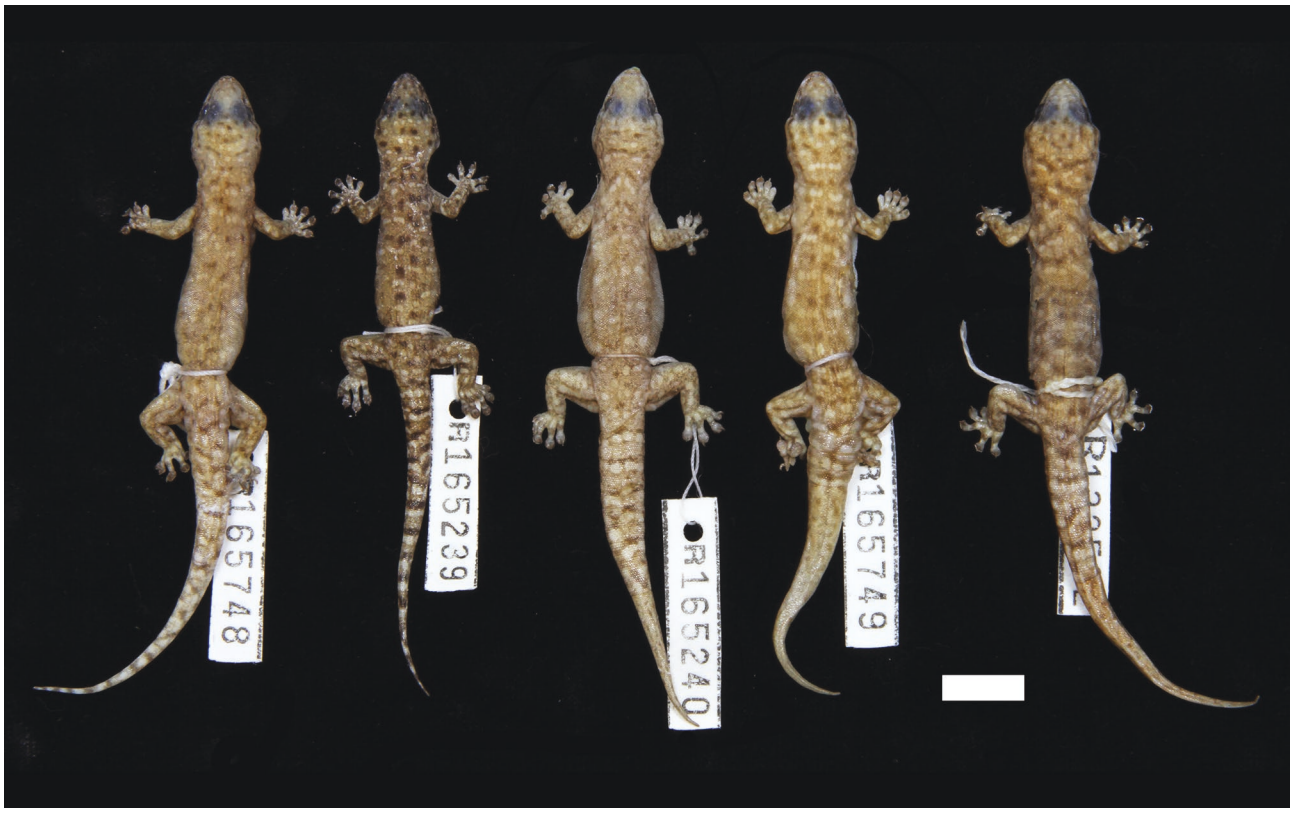

FIGURE 17 Variation among *Gehyra peninsularis* sp. nov. specimens. Holotype specimen is second from the right. Scale bar = 10 mm.

VARIATION

Table 2 and Appendix 2 present variation in quantitative characters, and Figure 17 shows a range of dorsal patterns. The smallest male with fully expressed pre-cloacal pores was 35.5 mm SVL. Most adult body sizes were in the 35–45 mm SVL range, but with a maximum of 48.5 mm SVL.

In life, the background colour is a rich reddish-brown (Figure 6), with yellowish-white pale spots and dark brown markings; in preservative, background colour varied from a light to medium-dark brown. The spots on the dorsum sometimes were so close as to form almost continuous rows (cf. WAM R132562), ranging to more widely separated (WAM R165748).

ECOLOGY AND HABITAT

There are almost no habitat notes for this species, other than a single mention of 'creek line' on the WAM database for one specimen (WAM R164116). Given the habitats where it occurs and the reddish, spotted pattern it is likely to be a terrestrial species living among rocks and stones (i.e. not vertical crevices in boulders as for the *G. punctata* species-group members).

DISTRIBUTION

Confined to the Burrup Peninsula and offshore islands in the northern Pilbara near Karratha, including the Dampier port and West Intercourse Island (Figure 3).

REMARKS

This species is closely related to *G. micra* sp. nov., with *G. peninsularis* appearing as a lineage within this species in the mtDNA data (Figure 1) but positioned as a basal lineage within the Ashman et al. (2018) exon capture data set and distinctive with respect to allozymes as well (M. Adams and P. Doughty, unpublished data). Coupled with the slightly elongate body shape, large rows of spots on the dorsum and geographical isolation on the Burrup Peninsula, the combined evidence indicates this is a distinctive independently evolving lineage. Populations of *Crenadactylus pilbarensis* Doughty, Ellis and Oliver, 2016 from the Burrup Peninsula were also slightly genetically distinctive (Oliver et al. 2010) as well as *G. punctata* with differences in allozymes (M. Adams and P. Doughty, unpublished data). The history of the Burrup Peninsula as a potential refugium may be of interest biogeographically, especially coupled with studies of the effects of changes in sea levels connecting current offshore islands, including Barrow Island, and the mainland.

Owing to this species' restricted distribution, we regard its conservation status as 'data deficient'.

ETYMOLOGY

The specific name of *peninsularis* refers to this species' occurrence on the Burrup Peninsula on the northern Pilbara coast.

DISCUSSION

Storr's (1982) taxonomic conservatism with respect to the reddish-brown spotted *Gehyra* of the Pilbara was understandable, given the paucity of collections then available and the lack of genetic analyses with which to evaluate phylogenetic structure and species boundaries. However, both general surveys and directed fieldwork in the Pilbara have generated large collections of *Gehyra* in recent decades, yielding geographically representative genetic samples and series of specimens large enough to meaningfully evaluate intra- vs. interspecific variation. This has permitted us to make progress in the face of what King (1979) rightly considered a 'taxonomist's nightmare'. Our method followed the approach of integrative taxonomy (Padial et al. 2010) in which molecular data and morphology provide independent lines of evidence to support the recognition of species level lineages that are both monophyletic and morphologically diagnosable and are broadly consistent with the general lineage species concept (de Querioz 1998).

We relied on three main lines of evidence in this study, including morphology, a mtDNA data set that screened hundreds of individuals across the region, and a recently published phylogeny that sequenced hundreds of nDNA genes but with very few individuals per lineage sampled. Each data source excels in some areas but has weaknesses in others. For morphology, phenotypic expression of colouration can be highly variable and convergent, with patterns fading in preservation leading to the loss of characters. Moreover, the body plan of *Gehyra* is highly conserved across this old and widespread group, with only subtle changes in shape across widely divergent lineages (Heinicke et al. 2011; Ashman et al. 2018; Doughty et al. 2018; Kealley et al. 2018). However, the benefit of working with morphology is that many potentially informative characters can be inexpensively assessed. For the mtDNA evidence, incomplete lineage sorting and introgression after divergence can obscure patterns of evolutionary history (Maddison and Knowles 2006). On the other hand, sufficient numbers of specimens can be incorporated into such analyses to evaluate putative morphologically-derived clusters of specimens and to estimate true geographic distribution, an important outcome when working with cryptic species (Kealley et al. 2018). Obtaining and analysing nDNA sequences is far more laborious in terms of time and cost, resulting in very few individuals being sequenced. However, the insight gained from such analyses can provide robust tests of whether putative taxa behave as independently-evolving lineages, a crucial step in evaluating whether to refer to such lineages as species (Fujita et al. 2012; Sukumaran and Knowles 2017).

In practice, the key to assigning names to lineages in this study first required the stabilisation of the name *G. punctata*, the application of which had been uncertain since its first use more than a century ago. After this was accomplished, we needed to evaluate the validity of *G. fenestra*, itself an unstable and uncertain entity since its proposal by Mitchell (1965). Having identified the genetic lineage to which both of these names correctly apply, all other lineages recognised through genetic means could be characterised and diagnosed morphologically and formally described. This integrative approach taken here and elsewhere recently (e.g. Sistrom et al. 2009; Doughty et al. 2012, 2018; Hutchinson et al. 2014; Oliver et al. 2016; Kealley et al. 2018) has proved highly effective at resolving cryptic diversity in conservative *Gehyra* lineages.

The resolution of the *Gehyra punctata* species complex here reveals an intriguing large-scale biogeographic pattern that can provide insights into the evolution of the Australian arid zone fauna. The most apparent pattern of Pilbara region *Gehyra* is the high species diversity for saxicoline species compared to arboreal and generalist species such as *G. variegata* and *G. purpurascens* in the arid zone (see also Pepper et al. 2014; Heineke et al. 2017; Ashman et al. 2018). The arboreal-generalist species tend to have massive distributions across the arid zone, whereas the saxicoline species have much smaller distributions, possibly reflecting patterns of diversity related to the rocky regions such as the Pilbara and Central Ranges that serve as ancient refugia that are able to promote speciation through time (Doughty et al. 2011; Pepper et al. 2013; Ashman et al. 2018). The lower diversity of arboreal-generalist species may be correlated with their habitat preferences for trees and shrubs because arboreal habitats are continuous through the arid zone compared to the clumped nature of rocky refugia. Interestingly, within the arboreal lineages the evolution of saxicoline forms has occurred multiple times, e.g. *G. minuta*, *G. einasleighensis* and other occasions in the *G. variegata* species-group (Ashman et al. 2018; Kealley et al. 2018).

Within the saxicoline species of the Pilbara region there were interesting patterns of body size and distribution. For instance, the *G. punctata* species-group and *G. media* species-group members with generally large differences in body size and habitat preferences had wide overlap within the Pilbara craton. For the large-bodied species of the *G. punctata* species-group, they appeared to be parapatric with *G. macra* sp. nov. occurring exclusively in the northern Pilbara and *G. punctata* to the south. The nature of the rock outcrops within these distributions also differs with ironstones to the south and more granitoids in the north, and the species may be adapted to these different substrates (Pepper et al. 2013), bearing in mind the complex matrix of habitat types in close proximity in the Pilbara (Doughty et al. 2011). The Hamersley endemic species *G. fenestrula* sp. nov. is a basal member of the *G. punctata* species-group and has a moderate body size more typical of other arid clade members of the *G. variegata* group (see also Ashman et al. 2018). It overlaps broadly with *G. punctata* and *G. micra* sp. nov., possibly indicating a different habitat preference from those more recently evolved species. For the

two southern *G. punctata* species-group members, *G. punctulata* sp. nov. and *G. polka* sp. nov., these species did not overlap with either the larger-bodied members of their species-group to the north and no *G. media* species-group members occur south of the Pilbara. These southern species possessed body sizes that were intermediate, possibly reflecting evolution of a more generalised saxicoline body size in the absence of other competition. Within the *G. media* species-group, *G. media* sp. nov. and *G. micra* sp. nov. differed slightly in body size and had areas of wide overlap throughout the Pilbara, but with the northern (*G. media* sp. nov. only) and Hamersley Range (*G. micra* sp. nov. only) areas where there was only a single species. *Gehyra peninsularis* sp. nov. appears to be an allopatric replacement of other *G. micra* sp. nov. lineages on the Burrup Peninsula. These speculations and more sophisticated biogeographic scenarios could be further tested, but the description of the species here and in Kealley et al. (2018) and other works on *Gehyra* provide a fertile field of further enquiry.

In addition to being ideal groups for studying a variety of evolutionary questions, much of biodiversity may remain hidden in highly variable species complexes, which can have impact on the design of reserves to capture the most phylogenetic diversity (Rosauer et al. 2018). In this instance the resolution of the reddish-brown spotted *Gehyra* provides further evidence of the now well established distinctiveness and high endemism of the Pilbara (Powney et al. 2010; Doughty et al. 2011; Pepper et al. 2013), but it also reveals patterns of endemism and richness within the Pilbara that had not been previously appreciated. With at least an initial understanding of the spatial distribution of the species treated in this study we can begin to evaluate the ways in which body size and microhabitat use are associated with lineage diversification in what we now know to be a relatively species rich radiation of *Gehyra*.

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REFERENCES

Adler, K. (2007). *Contributions to the history of herpetology, part 2.* Society for the Study of Amphibians and Reptiles: Saint Louis, U.S.A.

Ashman, L.G., Bragg, J.G., Doughty, P., Hutchinson, M.N., Bank, S., Matzke, N.J., Oliver, P.M., and Moritz, C. (2018). Diversification across biomes in a continental lizard radiation. *Evolution*: in press.

Bauer, A.M., Jackman, T., Sadlier, R.A. & Whitaker, A.H. (2006) A revision of the *Bavayia validiclavis* group (Squamata: Gekkota: Diplodactylidae), a clade of New Caledonian geckos exhibiting microendemism. *Proceedings of the California Academy of Sciences* **57**: 503–547.

Bergmann, P.J. and Russell, A.P. (2007) Systematics and biogeography of the widespread Neotropical gekkonid genus *Thecadactylus* (Squamata), with the description of a new cryptic species. *Zoological Journal of the Linnaean Society* **149**: 339–370.

Börner, A.R. and Schüttler, B.I. (1983). An additional note on the Australian geckos of the genus *Gehyra*. *Miscellaneous Articles in Saurology* **12**: 1–4.

Bourke, G., Pratt, R.C., Vanderduys, E. and Moritz, C. (2017). Systematics of a small *Gehyra* (Squamata: Gekkonidae) from the Einasleigh Uplands, Queensland: description of a new range restricted species. *Zootaxa* **4231**: 85–99.

Bush, B., Maryan, B., Browne-Cooper, R. and Robinson, D. (1997). Reptiles and frogs in the bush: Southwestern Australia. University of Western Australia Press, Crawley, Western Australia.

Bustard, H.R. (1965a). The systematic status of the Australian gecko, *Gehyra variegata punctata* (Fry). *Herpetologica* **21**: 157–158.

Bustard, H.R. (1965b). The systematic status of the Australian geckos *Gehyra variegata* (Duméril and Bibron, 1836) and *Gehyra australis* Gray, 1845. *Herpetologica* **20**: 259–272.

Camargo, A. and Sites, J.W., Jr. (2013). Species delimitation: a decade after the Renaissance (pp. 225–247). *In*: Pavlinov, I. Ya. (ed.), *The species problem – ongoing issues*. InTech Publishing: Rijeka, Croatia.

Chrapliwy, P.S., Smith, H.M. and Grant, C. (1961). Systematic studies of the gekkonid lizard genera *Gehyra*, *Peropus*, *Hoplodactylus* and *Naultinus*. *Herpetologica* **17**: 5–12.

de Queiroz, K. (1998). The general lineage concept of species, species criteria, and the process of speciation (pp. 57–75). *In*: Howard, D.J. and Berlocher, S.H. (eds), *Endless forms: species and speciation*. Oxford University Press: Oxford, United Kingdom.

de Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology* **56**: 879–886.

Doughty, P., Oliver, P. and Adams, M. (2007). Systematics of stone geckos in the genus *Diplodactylus* (Reptilia: Diplodactylidae) from northwestern Australia, with a description of a new species from the Northwest Cape, Western Australia. *Records of the Western Australian Museum* **24**: 247–265.

Doughty, P., Ellis, R.J. and Oliver, P.M. (2016). Many things come in small packages: Revision of the clawless geckos (*Crenadactylus*: Diplodactylidae) of Australia. *Zootaxa* **4168**: 239–278.

Doughty, P., Rolfe, J.K., Burbidge, A.H., Pearson, D.J. and Kendrick, P.G. (2011). Herpetological assemblages of the Pilbara biogeographic region, Western Australia: ecological associations, biogeographic patterns and conservation. *Records of the Western Australian Museum, Supplement* **78**: 315–341.

Doughty, P., Palmer, R., Sistrom, M.J., Bauer, A.M. and Donnellan, S.C. (2012). Two new species of *Gehyra* (Squamata: Gekkonidae) geckos from the north-west Kimberley region of Western Australia. *Records of the Western Australian Museum* **27**: 117–134.

Doughty, P., Bourke, G., Tedeschi, L.G., Pratt, R.C., Oliver, P.M., Palmer, R.A. and Moritz, C. (2018). Species delimitation in the *Gehyra nana* (Squamata: Gekkonidae) complex: cryptic and divergent morphological evolution in the Australian Monsoonal Tropics, with the description of four new species. *Zootaxa* **4403**: 201–244.

Duméril, A.M.C. and Bibron, G. (1836). *Erpetologie générale ou histoire naturelle complete des reptiles. vol. 3.* Libr. Encyclopédique Roret: Paris.

Edgar, R.C. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Ressearch* **32**: 1792–1797.

Ellis, R.J., Doughty, P. and Bauer, A.M. (2018). An annotated type catalogue of the geckos and pygopods (Squamata: Gekkota: Carphodactylidae, Diplodactylidae, Gekkonidae, Pygopodidae) in the collection of the Western Australian Museum. *Records of the Western Australian Museum* **33**(1): 51–94. doi: 10.18195/issn.0312-3162.33(1).2018.051-094.

Frost, D.R. and Hillis, D.M. (1990). Species in concept and practice: herpetological applications. *Herpetologica* **46**: 87–104.

Frost, D.R., Kluge, A.G. and Hillis, D.M. (1992). Species in contemporary herpetology: comments on phylogenetic inference and taxonomy. *Herpetological Review* 23: 46–54.

Fry, D.B. (1914). On a collection of reptiles and batrachians from Western Australia. *Records of the Western Australian Museum and Art Gallery* **1**: 174–210.

Fujita, M.K., Leaché, A.D., Burbrink, F.T., McGuire, J.A. and Moritz, C. (2012). Coalescent- based species delimitation in an integrative taxonomy. *Trends In Ecology & Evolution* **27**: 480– 488.

Gamble, T., Greenbaum, E., Jackman, T.R., Russell, A.P. and Bauer, A.M. (2012). Repeated origin and loss of adhesive toepads in geckos. *PLoS ONE* **7(6)**:e39429

Gray, J.E. (1834). Characters of two new genera of reptiles (*Geoemyda* and *Gehyra*). *Proceedings of the Zoological Society of London* **1834**: 99–100.

Gray, J.E. (1845). Catalogue of the specimens of lizards in the collection of the British Museum, 1st edition. British Museum: London, xxviii + 259 pp.

Heinicke, M.P., Greenbaum, E., Jackman, T.R. and Bauer, A.M. (2011). Phylogeny of a trans-Wallacean radiation (Squamata, Gekkonidae, *Gehyra*) supports a single early colonization of Australia. *Zoologica Scripta* **40**: 584–602.

Heineke, M.P., Jackman, T.R. and Bauer, A.M. (2017). The measure of success: geographic isolation promotes diversification in *Pachydactylus* geckos. *BMC Evolutionary Biology* **17**: 9.

Horner, P. (2005). *Gehyra koira* sp. nov. (Reptilia: Gekkonidae), a new species of lizard with two allopatric subspecies from the Ord-Victoria region of north-western Australia and a key to the *Gehyra australis* species complex. *The Beagle* **21**: 165–174.

Hutchinson, M., Sistrom, M., Donnellan, S. and Hutchinson R. (2014). Taxonomic revision of the Australian arid zone lizards *Gehyra variegata* and *G. montium* (Squamata, Gekkonidae) with description of three new species. *Zootaxa* **3814**: 221–241.

Kealley, L., Doughty, P., Pepper, P., Keogh, J.S., Hillyer, M. and Huey, J. (2018). Conspicuously concealed: Revision of the arid clade of the *Gehyra variegata* (Gekkonidae) group in Western Australia using an integrative molecular and morphological approach, with the description of five cryptic species. *PeerJ* **6**: e5334.

King, M. (1979). Karyotypic evolution in *Gehyra* (Gekkonidae: Reptilia) I. The *Gehyra variegata-punctata* complex. *Australian Journal of Zoology* **27**: 373–393.

King, M. (1981). Notes on the distribution of *Gehyra nana* Storr and *Gehyra punctata* (Fry) in Australia. *Australian Journal of Herpetology* **1**: 55–56.

King, M. (1982a). Karyotypic evolution in *Gehyra* (Gekkonidae: Reptilia). II. A new species from the Alligator Rivers region in northern Australia. *Australian Journal of Zoology* **30**: 92–101.

King, M. (1982b). A new species of *Gehyra* (Reptilia, Gekkonidae) from central Australia. *Transactions of the Royal Society of South Australia* **106**: 155–158.

King, M. (1983). Karyoptic evolution in *Gehyra* (Gekkonidae: Reptilia). III. The *Gehyra australis* complex. *Australian Journal of Zoology* **31**: 723–741.

King, M. (1984a). The *Gehyra australis* species complex (Sauria: Gekkonidae). *Amphibia-Reptilia* **4 (1983)**: 147–169.

King, M. (1984b). A new species of *Gehyra* (Reptilia: Gekkonidae) from northern Western Australia. *Transactions of the Royal Society of South Australia* **108**: 113–117.

Lanfear, R., Calcott, B., Ho, S.Y.W. and Guindon, S. (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29**: 1695–1701.

Lesson, R.P. (1830). Description de quelques reptiles nouveaux ou peu connus. *In:* M.L.I. Duperrey (ed)., Voyage Autour du Monde Execute par Ordre du Roi, sur la Corvette de La Majeste, La Coquille, exécuté Pendant les Annees 1822, 1823, 1824 et 1825. 2. Zoologie 2 (1). Arthur Bertrand, Paris: 1–65.

Loveridge, A. (1934). Australian reptiles in the Museum of Comparative Zoology, Cambridge, Mass. *Bulliten of the Museum of Comparative Zoology* **77**: 243–283.

Low, T. (1978). A new species of gecko, genus *Gehyra* (Reptilia: Gekkonidae) from Queensland. *Victorian Naturalist* **96:** 190–196.

Lucas, A.H.S. and Frost, C. (1896). Reptilia. *In:* Spencer, W. B. (ed.) *Report on the work of the Horn Scientific Expedition to Central Australia. Part II. – Zoology.* Dulau and Co., London and Melville, Mullen and Slade, Melbourne, pp. 112–175.

Macey, J.R., Schulte, J.A., Ananjeva, N.B., Larson, A., Rastegar-Pouyani, N., Shammakov, S.M. and Papenfuss, T.J. (1998). Phylogenetic relationships among agamid lizards of the Laudakia caucasia species group: testing hypotheses of biogeographic fragmentation and an area cladogram for the Iranian Plateau. *Molecular Phylogenetics and Evolution* **10**: 118–131.

Macey, J.R., Schulte, J.A., Larson, A., Ananjeva, N.B., Wang, Y., Pethiya- goda, R., Rastegar-Pouyani, N. and Papenfuss,

T.J. (2000). Evaluating trans-Tethys migration: an example using acrodont lizard phylogenetics. *Systematic Biology* **49**: 233–256.

Macleay, W. (1877). The lizards of the Chevert Expedition. Second paper. *Proceedings of the Linnaean Society of New South Wales* **2**: 97–104.

Maddison, W.P. and Knowles, L.L. (2006). Inferring phylogeny despite incomplete lineage sorting. *Systematic Biology* **55**: 21–30.

Mayden, R.L. (1997) A hierarchy of species concepts: the denouement in the saga of the species problem (pp 381–424). *In*: Claridge M.F., Dawah H.A. & Wilson M.R. (eds), *Species: the units of biodiversity*. Chapman and Hall: New York.

McKenzie, N.L., van Leeuwen, S. and Pinder, A.M. (2009). Introduction to the Pilbara Biodiversity Survey, 2002–2007. *Records of the Western Australian Museum, Supplement* **78**: 3–89.

Mitchell, F.J. (1955). Preliminary account of the Reptilia and Amphibia collected by the National Geographic Society-Commonwealth Government-Smithsonian Institute Expedition to Arnhem Land. *Records of the South Australian Museum* **11**: 373–408.

Mitchell, F.J. (1965). Australian geckos assigned to the genus *Gehyra* Gray (Reptilia, Gekkonidae)**.** *Senckenbergiana Biologica* **46**: 287–319.

Moritz, C. (1986). The population biology of *Gehyra* (Gekkonidae): chromosome change and speciation. *Systematic Zoology* **35**: 46–67.

Moritz, C., Pratt, R.C., Bank, S., Bourke, G., Bragg, J.G., Doughty, P., Keogh, J.S., Laver, R.J., Potter, S., Teasdale, L.C., Tedeschi, L.G. and Oliver, P.M. (2018). Cryptic lineage diversity, body size divergence and sympatry in a species complex of Australian lizards (*Gehyra*). *Evolution* **72**: 54–66.

Oliver, P.M., Bourke, G., Pratt, R.C., Doughty, P. and Moritz, C. (2016). Systematics of small *Gehyra* (Squamata: Gekkonidae) of the southern Kimberley, Western Australia: redescription of *G. kimberleyi* Börner & Schüttler, 1983 and description of a new restricted range species. *Zootaxa* **4107**: 49–64.

Oliver, P.M., Adams, M. and Doughty, P. (2010). Molecular evidence for ten species and Oligo-Miocene vicariance within a nominal Australian gecko species (*Crenadactylus ocellatus*, Diplodactylidae). *BMC Evolutionary Biology* **10**: 386.

Oliver, P.M., Adams, M., Lee, M.S.Y., Hutchinson, M.N. and Doughty, P. (2009) Cryptic diversity in vertebrates: molecular data double estimates of species diversity in a raditation of Australian lizards (*Diplodactylus*, Gekkota). *Proceedings of the Royal Society B* **276**: 2001–2007.

Padial, J.M., Miralles, A., De la Riva, I. and Vences, M. (2010). The integrative future of taxonomy. *Frontiers in Zoology* **7**: 16. doi: 10.1186/1742-9994-7-16

Pepper, M., Doughty, P. and Keogh, S.J. (2013). Synthesis: Geodiversity and endemism in the iconic Australian Pilbara region: a review of landscape evolution and biotic response in an ancient refugium. *Journal of Biogeography* **40**: 1225–1239.

Powney, G.D., Grenyer, R., Orme, C.D.L., Owens, I.P.F. and Meiri, S. (2010). Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. *Global Ecology and Biogeography* **19**: 386–396.

Rambaut, A. (1996). Se-Al: sequence alignment editor software. <http:// tree.bio.ed.ac.uk/software/seal>

Read, K., Keogh, J.S., Scott, I.A.W., Roberts, J.D. and Doughty, P. (2001). Molecular phylogeny of the Australian frog genera *Crinia*, *Geocrinia* and allied taxa (Anura: Myobatrachidae). *Molecular Phylogenetics and Evolution* **21**: 294–308.

Rodriguez, F., Oliver, J.L., Marin, A. and Medina, J.R. (1990). The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology* **142**: 485–501.

Rosauer, D.F., Byrne, M., Blom, M.P.K., Coates, D.J., Donnellan, S., Doughty, P., Keogh, J.S., Kinloch, J., Laver, R.J., Myers, C., Oliver, P.M., Potter, S., Rabosky, D.L., Afonso Silva, A.C., Smith, J. and Moritz, C. (2018). Real-world conservation planning for evolutionary diversity in the Kimberley, Australia, sidesteps uncertain taxonomy. *Conservation Letters*: early on-line view.

Sistrom, M.J., Hutchinson, M.N., Hutchinson, R.G., Donnellan, S.C. (2009). Molecular phylogeny of Australian *Gehyra* (Squamata: Gekkonidae) and taxonomic revision of *Gehyra variegata* in south-eastern Australia. *Zootaxa* **2277**: 14–32.

Sistrom, M.J., Edwards, D.L., Donnellan, S. and Hutchinson, M. (2012). Morphological differentiation correlates with ecological but not genetic divergence in a *Gehyra* gecko. *Journal of Evolutionary Biology* **25**: 647–660.

Sistrom, M., Donnellan, S. and Hutchinson, M. (2013). Delimiting species in recent radiations with low levels of morphological divergence: A case study in Australian *Gehyra* geckos. *Molecular Phylogenetics & Evolution* **68**: 135–143.

Sistrom, M., Hutchinson, M., Bertozzi, T. and Donnellan, S. (2014). Evaluating evolutionary history in the face of high gene tree discordance in Australian *Gehyra* (Reptilia: Gekkonidae). *Heredity* **113**: 52–63.

Sites, J.W., Jr. and Marshall, J.C. (2003). Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology and Evolution* **18**: 462–470.

Sites, J.W., Jr. and Marshall, J.C. (2004). Operational criteria for delimiting species. *Annual Review of Ecology and Systematics* **35**: 199–227.

Stamatakis, A. (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.

Storr, G.M. (1978). Seven new gekkonid lizards from Western Australia. *Records of the Western Australian Museum* **6**: 337–352.

Storr, G.M. (1982). Two new *Gehyra* (Lacertilia: Gekkonidae) from Australia. *Records of the Western Australian Museum* **10**: 53–59.

Storr, G.M., Smith, L.A. and Johnstone, R.E. (1990). *Lizards of Western Australia. III. Geckos and pygopods.* Western Australian Museum Press: Perth.

Sukumaran, J. and Knowles, L.L. (2017). Multispecies coalescent delimits structure, not species. *Proceedings of the National Academy of Sciences* **114**: 1607–1612.

Thackway, R. and Cresswell, I.D. (1995). *An interim biogeographic regionalisation of Australia*. Australian Nature Conservation Agency: Canberra.

Wells, R.W. and Wellington, C.R. (1983). A synopsis of the Class Reptilia in Australia. *Australian Journal of Herpetology* **1**: 73-129.

Wilson, S.K. and Swan, G. (2008). *A complete field guide to reptiles of Australia, 2nd edition.* Reed New Holland: Sydney, 512 pp.

Wiens, J.J. and Penkrot, T.A. (2002). Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). *Systematic Biology* **51**: 69–91.

Zietz, F.R. (1920). Catalogue of Australian lizards. *Records of the South Australian Museum* **1**: 181– 228.

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APPENDIX 1 Specimens used in this study. WAM R- prefixes not shown. Codes: mtDNA – this study; Allozymes – an unpublished study by M. Adams and P. Doughty; Exon capture – from Ashman et al. (2018); Morphology – this study; Location – all from Western Australia; Latitude and Longitude in decimal degrees.

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
G. punctata							
90607	X	X			Woodstock Station	-21.6166	119.0233
90608	X	X			Woodstock Station	-21.6166	119.0233
90645		X			Gallery Hill	-21.6675	119.0408
90665		X			Woodstock Station	-21.6166	119.0233
90768		X			Woodstock Station	-21.6111	119.0397
90808		X			Woodstock Station	-21.6069	119.0306
90822		X			Gallery Hill	-21.6675	119.0408
90823		X			Gallery Hill	-21.6675	119.0408
90828		X			Gallery Hill	-21.6675	119.0408
90850		X			Woodstock Station	-21.6166	119.0233
90851		X			Woodstock Station	-21.6166	119.0233
90870		X			Gallery Hill	-21.6675	119.0408
90871		X			Woodstock Station	-21.6597	119.0417
90896		X			Woodstock Station	-21.6111	119.0397
90911		X			Cadjeput Rock Hole	-21.5355	119.1358
90912		X			Cadjeput Rock Hole	-21.5355	119.1358
99140		X			Woodstock Station	-21.6111	119.0397
99168		X			Woodstock Station	-21.6069	119.0306
100651		X			Woodstock Station	-21.6166	119.0231
100652		X			Woodstock Station	-21.6166	119.0231
100667		X			Woodstock Station	-21.5888	118.9831
100668	X	X			Woodstock Station	-21.5888	118.9831
100669		X			Woodstock Station	-21.5888	118.9831
100752	X	X			Woodstock Station	-21.6675	119.0406
100753	X	X			Woodstock Station	-21.6675	119.0406
100754		X			Woodstock Station	-21.6675	119.0406
100755	X	X			Woodstock Station	-21.6675	119.0406

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
104115		X			Woodstock Station	-21.675	119.0442
104116		X			Woodstock Station	-21.675	119.0442
104117		X			Woodstock Station	-21.675	119.0442
104118		X			Woodstock Station	-21.675	119.0442
104119		X			Woodstock Station	-21.6675	119.0406
104120		X			Woodstock Station	-21.6675	119.0406
104122		X			Woodstock Station	-21.6675	119.0406
104131		X			Woodstock Station	-21.675	119.0442
104132		X			Woodstock Station	-21.675	119.0442
104148		X			Woodstock Station	-21.6219	118.9531
104149		X			Woodstock Station	-21.6219	118.9531
104174		X			Woodstock Station	-21.6066	119.0394
104198		X			Woodstock Station	-21.6675	119.0406
104199		X			Woodstock Station	-21.6675	119.0406
104221		X			Woodstock Station	-21.5263	119.1492
104237		X			Woodstock Station	-21.5527	119.1167
104238		X			Woodstock Station	-21.6219	118.9531
104241		X			Woodstock Station	-21.6219	118.9531
106156	X				31.5 km SSW Turee Creek Homestead	-23.8666	118.5667
108841		X			42 km NNE Munjina Roadhouse	-21.9833	119.75
108850	X				Cherralta Homestead	-21.0333	116.8167
108851	X				Cherralta Homestead	-21.0333	116.8167
110019		X			5 km N Lake Poongkaliyarra	-20.9346	117.115
110047	X	X			3.5 km WNW Mount Gregory	-20.8526	117.096
110048	X	X			3.5 km WNW Mount Gregory	-20.8526	117.096
110117	X				5 km NW Mount Florance Homestead	-21.7665	117.825
111897		X			9 km NE Sylvania	-23.525	120.107
111898		X			9 km NE Sylvania	-23.525	120.107
111900	X	X			9 km NE Sylvania	-23.525	120.107
111959		X			23 km WNW Balfour Downs Homestead	-22.7183	120.646

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
111960		X			23 km WNW Balfour Downs Homestead	-22.7183	120.646
111961		X			23 km WNW Balfour Downs Homestead	-22.7183	120.646
111963	X	X			23 km WNW Balfour Downs Homestead	-22.7183	120.646
111966		X			25 km NW Balfour Downs Homestead	-22.6111	120.729
111967		X			25 km NW Balfour Downs Homestead	-22.6111	120.729
113239		X			Junction of Jimmawurrada Creek and Robe River	-21.7333	116.25
114301	X				Bulloo Downs Homestead	-24	119.5667
114308	X				Nichol (Bamboo) Spring, On Ethel Creek	-24.4666	118.5667
114540	X	X			Yangadee Gorge, 15 km SW Pannawonica	-21.7166	116.5
114917	X	X			25 km N Nullagine	-21.65	120.0833
116893	X		X		25 km ESE Kooline Homestead	-22.7894	116.5461
116894	X				25 km ESE Kooline Homestead	-22.7894	116.5461
117008	X				3 km SE Yilbrinna Pool	-24	118.5333
117009	X				3 km SE Yilbrinna Pool	-24	118.5333
117113	X				Wyloo Homestead	-22.7	116.7167
117114	X	X			Wyloo Homestead	-22.7	116.7167
125086	X				15 km E Newman	-23.3666	119.9
125087		X			15 km E Newman	-23.3666	119.9
125459	X				30 km E Newman	-23.3166	120.0333
125480	X	X			30 km E Newman	-23.3166	120.0333
129932	X		X		West Angelas, 100 km WNW Newman	-23.25	118.6667
131757		X			Millstream-Chichester Range National Park	-21.3438	117.135
132523	X				Burrup Peninsula	-20.6705	116.7561
132735	X	X			25 km WNW Abydos	-21.4013	118.7061
135009	X	X			Mount Whaleback	-23.4066	119.6242
138946	X				West Angelas	-23.1947	118.5964
139311		X			Meentheena	-21.4391	120.4025
139377		X			Meentheena	-21.2163	120.3406
139389	X	X			Old Meentheena Homestead	-21.2663	120.4553
140014	X	X			Millstream-Chichester National Park	-21.2658	117.0742

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
140307	X	X			Millstream-Chichester National Park	-21.2658	117.0742
141312	X				Cape Preston Area	-20.9052	116.2169
141333	X	X			Cape Preston Area	-20.9052	116.2169
141338	X	X			Vicinity Of Cape Preston	-21.0438	116.1872
141387	X	X			Cape Preston Area	-20.9052	116.2169
141388		X			Cape Preston Area	-20.9052	116.2169
145251	X	X			5 km S Mount Tom Price Mine	-22.8072	117.75
146498		X			Burrup Peninsula	-20.6211	116.7758
154306	X	X		X	Chichester Range	-22.0519	118.9878
154308		X			Chichester Range	-22.0519	118.9878
154776	X				Brockman Ridge	-23.3211	119.9378
157722	X				Packsaddle Range	-22.9408	118.905
160222	X				12.5 km N Nullagine	-21.7703	120.092
160939		X			5 km N Lake Poongkaliyarra	-20.9346	117.115
161041				X	3.5 km S Marda Pool	-21.0655	116.15
163610				X	Cape Preston	-20.9366	116.1997
163611				X	Cape Preston	-20.9366	116.1997
165026		X		X	24.5 km N Cowra Line Camp	-22.1347	119.024
165102	X				8 km NNW Millstream Homestead	-21.518	117.043
165120		X			2.6 km WNW Python Pool	-21.326	117.215
165122				X	Black Hill Pool	-21.334	117.253
165190	X				3 km SW Harding Dam	-20.994	117.082
165236		X			Hearson Cove, Burrup Peninsula	-20.635	116.799
165249	X				14.9 km E Karratha	-20.7588	116.6853
165250	X				14.9 km E Karratha	-20.7588	116.6853
165253	X				14.9 km E Karratha	-20.7588	116.6853
165255				X	14.9 km E Karratha	-20.7588	116.6853
165256					14.9 km E Karratha	-20.7588	116.6853
165527	X				West Intercourse Island	-20.6852	116.63
165601	X		X		Dampier Area	-20.6744	116.7156

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
165738		X		X	Barrow Island	-20.85	115.4
165740	X	X		X	Barrow Island	-20.85	115.4
165742	X	X		X	Barrow Island	-20.85	115.4
170008	X				22.5 km Sse Wodgina	-21.3644	118.701
170581		X			22 km Ne Peedamulla Homestead	-21.7319	115.807
170815	X				Old Pilga Homestead	-21.48	119.414
174328	X				Glen Herring Gorge, 25 km SSW Marble Bar	-21.3529	119.6145
174330	X				Glen Herring Gorge, 25 km SSW Marble Bar	-21.3529	119.6145
174331	X				Glen Herring Gorge, 25 km SSW Marble Bar	-21.3529	119.6145
174332				X	Glen Herring Gorge, 25 km SSW Marble Bar	-21.3529	119.6145
174333	X			X	Glen Herring Gorge, 25 km SSW Marble Bar	-21.3529	119.6145
174334	X			X	Glen Herring Gorge, 25 km SSW Marble Bar	-21.3529	119.6145
175321					Opthalmia Dam, 15 km NNE Newman	-23.31534	119.86948
175325					Opthalmia Dam, 15 km NNE Newman	-23.31534	119.86948
***G. macra* sp. nov.**							
132679	X	X			Yarrie, 20 km SSE Shay Gap	-20.5788	120.0053
154517	X	X		X	Yarri Mining Camp	-20.5477	120.2453
156586	X				Cundaline Gap	-20.5488	120.1681
156587	X		X	X	Cundaline Gap	-20.5488	120.1681
160096	X	X	X	X	13 km SE Braeside	-21.289	121.096
160097	X	X		X	13 km SE Braeside	-21.289	121.096
160098	X	X		X	13 km SE Braeside	-21.289	121.096
162688		X		X	Baldy Rock	-21.05	118.8
162701	X	X	X	X	Baldy Rock	-21.05	118.8
162702		X		X	Baldy Rock	-21.05	118.8
162703	X	X		X	Baldy Rock	-21.05	118.8
173362	X				Roy Hill Rail Chainage 75, 67 km S South Hedland	-20.9618	118.6846
173363	X			X	Roy Hill Rail Chainage 76, 65 km S South Hedland	-20.9588	118.6844
173364	X				Roy Hill Rail Chainage 75, 67 km S South Hedland	-20.9618	118.6846

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
173365	X			X	Roy Hill Rail Chainage 76, 65 km S South Hedland	-20.9588	118.6844
173366	X			X	Roy Hill Rail Chainage 75, 67 km S South Hedland	-20.9618	118.6846
***G. punctulata* sp. nov.**							
97165		X			10.9 km SE Kalli Homestead	-26.9166	117.2
97166		X			10.9 km SE Kalli Homestead	-26.9166	117.2
97171		X			Yaloo Peak	-26.8	117.1833
113599	X			X	30 km ENE Nanutarra	-22.4166	115.6167
113633	X			X	30 km ENE Nanutarra	-22.4166	115.6167
114315	X			X	Lallytharra Springs Homestead	-25.8166	115.3833
114316	X			X	Lallytharra Springs Homestead	-25.8166	115.3833
114320		X			16 km NNE Mulgul Homestead	-24.6833	118.5167
117038	X			X	18 km W Mount Stuart Homestead	-22.4333	115.8833
117039	X				18 km W Mount Stuart Homestead	-22.4333	115.8833
117040	X			X	18 km W Mount Stuart Homestead	-22.4333	115.8833
120534	X	X			39 km ESE Gascoyne Junction	-25.21	115.5142
123764	X		X	X	39 km ESE Gascoyne Junction	-25.21	115.5142
123769	X				39 km ESE Gascoyne Junction	-25.21	115.5142
123770	X				39 km ESE Gascoyne Junction	-25.21	115.5142
131769	X	X		X	Muggon Station	-26.6166	115.5333
136281	X	X			Muggon Station	-26.8169	115.5478
139194	X	X			Mount Minnie	-22.265	115.4072
139444	X	X	X	X	Cane River	-22.1352	115.6889
163044	X			X	Cane River Homestead	-22.089	115.626
163106	X			X	19.5 km SSW Mount Amy	-22.4193	115.838
163126	X				19.5 km SSW Mount Amy	-22.4193	115.838
167604	X				North West Coastal Highway, 147 km E Ningaloo	-22.7819	115.0842
167605	X				North West Coastal Highway, 147 km E Ningaloo	-22.7816	115.0842
167623	X				Near Nanutarra Roadhouse	-22.4694	115.5211
167627	X				Near Nanutarra Roadhouse	-22.4686	115.5214

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
172404	X				Cane River	-22.4295	115.351
***G. polka* sp. nov.**							
97169		X			4.2 km E Yalgoo	-28.35	116.7167
106086	X				Mount Welcome	-27.0666	116.2667
106087	X	X			Mount Welcome	-27.0666	116.2667
106088	X	X		X	Mount Welcome	-27.0666	116.2667
106089	X	X		X	5 km NE Mount Welcome	-27.0333	116.3
106090	X	X		X	5 km NE Mount Welcome	-27.0333	116.3
106164	X				Mount Frazer	-25.6333	118.3833
106202	X	X			Pia Aboriginal Reserve (Near Wooleen)	-27.1333	116.3333
114251	X				NW End Of Mount Fraser	-25.5833	118.3667
114329	X				Myaree Pool	-20.85	116.6
114330	X	X			Myaree Pool	-20.85	116.6
116895	X				22 km S Mount Phillip Homestead	-24.7666	116.2167
116896	X	X		X	22 km S Mount Phillip Homestead	-24.7666	116.2167
116897	X	X			22 km S Mount Phillip Homestead	-24.7666	116.2167
116898	X		X		22 km S Mount Phillip Homestead	-24.7666	116.2167
117036	X				20 km SW Cobra Homestead	-24.3	116.35
117070	X			X	50 km W Mt Augustus	-24.3666	116.3167
119278	X				20 km WSW Mount Levra Station Homesteadd	-26.4333	117.15
119368		X		X	50 km SW Yalgoo	-28.65	116.3
119369	X	X		X	50 km SW Yalgoo	-28.65	116.3
127414	X	X		X	10.3 km S Yinnietharra Homestead	-24.7202	116.1197
127415	X	X		X	10.3 km S Yinnietharra Homestead	-24.7202	116.1197
127543	X	X		X	Barnong Homestead	-28.6333	116.2833
132290	X	X			6 km NW Noondie Outstation	-27.0744	117.0789
132291		X		X	6 km NW Noondie Outstation	-27.0744	117.0789
132294	X	X		X	Marlandy Hill	-28.1216	117.2331
167695	X				Meekatharra	-26.4241	118.5883

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
***G. fenestrula* sp. nov.**							
71633				X	21 km WSW Marilliana Homestead	-22.6666	119.2167
71634				X	21 km WSW Marilliana Homestead	-22.6666	119.2167
111769	X	X		X	34 km E Wheelarra Hill	-23.3586	120.459
114334	X	X			35 km SE Prairie Downs	-23.7166	119.4333
114335	X	X	X		35 km SE Prairie Downs	-23.7166	119.4333
114336	X	X			35 km SE Prairie Downs	-23.7166	119.4333
114337	X	X		X	35 km SE Prairie Downs	-23.7166	119.4333
125083	X			X	15 km E Newman	-23.3666	119.9
127475	X	X		X	32 km S Newman	-23.65	119.7167
129925	X		X	X	West Angelas, 100 km WNW Newman	-23.25	118.6667
129926	X			X	West Angelas, 100 km WNW Newman	-23.25	118.6667
135013	X	X		X	Mount Whaleback	-23.403	119.6961
135018	X	X		X	Mount Whaleback	-23.3347	119.6694
157507	X				Packsaddle Range	-22.9102	118.9417
157510				X	Packsaddle Range	-22.9194	118.8733
162244	X				9 km NE Weelie Wollie Spring	-22.8524	119.265
167680	X				Millstream-Chichester National Park	-23.7013	119.7403
***G. media* sp. nov.**							
110146	X	X	X		2 km E Ti Tree Pool	-21.8336	117.611
110219		X			16 km NE Goolbung Hill	-21.3841	117.061
114291	X				Myaree Pool	-20.85	116.6
114343	X				8-10 km S Cleaverville	-20.7333	117
114570		X			Poonthune Pool, East Turner River	-20.7833	118.7167
114571	X		X		Poonthune Pool, East Turner River	-20.7833	118.7167
114926	X			X	37 km ENE Port Hedland	-20.4	118.95
120703	X				Boodarie Stn	-20.4	118.4667
120738	X				Boodarie Hill	-20.4	118.5167

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
120739	X				Boodarie Hill	-20.4	118.5167
120740	X				Boodarie Hill	-20.4	118.5167
127645	X				Nifty Mine	-21.6666	121.5833
129949	X				Mount Herbert Area	-21.33	117.1889
131002	X				Mount Herbert Area	-21.1383	117.1158
131758	X				Millstream-Chichester Range National Park	-21.3236	117.1253
132736	X	X			25 km WNW Abydos	-21.4	118.7061
139365	X	X			Meentheena	-21.2888	120.4719
145683	X	X			Abydos Station	-21.2583	118.8161
158086	X	X			5 km WSW Python Pool	-21.3413	117.189
159912	X			X	53 km NNE Whim Creek Hotel	-20.4302	118.064
160940	X	X		X	9 km NW Lake Poongkaliyarra	-20.9399	117.035
160961	X				13.5 km W Wickham	-20.6884	117.007
161014	X	X		X	3.5 km S Marda Pool	-21.0655	116.15
161088	X	X		X	9.5 km ESE Marda Pool	-21.0633	116.234
161124	X				31 km NNW Marble Bar	-20.9231	119.61
161242	X				53 km NNE Whim Creek Hotel	-20.4302	118.064
161245	X			X	53 km NNE Whim Creek Hotel	-20.4302	118.064
161249	X				53 km NNE Whim Creek Hotel	-20.4302	118.064
161258	X				53 km NNE Whim Creek Hotel	-20.4302	118.064
161635	X				36.5 km W Goldsworthy	-20.3264	119.175
161663	X				36.5 km W Goldsworthy	-20.3264	119.175
161664	X				36.5 km W Goldsworthy	-20.3264	119.175
161998	X				2 km E Mount Minnie	-22.1041	115.568
162410	X				8 km SW Roebourne	-20.808	117.073
162686	X	X		X	Baldy Rock	-21.05	118.8
162687	X	X		X	Baldy Rock	-21.05	118.8
162704	X	X		X	Baldy Rock	-21.05	118.8
162915	X				North West Coastal Highway, 8 km SW Mount Negri, Sherlock	-20.8455	117.7958

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
162916	X				North West Coastal Highway, 8 km SW Mount Negri, Sherlock	-20.8455	117.7956
165091	X				5 km WSW Python Pool	-21.3413	117.189
165106	X				5 km WSW Python Pool	-21.3413	117.189
165181	X	X			7 km SE Marda Pool	-21.0699	116.207
167635	X				48 km N Nanutarra Roadhouse	-22.0797	115.5742
170795	X	X			17.5 km E Pannawonica	-21.6331	116.492
170866	X				21 km SW Marble Bar	-21.3108	119.604
172380	X			X	Port Hedland	-20.5291	118.6497
172381	X			X	Port Hedland	-20.5291	118.6497
174289	X			X	Nanutarra Roadhouse	-22.46434	116.03714
***G. micra* sp. nov.**							
102506	X				Barlee Range Nature Reserve	-23.1058	116.9978
110011		X		X	6 km NW Roebourne	-20.7364	117.099
110012		X			9 km NW Lake Poongkaliyarra	-20.9399	117.035
110013	X	X	X	X	5 km S Lake Poongkaliyarra	-21.0364	117.106
110045	X	X		X	13.5 km W Wickham	-20.6884	117.007
110073	X	X		X	13.5 km W Wickham	-20.6884	117.007
110113	X				0.2 km N Mount Florance Homestead	-21.7868	117.862
111846	X	X			10 km SSE Wheelarra Hill	-23.4583	120.156
111919	X				25 km NW Balfour Downs Homestead	-22.6111	120.729
111956	X				25 km NW Balfour Downs Homestead	-22.6111	120.729
114290	X				Myaree Pool	-20.85	116.6
114292	X				Myaree Pool	-20.85	116.6
117011	X				21 km WNW Ashburton Downs Homestead	-23.2666	116.85
117027	X		X		15 km NW Paraburdoo	-23.1333	117.5667
120067	X				50 km E Newman (Jimblebar Mine Site)	-23.3791	120.1236
125029	X	X		X	Yandicoogina	-22.7125	119.0672
125036	X				Yandicoogina	-22.74	119.0525
125472	X		X		30 km E Newman	-23.3166	120.0333

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
125485	X				30 km E Newman	-23.3166	120.0333
129655	X				120 km NW Newman	-22.9958	119.0917
129933	X				West Angelas, 100 km WNW Newman	-23.25	118.6667
131008	X		X		Mount Herbert Area	-21.3127	117.2339
141314	X				Cape Preston Area	-20.9052	116.2169
141332	X		X	X	Cape Preston Area	-20.9052	116.2169
141352	X				Cape Preston Area	-20.9052	116.2169
145755	X				Chichester Range	-21.9438	118.9628
154311	X				Weeli Wolli Creek	-22.9577	119.1789
156615	X				Woodie Woodie Minesite	-21.6541	121.2244
158267	X		X		47.5 km W Roy Hill	-22.6333	120.4111
159971	X				5 km E Whim Creek Hotel	-20.8485	117.855
160106	X				58 km ESE Meentheena Outcamp	-21.3219	121.002
160184	X				27.5 km NNW Nullagine	-21.6442	120.063
160221	X				27.5 km NNW Nullagine	-21.6442	120.063
160233	X				45 km N Nullagine	-21.4799	120.091
160255	X				45 km N Nullagine	-21.4799	120.091
160271	X				24.5 km N Cowra Line Camp	-22.1347	119.024
160879		X		X	3.5 km S Marda Pool	-21.0655	116.15
160943	X				3.5 km WNW Mount Gregory	-20.8526	117.096
161324	X				55 km N Nullagine	-21.3923	120.071
161376	X				35 km NNW Marble Bar	-20.8983	119.591
161441	X			X	39 km NNW Marble Bar	-20.8522	119.593
161480	X				9.5 km SE Yarrie Homestead	-20.7483	120.258
161891	X				21 km SW Marble Bar	-21.3108	119.604
161969	X				2.8 km SE Mount Minnie	-22.1201	115.57
161970	X				2.8 km SE Mount Minnie	-22.1201	115.57
162082	X				16 km W Mount De Courcey	-22.7402	116.461
162359	X				0.2 km N Mount Florance Homestead	-21.7868	117.862
162630	X				27.5 km ENE Wodgina	-21.0628	118.911

WAM registration number	mtDNA	Allozymes	Exon capture	Morphology	Location	Latitude	Longitude
162861	X				30 km SSE Paraburdoo	-23.4189	117.842
163088	X				4.5 km NNE Weeli Wolli Spring	-22.883	119.236
163089	X				4.5 km NNE Weeli Wolli Spring	-22.883	119.236
163232	X				Jinayri Mine	-23.04	119.2794
163244	X				24.8 km S Roebourne	-20.9963	117.0847
163909	X				27 km ENE Warrawagine Homestead	-20.7481	120.931
165157	X				3.5 km N Karratha Station	-20.8539	116.669
165158	X	X		X	3.5 km N Karratha Station	-20.8539	116.669
165171	X				26 km WNW Mount Berry	-22.4253	116.215
165211	X			X	5 km S Lake Poongkaliyarra	-21.0364	117.106
169960	X				Packsaddle Range	-22.905	119.1769
170006	X				26 km ENE Wodgina	-21.0664	118.899
170574	X				22 km NE Peedamulla Homestead	-21.7319	115.807
170756	X	X		X	5.2 km WSW Pannawonica	-21.663	116.279
170869	X				14.5 km S Dresser Mining Center	-21.2794	119.412
170899	X				14.5 km S Dresser Mining Center	-21.2794	119.412
***G. peninsularis* sp. nov.**							
125740	X			X	Burrup Peninsula	-20.55	116.8333
132562	X	X		X	Burrup Peninsula	-20.6161	116.785
132563	X	X	X	X	Burrup Peninsula	-20.6161	116.785
146581	X	X		X	Burrup Peninsula	-20.6166	116.785
165237	X				Hearson Cove, Burrup Peninsula	-20.635	116.799
165239	X				2.4 km W Hearson Cove	-20.617	116.772
165240	X				3.4 km NE Dampier, Burrup Peninsula	-20.658	116.741
165508	X		X	X	West Intercourse Island	-20.7	116.5833
165517	X			X	West Intercourse Island	-20.7	116.5833
165534	X			X	West Intercourse Island	-20.6858	116.6306
165748	X	X		X	Dampier Port	-20.6166	116.75
165749	X	X		X	Dampier Port	-20.6166	116.75

APPENDIX 2 Summary of morphological measurements for members of the *Gehyra punctata* species complex: continuous variables, counts and ratios. See Table 1 for an explanation of characters.

Character	*G. punctata* Fry	*G. macra* sp. nov.	*G. punctulata* sp. nov.	*G. polka* sp. nov.	*G. fenestrula* sp. nov.	*G. media* sp. nov.	*G. micra* sp. nov.	*G. peninsularis* sp. nov.
SVL (mm)	59.3	66.0	51.8	53.8	41.3	43.2	37.4	42.2
Mean (range)	(55.5–65.0)	(59.0–73.5)	(48.0–56.0)	(49.0–61.0)	(36.0–48.0)	(36.5–50.0)	(34.0–46.5)	(36.0–48.5)
TailL	70.0	70.3	52.1	54.1	40.4	43.3	38.9	44.4
N	(65–75)	(52 – 83)	(46–60)	(47–63)	(35–45)	(37–52)	(35–50)	(39–55)
	8	10	8	9	5	8	8	12
HeadL	17.2	18.5	14.4	14.9	12.6	11.9	10.2	11.6
	(15.7–19.0)	(16.6–20.3)	(13.2–15.9)	(7–9)	(10.9–15.3)	(10.7–13.4)	(8.7–11.4)	(9.6–14.4)
HeadW	12.8	14.0	11.1	11.3	9.0	9.4	7.7	8.4
	(11.9–14.2)	(12.0–15.6)	(10.0–12.2)	(7–9)	(7.8–10.0)	(7.8–10.9)	(7.0–9.2)	(7.1–10.6)
HeadD	6.6	7.0	5.6	5.5	4.4	4.7	4.0	4.5
	(5.3–7.9)	(6.1–8.4)	(4.9–6.0)	(7–9)	(3.7–5.5)	(3.8–5.5)	(3.5–4.6)	(3.6–5.4)
LegL	8.7	10.3	8.0	8.3	6.6	6.7	5.4	6.2
	(7.9–9.6)	(9.0–11.6)	(7.3–8.7)	(7–9)	(5.9–8.5)	(5.6–7.7)	(4.8–6.4)	(5.0–8.5)
SupLab	10.0	9.3	9.3	9.3	9.3	8.0	8.3	8.4
	(9–12)	(9–10)	(9–10)	(9–10)	(8–10)	(7–9)	(8–9)	(7–10)
InfLab	8.5	8.1	8.5	8.0	7.9	7.7	7.6	7.4
	(8–10)	(7–9)	(7–9)	(7–9)	(7–9)	(7–9)	(7–8)	(7–8)
SupNas: separate/ contact	5/6	7/5	5/7	9/3	2/9	6/6	6/6	10/2
4TLam	7.8	9.2	7.3	7.2	6.3	5.9	5.8	6.6
	(7–8)	(7–10)	(7–8)	(7–8)	(6–7)	(5–6)	(5–6)	(6–7)
PCP	13.3	17.0	10.8	11.3	10.8	10.8	14.5	12.1
N males	(9–15)	(14–21)	(8–13)	(10–13)	(9–12)	(8–15)	(10–19)	(7–15)
	27	9	9	11	4	18	22	9
HeadW/HeadL	0.742	0.755	0.771	0.761	0.720	0.789	0.753	0.729
	(0.718–0.770)	(0.695–0.813)	(0.719–0.834)	(0.721–0.797)	(0.608–0.797)	(0.729–0.840)	(0.708–0.805)	(0.675–0.794)
HeadD/HeadL	0.381	0.380	0.388	0.373	0.356	0.398	0.397	0.389
	(0.338–0.417)	(0.344–0.433)	(0.350–0.432)	(0.301–0.430)	(0.266–0.407)	(0.328–0.442)	(0.330–0.471)	(0.340–0.450)