RECORDS OF THE WESTERN AUSTRALIAN MUSEUM 26 115–137 (2011) DOI: 10.18195/issn.0312-3162.26(2).2011.115-137

Revision of the Pygmy Spiny-tailed Skinks (*Egernia depressa* species-group) from Western Australia, with descriptions of three new species

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ABSTRACT – *Egernia depressa* is an extremely spiny species of scincid lizard that occurs in several populations with highly variable morphology in western Australia. Using a combination of fixed morphological character differences and mitochondrial DNA sequence data, we found evidence for four species level groups within the complex. We restrict *E. depressa* to the log-inhabiting population from south-western Australia and resdescribe the species, and describe three new species from the arid zone: two from the Pilbara and one from the central ranges. In addition to the genetic differences, the species differ in head size, limb length, tail shape, colouration and scalation. Many of the morphological characters appear to be adaptations to log or rock-dwelling, with the log-dwelling *E. depressa* having brown colouration, large head, limbs and tail and long thin spines on the body and tail. The two Pilbara species are not each other's closest relatives, yet they resemble each other the closest, probably owing to a suite of characters adapted for living in rock crevices such as yellow to reddish colouration, smaller head and limbs, narrower tail and short strong spines on the body and tail. The central ranges species appears to have a combination of characters from log and rock-dwelling forms and is the most isolated of the four species.

KEYWORDS: new species, *Egernia*, skink, Australia, mitochondrial DNA.

INTRODUCTION

Scincid lizards of the genus *Egernia* Gray, 1839 (*sensu* Gardner et al. 2008) are medium to large-bodied Australian *Egernia* group skinks with moderate morphological diversity and a tendency towards sociality (Storr et al. 1999; Chapple 2003). Many *Egernia* species rely on crevices for shelter in either rocks or trees, especially fallen logs. The Pygmy Spiny-tailed Skink, *E. depressa* (Günther, 1875), occurs in arid regions in the southern and western portion of Western Australia (WA), with widely scattered localities in the western half and also south-western Northern Territory (Figure 1). They are interesting lizards owing to their relatively large body size for a skink and unusual appearance featuring complex patterns on a brown to reddish colouration and spinose scales along the body, especially the tail. Storr (1978) systematically reviewed all *Egernia* occurring in Western Australia, including *E. depressa*. He commented on morphological and colour pattern variation within *E. depressa* and specifically mentioned the Pilbara populations as having 'almost diverged to the extent of being a separate subspecies' (p. 154). However, he took a conservative approach owing to individuals that appeared to be intermediate to the southern and Pilbara forms in the upper Ashburton-Jiggalong region and also that the central population approached the colouration of skinks from the Pilbara.

More extensive collections are available now, including tissue samples for molecular genetic analyses, and the morphological variation apparent in southern, Pilbara and central populations, allowing a more comprehensive taxonomic review of the species and the variation identified by Storr (1978). In the present paper, we assess the morphological and molecular genetic

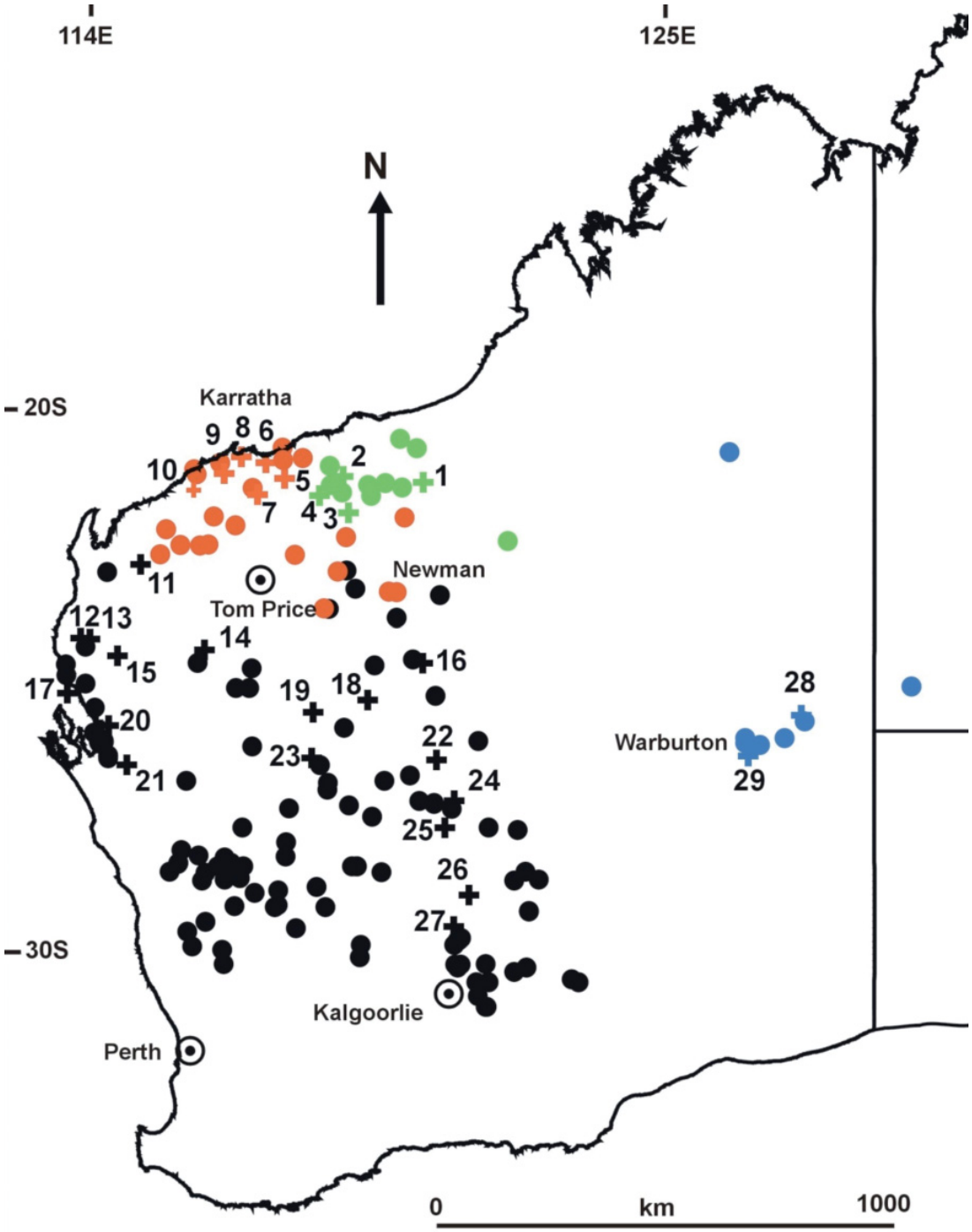

FIGURE 1 Distribution of the *Egernia depressa* species-group in Australia.

variation across the range of *E. depressa*. We found considerable depth and complexity in the patterns of genetic and morphological divergence among regions, supporting the recognition of four species level lineages. We redescribe *E. depressa sensu stricto* and describe the three other lineages as new species.

MATERIALS AND METHODS

MITOCHONDRIAL DNA ANALYSES

We obtained nucleotide sequences of the mitochondrial *ND4* gene and flanking tRNAs (Histidine and Serine) from 65 lizards (see Figure 1 and Appendices 1 and 2 for details of specimens examined and GenBank accession numbers). Outgroup taxa were selected on the basis of the phylogenetic analysis of the *Egernia* group by Gardner et al. (2008).

DNA was extracted from tissue samples with a Gentra Purgene kit (Qiagen) from frozen or alcohol preserved tissues and stored at -20°C. For polymerase chain reaction (PCR) amplifications, 50–100 ng of the extracted total DNA samples were added to 50 µl reaction mixtures containing 2 or 4 mM $MgCl_2$, 1X *Taq* DNA buffer, 0.2 mM each of dNTPs, 0.25 mM each primer and 0.75 unit of Promega *Taq* DNA Polymerase. The primers used for amplification and direct sequencing of part of the mitochondrial *ND4* gene are listed in Gardner et al. (2008). Amplification was carried out on a Corbett FTS-320 Thermal Sequencer and comprised a single cycle of denaturation for 3 min at 94°C, annealing for 45 s at 47°C or 55°C and extension for 1 min at 72°C, followed by 34 cycles of 94°C for 45 s, 47°C or 55°C for 45 s and 72°C for 1 min, ending with a single extension step of 72°C for 6 min. PCR products were purified for sequencing using BRESAspin™ PCR Purification Kit from Bresatec, following the manufacturer's protocol. Each sample had both strands sequenced directly from the PCR product using the original PCR primers. Products were sequenced on a Corbett FTS-1 Thermal Sequencer using the ABI PRISM™ Dye Terminator Cycle Sequencing Ready Reaction Kit from Perkin Elmer, following the manufacturer's instructions. The sequencing program consisted of 25 cycles of 94°C for 30 s, 50°C for 15 s and 60°C for 4 min. Sequencing products were electrophoresed on an ABI PRISM 377 Sequencer.

Evolutionary trees were constructed with the maximum likelihood (ML) criterion of optimality implemented in the web server version of RAxML (Stamatakis et al. 2008), which uses the GTR+Γ model of nucleotide substitution. We applied four partitions to the data: first, second and third codon positions for the *ND4* gene and the tRNA genes. The robustness of phylogenetic hypotheses was tested with non-parametric bootstrapping from 1000 pseudoreplicates.

MORPHOLOGY

We examined specimens in the collections of the Western Australian Museum (WAM; hereafter, WAM prefixes are excluded from specimen numbers). Table 1 presents the morphological variables assessed. Measurements were made with electronic callipers to the nearest 0.1 mm, with SVL, TailL and TrunkL to 0.5 mm. Individuals were sexed by direct examination of the gonads and observations of conspicuous young or everted hemipenes. Based on the genetic groupings (see Results, below), we measured approximately 20 individuals from each genetic lineage.

For the statistical tests, we excluded individuals that were 91 mm SVL or less to produce homogeneous samples of adult body sizes. We tested for significant differences in SVL as a function of sex and group with a 2-factor ANOVA. For TrunkL, we used SVL as a covariate and sex and group as factors in a 2-way ANCOVA. As there were no sex or group differences for SVL or TrunkL (see Results, below), we pooled males and females for all subsequent analyses. We used 1-way ANOVAs to test whether there were significant differences in the following characters among lineages: HeadL, HeadW, HeadD, ArmL, LegL, TailL, TailW, SupLab, InfLab, SupCil, EarLob, MBSR, 4FLam and 4TLam. We used Tukey's post-hoc test (alpha = 0.05) to determine which populations differed significantly from each other when the overall ANOVA was significant.

Other abbreviations: Australian Museum, Sydney (AMS), Natural History Museum, London (BMNH), Northern Territory Museum and Art Gallery, Darwin (NTM), South Australian Museum, Adelaide (SAMA).

RESULTS

MOLECULAR GENETICS

Figure 2 shows the Maximum Likelihood phylogenetic tree of mitochondrial nucleotide sequences of the *E. depressa* species-group and a range of outgroups. Samples identifiable as members of the *E. depressa* species-group fell into four major clades which we refer to as the southern group, central group, eastern Pilbara group and western Pilbara group (up to the Taxonomy section, below). Each clade received strong bootstrap support. The eastern Pilbara group is the well-supported sister to the remaining three clades, within which the central and the western Pilbara groups form a sister clade but without strong support (effectively forming an unresolved trichotomy). Mean uncorrected genetic distances (p-distance) among the four clades range from 4.0% (between the southern and central groups) to 7.3% (between the eastern and western Pilbara groups), contrasting with mean p-distances within groups of a minimum of 0.5% within the central group to a maximum of 1.8% within the southern group (Table 2).

MORPHOLOGY

Table 3 summarizes the morphological measurements for the four groups of *E. depressa* and presents the results of the statistical tests. The 2-way ANOVA on

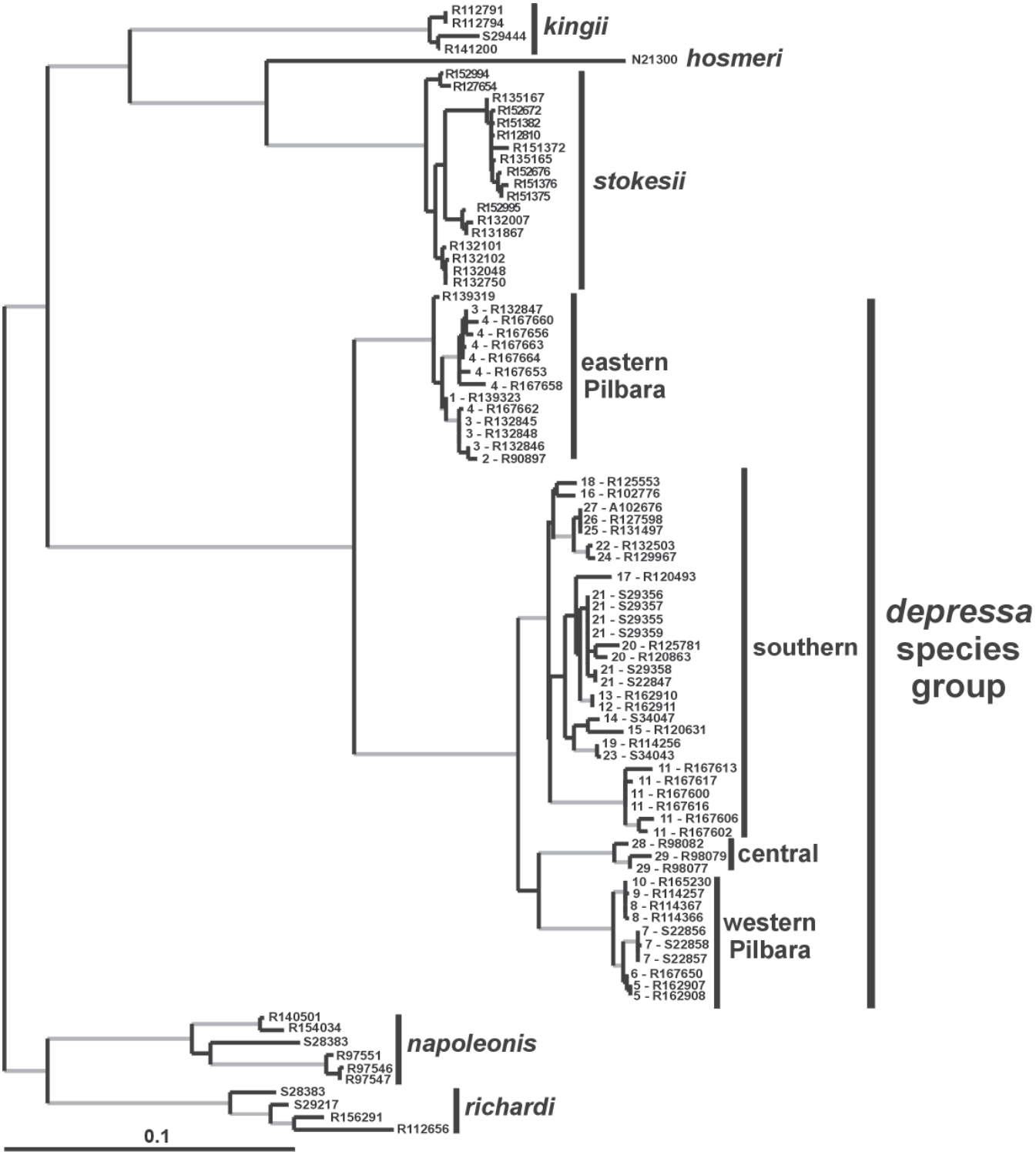

FIGURE 2 Maximum likelihood phylogeny of mitochondrial *ND4* nucleotide sequences of the *Egernia depressa* species-group. Branches in grey had bootstrap proportions > 70%.

TABLE 1 Meristic characters and their abbreviations.

Character	Description
SVL	Snout-vent length
TrunkL	Trunk length from axilla to groin
HeadL	Head length from tip of snout to anterior margin of the ear
HeadW	Head width, measured level with centre of the ear opening, below the spines
HeadD	Head depth, measured level with centre of the ear, in between two spine rows
ArmL	Measured from the base of wrist to the elbow
LegL	Measured from the base of the heel to the knee
TailL	Tail length from vent to tip
TailW	Width of the tail at the widest point just below the outer row of spines
SupLab	Number of supralabial scales
InfLab	Number of infralabial scales, ending with the last small scale in contact with the posterior margin of the last upper labial
SupCil	Number of supracilaries, beginning with the scale adjoining the prefrontal and loreal, and ending with the scale still contacting cilaries and last supraocular
MBSR	Number of midbody scale rows, counted midway between axilla and groin
4FLam	Number of enlarged subdigital lamellae under fourth finger, counted from finger junction to base of claw
4TLam	Number of enlarged subdigial lamellae under fourth toe, counted from toe junction to base of claw

TABLE 2 Uncorrected pairwise sequence divergences (%) within (diagonal, bold for emphasis) and between (below diagonal) the four lineages in the *Egernia depressa* species-group. Entries show the range with means in parentheses.

Character	southern	central	western Pilbara	eastern Pilbara
southern	**1.8**			
central	3.7–4.6 (4.0)	**0.5**		
western Pilbara	3.8–5.3 (4.3)	3.8–4.4 (4.1)	**0.6**	
eastern Pilbara	6.1–8.6 (6.9)	7.3–8.0 (7.7)	6.5–8.0 (7.3)	0.8

TABLE 3 Summaries of characters and ratios measured for four groups of the *Egernia depressa* species-group. Mean±SD (range). See Table 1 for abbreviations and Materials and Methods for details of statistical tests (NS, not significant: $P>0.10$, * $P<0.05$, ** $P<0.01$, *** $P<0.001$, **** $P<0.0001$). Sample sizes for all individuals measured are presented in the column headings. Subadult (<90 mm) individuals, however, were removed from all comparisons involving quantitative variables. Thus, for the first nine characters sample sizes for the two Pilbara groups were: western, 12♀, 5♂, eastern, 10♀, 3♂. †N = 18.

Character	southern N=22 (14♂, 8♀)	central N=20 (10♂, 10♀)	western Pilbara N = 19 (8♂, 12♀)	eastern Pilbara N = 22 (8♂, 13♀)	Statistics
SVL	♀♀: 100.1±3.6	♀♀: 98.3±5.7	♀♀: 102.8±6.6	♀♀: 99.6±3.8	Overall: $F_{3,68} = 1.575^{NS}$
	(97.5–107.5)	(91.5–108.5)	(91.5–117.5)	(91.0–110.0)	
	♂♂: 99.1±3.8	♂♂: 101.6±5.0	♂♂: 94.9±2.1	♂♂: 101.4±4.7	
	(93.0–105.0)	(95.5–110.0)	(92–97.0)	(94.0–105.5)	
TrunkL	♀♀: 51.1±3.5	♀♀: 49.5±5.8	♀♀: 54.0±4.0	♀♀: 49.5±5.7	GROUP: $F_{3,67} = 2.913^{NS}$
	(45.5–54.9)	(40.4–58.2)	(46.6–58.3)	(38.4–57.1)	SEX: $F_{1,67} = 1.017^{NS}$
	♂♂: 48.4±2.2	♂♂: 53.0±2.3	♂♂: 48.0±3.4	♂♂: 50.0±4.0	COVARIATE (SVL): $F_{1,67} = 115.770^{****}$
	(43.7–51.9)	(49.6–56.1)	(43.0–51.2)	(43.5–56.5)	$F_{3,72} = 5.094^{**}$
HeadL	18.3±0.8	18.1±0.8	17.4±0.7	17.8±0.9	
	(17.4–20.5)	(16.3–19.5)	(16.3–19.1)	(16.0–19.5)	$F_{3,72} = 5.425^{**}$
HeadW	14.9±1.2	15.5±1.5	13.6±1.4	14.9±1.4	
	(13.4–19.1)	(12.9–17.9)	(11.0–17.3)	(11.6–16.7)	$F_{3,72} = 4.291^{**}$
HeadD	12.0±0.6	12.1±1.0	11.1±0.9	11.7±0.8	
	(11.2–13.1)	(10.6–13.8)	(9.8–12.7)	(10.4–13.3)	$F_{3,72} = 3.196^{**}$
ArmL	12.1±0.5	12.0±0.6	11.6±0.7	11.7±0.8	
	(11.1–13.0)	(10.9–12.8)	(10.1–12.6)	(10.5–13.2)	$F_{3,72} = 14.553^{****}$
LegL	12.8±0.6	12.3±0.5	11.7±0.6	11.8±0.6	
	(11.8–14.2)	(11.5–13.1)	(10.5–12.6)	(10.8–12.8)	$F_{3,72} = 4.832^{***}$
TailL	38.5±2.6	36.8±3.3	41.1±4.4	40.1±4.8	
	(34.5–43.0)	(31.0–44.5)	(33.5–49.8)	(31.2–47.5)	$F_{3,72} = 13.099^{****}$
TailW	17.6±1.1	17.3±1.0	15.4±1.4	16.8±1.2	
	(16.2–20.5)	(15.5–18.8)	(13.4–17.3)	(13.6–18.5)	$F_{3,79} = 0.399^{NS}$
SupLab	6.0±0.1	6.1±0.3	6.0±0.5	6.1±0.4	
	(6–7)	(6–7)	(5–7)	(5–7)	$F_{3,79} = 2.623^{NS}$
InfLab	5.4±0.5	5.4±0.5	5.3±0.6	5.0±0.4	
	(5–6)	(5–6)	(4–7)	(4–6)	$F_{3,79} = 105.542^{****}$
SupCil	5.4±0.6	5.6±0.5	3.9±0.2	4.0±0.2	
	(4–6)	(5–7)	(3–4)	(3–5)	$F_{3,79} = 25.295^{****}$
MBSR	34.7±1.9	31.9±0.6	31.7±1.1	31.8±1.3	
	(32–38)	(31–33)	(30–34)	(30–34)	$F_{3,79} = 36.048^{****}$
4FLam	13.3±1.2	12.5±0.8	11.1±0.9	10.7±0.8	
	(12–16)	(11–15)	(10–13)	(9–13)	$F_{3,78} = 30.966^{****}$
4TLam	14.8±0.6	14.3±0.7	13.3±1.1†	12.7±0.9	
	(14–16)	(13–16)	(12–15)	(11–14)	

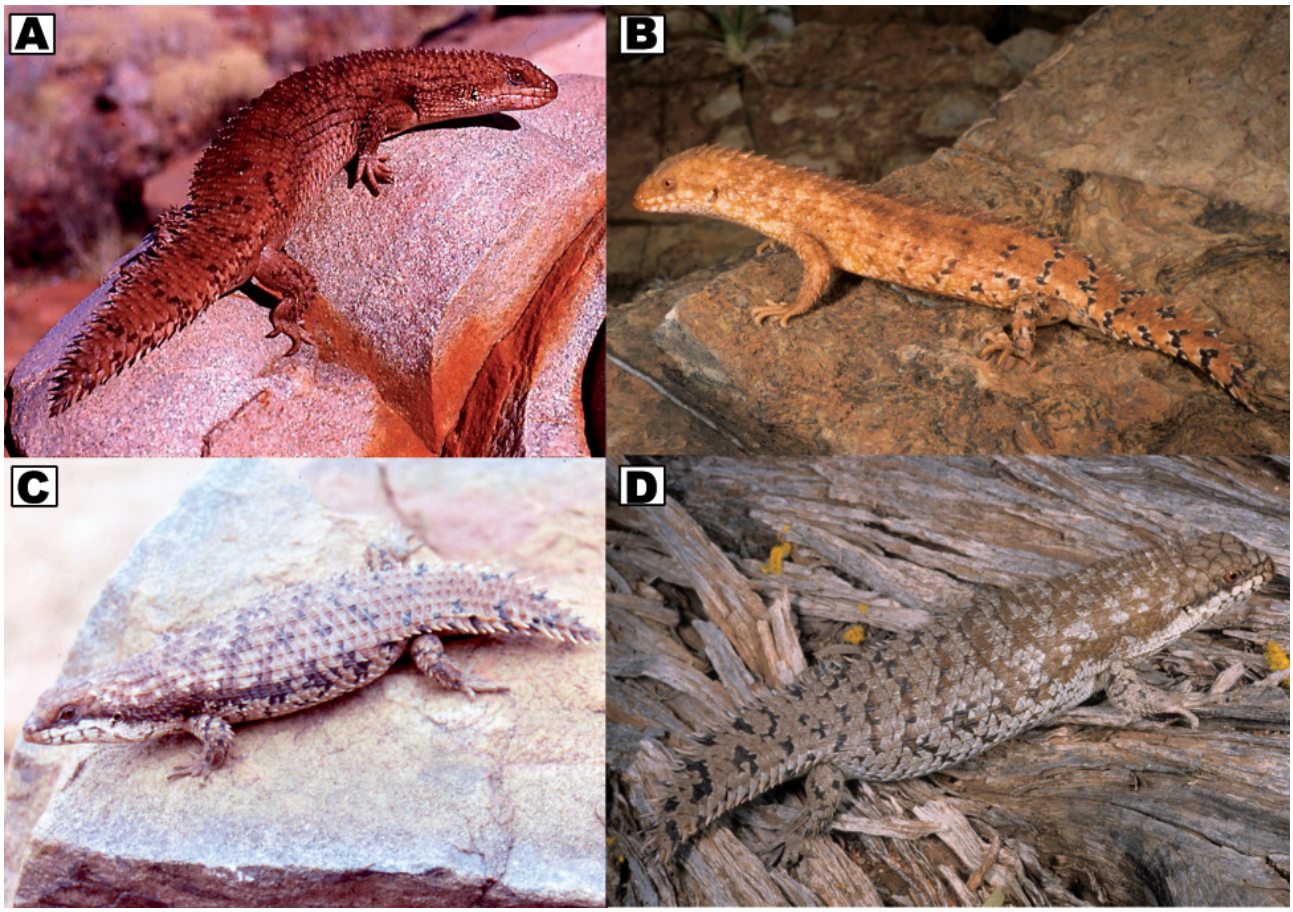

FIGURE 3 Photos in life of *Egernia depressa* species-group members: A) western Pilbara group (photo – G. Gaikhorst), B) eastern Pilbara group (B. Maryan), C) central group (G. Johnston), D) southern group (B. Maryan).

sex and group revealed no significant differences in SVL. For the 2-way ANCOVA on TrunkL, SVL was significant as a covariate, but sex and group were not significant. The ANOVAs for head size variables were all significant, with the post-hoc tests all combining the southern, central and eastern Pilbara groups together with higher values compared to the western Pilbara group which had a smaller head (Table 3). For HeadW and HeadD, the western Pilbara group had significantly lower values than the other three groups, and for HeadL both Pilbara populations had lower values than the southern and central groups. For ArmL, the western Pilbara group had significantly shorter limbs than the other three groups. LegL also differed significantly among groups, with the post-hoc tests combining the Pilbara groups together with the shortest legs, the next group with moderate-sized legs was the eastern Pilbara and central group and the southern group had the longest legs. TailL varied significantly among groups, with the central and southern populations having relatively short tails, and the southern and both Pilbara groups with the longest tails. TailW was significantly narrower in the western Pilbara group compared to the other three groups with wider tails (Table 3; Figures 3, 4). For scalation characters, numbers of labial scales did not differ, but the two Pilbara groups had significantly fewer supraciliary scales and subdigital lamellae than the southern and central groups (Table 3). For MBSR, the southern group had significantly higher counts than the other three groups (Table 3).

Qualitative differences in scalation were also apparent among groups. In the eastern Pilbara group the nasal scale is incompletely divided (grooved below but not above nare), whereas in the other three groups the nasal is clearly divided above and below the nare (Figure 5). In the southern group, the parietal and nearby scales are relatively flat, in the central group the posterior border is slightly raised with short spines and in the two Pilbara groups the posterior border is raised with a prominent row of spines. In the southern and central groups, ear openings are large and without projecting scales; in the two Pilbara groups, the ear opening is small with scales that project well into the opening from the anterior border. Palmar and plantar scales differed, with southern populations having flatter scales and the other three groups with slightly rounded, protruding scales. Dorsal spines on southern individuals are long and thin and lie nearly flat, whereas in the three other groups

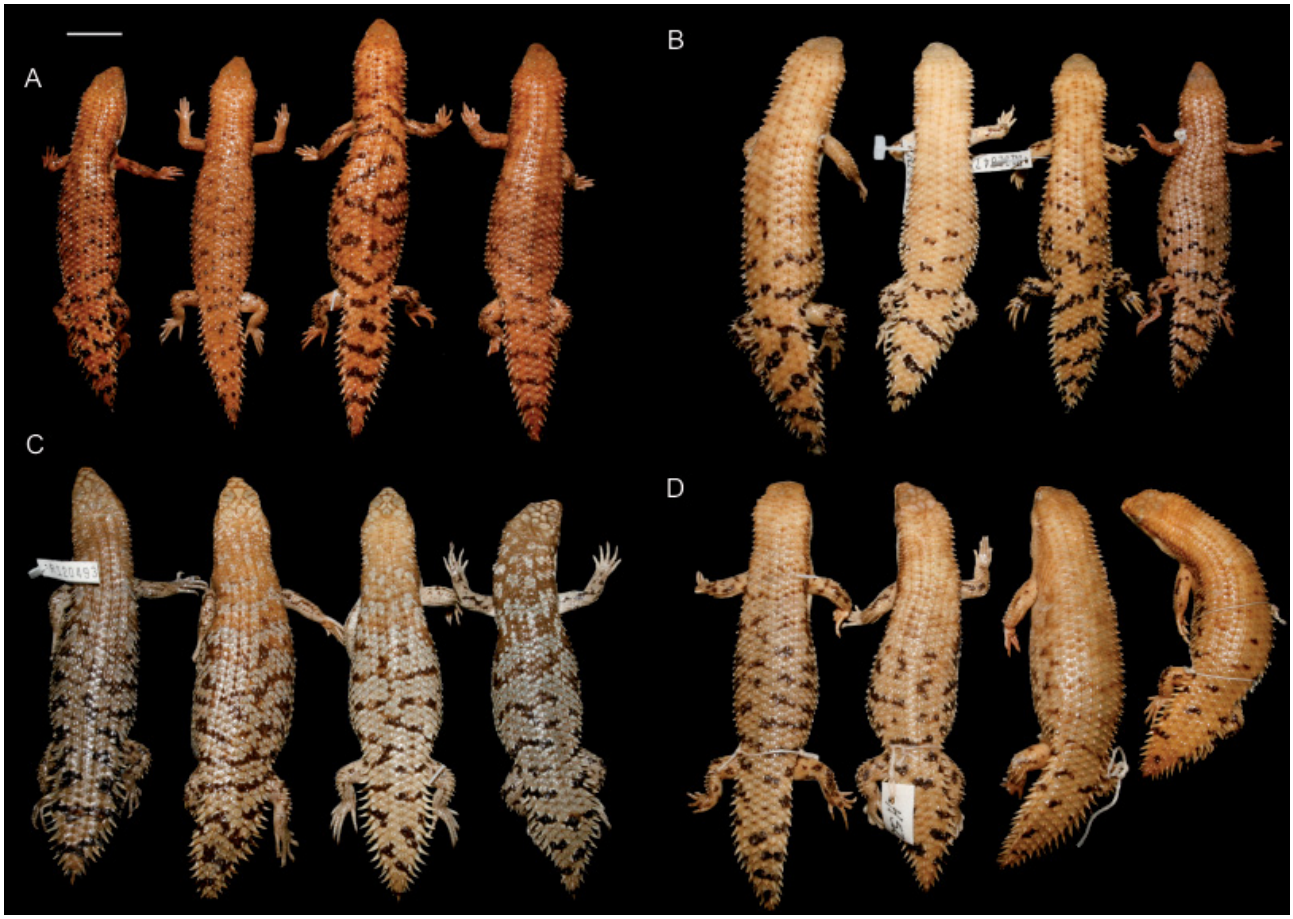

FIGURE 4 Range of variation in dorsal view among populations of the *Egernia depressa* species-group. A) western Pilbara group, B) eastern Pilbara group, C) southern group, D) central group.

they are shorter, stouter and project upwards. Spines on the eastern Pilbara specimens were the strongest, with a triangular appearance when viewed laterally and projecting away from the body (Figure 5). Viewed from above, lateral spines projected posteriorly at ~10° (i.e. almost parallel to body) in the southern group, increasing to about 30° in central and western Pilbara groups, and to about 45° in the eastern Pilbara group (Figure 4). The spines on the tails of southern group individuals are conspicuously longer and more recurved than the other three groups (Figure 4). Dorsal surface of tails of southern individuals are nearly flat, whereas tails in the other three groups have slightly tapered edges.

Colouration and pattern also differed among groups (Figures 3, 4). Individuals from the southern group have a grey background colouration posteriorly and brown head and anterior portion of the body, including a brown streak along the neck with a straight ventral edge. The other three groups had yellow to reddish-brown background colour, with the western Pilbara populations having the most reddish colour. The central group shares with the southern population the brown streak with a straight ventral edge. All populations have irregular dark transverse markings on the tail, but are variably expressed among them (Figure 4). In the western Pilbara group the bands often go up to the level of the arms, in the southern group they stop before the arms and in the central and eastern Pilbara groups the bands are usually confined to tail and posterior portion of body. The bands are usually edged with white in the eastern Pilbara and southern groups.

SYSTEMATIC CONCLUSIONS

Our molecular genetic and morphological analyses found evidence for four species-level lineages within *E. depressa*. In his review of *E. depressa*, Storr (1978) remarked on the Pilbara populations being noticeably distinct from southern populations. He listed several characters that we also measured that varied between the two regions, bearing in mind that his Pilbara sample combined two of our four groups. Phenotypically, the two Pilbara groups are most similar to each other. However, the genetic evidence indicates the western Pilbara group is more closely related to the southern and central groups, and not to the eastern Pilbara group. Among the remaining three closely-related groups, character state variation ranges from what appears to be a log-dwelling morphology (southern

group: brownish-grey colour, large head, limbs and tail, long thin spines), a rock-dwelling morphology (western Pilbara group: red colouration, small head, limbs and tail, short stout spines) and an intermediate morphology (central group: yellow-red colouration, large head, limbs and tail, short stout spines). In the Remarks sections for each taxon (below) we speculate further on the adaptive significance of these morphological characters and possible evolutionary history of the four groups. Regardless of these considerations, however, our combined molecular genetic and morphological data support the notion of four independent evolutionary lineages that are all morphologically diagnosable. Below we provide brief diagnoses for *Egernia* and the *E. depressa* species-group, redescribe *E. depressa sensu stricto* (the log-dwelling southern group) and describe the other three groups as new species.

TAXONOMY

Genus *Egernia* Gray, 1839

Egernia Gray, 1839: 288

TYPE SPECIES

Tiliqua cunninghami (Gray, 1832), by monotypy.

DIAGNOSIS (FROM GARDNER ET AL. 2008)

A genus of medium to large *Egernia* group skinks; usually dorsoventrally compressed, but with a more stout habitus in *E. kingii* and *E. rugosa*; MBSR 24–46; dorsal scales smooth, striated, multi-keeled and/or with long spine; postnarial groove (if present) on nasal scale in contact with first supralabial; parietals separated by interparietal; subocular scale row incomplete; eyes relatively small; eyelid colour similar to neighbouring scales.

INCLUDED SPECIES

Egernia cunninghami (Gray, 1832), *E. cygnitos* sp. nov., *E. depressa* (Günther, 1875), *E. douglasi* Glauert, 1956, *E. eos* sp. nov., *E. epsisolus* sp. nov., *E. formosa* Fry, 1914, *E. hosmeri* Kinghorn, 1955, *E. kingii* (Gray, 1838), *E. mcpheei* Wells and Wellington, 1984, *E. napoleonis* (Gray, 1838), *E. pilbarensis* Storr, 1978, *E. richardi* (Peters, 1869), *E. rugosa* de Vis, 1888, *E. saxatilis* Cogger, 1960, *E. stokesii* (Gray, 1845), *E. striolata* (Peters, 1870).

Egernia depressa species-group

DIAGNOSIS

Medium-sized (to 110 mm SVL) skinks with triangular head and blunt snout, spinose dorsal scalation with each scale usually possessing a long central spine flanked by two smaller spines, short non-fragile dorsoventrally compressed tail with long spines, no nuchal scales, litter size usually two.

Egernia depressa (Günther, 1875)

Southern Pygmy Spiny-tailed Skink

Figures 3–6

Silubosaurus depressus Günther, 1875: 15.

SYNTYPES

Australia: ***Western Australia*:** 2 syntypes, BMNH 1946.8.18.41–42, from southern interior of WA (Swan River).

DIAGNOSIS

A member of the *E. depressa* species-group, with a relatively long, deep and broad head, long limbs, long and thin dorsal spines that lie almost parallel to body and project clearly beyond scale, nasals in broad contact, divided nasal scale, numerous supraciliaries (4–6), head scales not raised and lacking spines on posterior border, ear opening large without lobules projecting over opening, 32–38 MBSR, numerous subdigital lamellae on fourth digits (fingers 12–16, toes 14–16), slightly raised flat scales on palmar and plantar surfaces, tail wide, dorsal surface of tail flat with long recurved spines. Colouration: head brown with black sutures, anterior of body light brown, posterior brownish-grey, irregular dark transverse bands on tail and posterior two-thirds of body, bands often edged with white.

DESCRIPTION

Medium (to 107.5 mm SVL) body size, with robust habitus and extremely spiny scalation, especially on the flattened tail. Head triangular and robust, snout tapering to rounded tip when viewed laterally, slightly concave snout when viewed dorsally, brows protruding; upper labials 6–7, lower labials 5–6, loreals 2, presuboculars 2, supraciliaries 4–6, nasals in contact, postnarial groove strong, prefrontals in contact and forming broad suture; parietal and neighbouring head scales flat and posterior edge without projecting spines; ear opening large, oblong and oriented vertically, without enlarged lobules or scales projecting over opening; no enlarged nuchal scales; neck only slightly narrower than widest part of head (above tympani); scales under chin enlarged to level between eye and ear, then abrupt shift to series of smaller scales that gradually enlarge on ventral surface of neck.

Dorsal scales with one long thin central spine flanked by two smaller spines that usually are only half the length of the central spine, central spine projecting clearly beyond posterior edge of scale; spines on neck and forebody angled very low (~20°), posteriorly the spines are directed more vertically (~30°) to almost vertical on the tail; body with 18–22 longitudinal rows of spines. On the upper lateral surfaces the spines are directed back towards midline; on lower lateral surfaces the spines gradually diminish in size until ventrolateral edge, scales in axillary region without spines. Ventral

FIGURE 5 Nasal scales (left) and dorsal scalation (right) of members of the *Egernia depressa* species-group. Dorsal scalation photo taken above the arm. Top row, southern group; second row, central group; third row, western Pilbara group; fourth row, eastern Pilbara group.

FIGURE 6 Syntypes of *Silubosaurus depressus* (upper – BMNH 1946.8.18.41; lower – BMNH 1946.8.18.42). Scale bar = 1 cm.

scales c. half the size of dorsal scales. Tail wide and dorsoventrally compressed, flat dorsally but with ventral portion cylindrical; dorsal surface with four longitudinal rows of spines, spines on outermost row following outline of tail two-thirds along length then enlarging to size of lateral rows; two lateral rows of especially long recurved spines, dorsal row ending halfway along tail; a ventro-lateral row runs most of the length of tail but spines are a quarter the size of lateral spines; ventral surface smooth, tail tip terminating in a spine.

Limbs relatively short and robust; 3–5 rows of spines on upper portion of limbs with moderately long spines; spines not protruding on anterior, posterior and ventral surfaces of limbs. Palmar and plantar surfaces with slightly raised flat scales; digits short and well-developed; finger length: 4>3>2>5>1, toe length: 4>5>3>2>1; smooth subdigital lamellae: fourth finger 12–16, fourth toe 14–16. Claws sharp and recurved.

Colouration

In life: Eyes red with black pupil. Anterior background colour yellowish-brown; brownish-grey posteriorly, but with broad intergrade zone centred on upper to mid torso; intergradation taking the form of alternating broad irregular transverse blocks of colour; dark brown to black angled transverse bars on tail and posterior portion of body, usually irregular and not forming long bands, erratically edged with white; top of snout pale with dark sutures. Upper surfaces of limbs brownish-grey, usually heavily marked with dark blotches. Pattern on sides of body a mixture of posterior brownish-grey with irregular dark blotching; on side of neck posterior to tympanum a brownish streak often discernable, usually with a straight ventral edge, becoming indistinct posterior to axillary region. Ventral surfaces pale, variably marked with dark blotches or flecks, sutures between scales under snout heavily pigmented, ventral surface of tail tending to be more heavily marked than the rest of the body, markings sometimes forming longitudinal blotches.

In spirit: Very similar to live colouration, except generally darker in appearance in older specimens.

VARIATION

Table 3 presents the ranges for morphological characters measured. The transverse bars on the tail and dorsum ranged from continuous bars across the body or smaller scattered blotches. The white edging on the

bars was also variable, with about half the individuals possessing them. The ventral edge of the brown streak on the side of the neck varied from straight to irregular; the dorsal edge of the streak was usually distinct from the anterior brown colouration but on many specimens the streak approached the background colour and so was ill-defined. As reported by Storr (1978), juveniles tend to have only the single central spine on the dorsal scales, with the flanking spines to either side developing more strongly as individuals approach adult size.

HABITAT

Prefers open woodland, especially mulga, where they will shelter in dead trees and fallen logs. Also occurs on granite outcrops where available (e.g. surrounded by mulga woodland).

DISTRIBUTION

Western Australia, from 100 km west of Kalgoorlie in the southeast of its range, west to the Wongon Hills, north and west to below the Northwest Cape and north and east to near Newman (but not occurring on the Pilbara craton). Older records from Perth and Albany are the result of accidental transportation. The specimens from two older records from Korrelocking and Marvel Loch cannot be located so we have excluded them from the map in Figure 1.

ETYMOLOGY

The adjective *depressa* (Latin) refers to the dorso-ventrally flattened appearance of this species.

COMPARISON WITH OTHER SPECIES-GROUP MEMBERS

Egernia depressa can be distinguished from the other three members of the species-group by browner colouration (v. yellow to reddish-brown colouration), flat scales on head and palmar and plantar surfaces, more MBSR (~ 35 v. 32), dorsal spines are long, thin and lie almost parallel to body (v. short and stout spines that project upwards) and wide tail with flat dorsal surface and long recurved spines (v. narrower tails with relatively short and straight spines). It differs further from the two Pilbara species by possessing a relatively large head and limbs, large ear opening without projecting scales, more numerous supraciliaries and subdigital lamellae and having the brown streak with straight ventral edge on the side of the neck. Further distinguished from *E. epsisolus* sp. nov. by a completely divided nasal scale (v. not divided above nare).

REMARKS

With the recognition of three other species from the *E. depressa* species-group, the range of *E. depressa sensu stricto* is reduced. The brown colouration, large head, limbs and tail and long thin spines on the dorsum and tail of *E. depressa* may represent adaptations to living in crevices in logs (see also Hollenshead 2011). However, the species is not restricted to logs, as small groups of individuals have been observed in crevices in granite outcrops surrounded by mulga woodlands (B. Maryan, G. Gaikhorst, pers. comm.). The long thin spines of *E. depressa* may be more advantageous in log hollows than in rock crevices with a relatively smooth and very hard texture. Perhaps the spines can catch irregularities inside logs to avoid dislodgment by a predator. Conversely, hollows in logs may result in less wear on spines compared to rock crevices, obviating the need to make the spines short, stout and projecting outwards (see also remarks below for rock-dwelling species). However, these ideas are speculative and functional tests of spine structure are needed to test them.

Conservation status of *E. depressa* appears to be secure, although the closely-related *E. stokesii badia* from the wheatbelt also shelters in similar logs and has suffered precipitous declines since the arrival of Europeans (How et al. 2003).

Egernia eos **sp. nov.**

Central Pygmy Spiny-tailed Skink

Figures 3–5, 7

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia*****:** R98077 (♂), Ainsley Gorge, 15.8 km ESE Warburton, 26°14'S, 126°42'E. Collected by G. Johnston on 14 December 1987.

Paratypes

Australia: ***Western Australia*****:** R14638 (♀), Warburton mission, 26°08'S, 126°35'E; R15697 (♀), 32 km E Warburton mission, 26°13'S, 126°52'E; R15734 (♀), 32 km E Warburton mission, 26°13'S, 126°52'E; R31363 (♂), Warburton mission, 26°08'S, 126°35'E; R98078 (♂), Ainsley Gorge, 15.8 km ESE Warburton, 26°14'S, 126°42'E; R98083 (♂), 6 km N Mantamaru, 25°46'S, 127°43'E.

Australia: ***Northern Territory*****:** NTM R36432 (formerly WAM R34201); 6 km N Mt Bowley, 25°06'S, 129°45'E.

DIAGNOSIS

A member of the *E. depressa* species-group, with a relatively long, deep and broad head, moderately long limbs, short and stout dorsal spines that project upwards, nasals in short contact, divided nasal scale, numerous supraciliaries (5–7), parietal and other head scales slightly raised posteriorly with low row of spines, ear opening large and without lobules projecting over opening, 31–33 MBSR, relatively large numbers subdigital lamellae on fourth digits (fingers 11–15, toes 13–16), slightly round scales on palmar and plantar surfaces, tail relatively short and wide with rounded edges dorsally and long lateral spines slightly recurved. Colouration: yellowish-brown with pale sides, short dark irregular transverse bands usually confined to tail, sides and upper surfaces of limbs, brownish streak from tympanum extending past arm, occasionally forward to snout.

FIGURE 7 Holotype of *Egernia eos* sp. nov. (WAM R98077), showing dorsal, lateral and ventral views. Scale bar = 1 cm.

DESCRIPTION

Medium (to 108.5 mm SVL) body size, with robust habitus and extremely spiny scalation, especially on the flattened tail. Head triangular and robust, snout tapering to rounded tip when viewed laterally, slightly concave snout when viewed dorsally with brow protruding; upper labials 6–7, lower labials 5–6, loreals 2, presuboculars 1–2, supraciliaries 5–7, nasals usually in short contact (from not in contact to about half the height of nasal scale), postnarial groove strong; prefrontals in contact and forming broad suture; parietal and neighbouring head scales with raised posterior border with a short row of spines; ear opening large, oblong and oriented vertically, with lobules not projecting into opening; no enlarged nuchal scales; neck only slightly narrower than widest part of head (above tympani); scales under chin enlarged to level between eye and ear, then abrupt shift to series of smaller scales that gradually enlarge on ventral surface of neck.

Dorsal scales with a stout central spine flanked by two slightly smaller spines that usually are greater than two-thirds the length of the central spine, central spine only slightly projecting beyond posterior edge of scale, spines on dorsum oriented c. 30° away from dorsum; body with 20–24 longitudinal rows of spines. On the upper lateral surfaces the spines are directed back towards midline; on lower lateral surfaces the spines gradually diminish in size until ventrolateral edge, scales in axillary region without spines. Ventral scales c. half the size of dorsal scales. Tail moderately wide and dorsoventrally compressed, almost flat dorsally but with rounded edges and ventral portion cylindrical; dorsal surface with four longitudinal rows of spines, the outer row following outline of tail near distal third or quarter, then enlarged to size of other lateral row; spines on a third ventrolateral row reduced to a quarter of the size of the first two lateral rows; lateral rows of spines longer and slightly recurved; ventral surface smooth, tail tip terminating in a spine.

Limbs relatively short and robust; 3–5 rows of spines on upper portion of limbs with moderately long spines; spines not protruding on anterior, posterior and ventral surfaces of limbs. Palmar and plantar surfaces with slightly rounded scales; digits short and well-developed; finger length: 4>3>2>5>1, toe length: 4>3>5>2>1; smooth subdigital lamellae: fourth finger 11–15, fourth toe 13–16. Claws sharp and recurved.

Colouration

In life: Background colour yellowy-brown; irregular blackish-brown short (up to about half the width of the body) transverse bars on tail, posterior portion of body, sides and upper surfaces of limbs. Conspicuous dark orangish-brown streak (2–3 scales high) from tympanum extending posteriorly to above arm and fading past arm or joining dark markings on sides; often extending anteriorly to eye above supralabial scales and to snout. Ventral surfaces yellowish white, with widely scattered dark blotches or flecks, sutures between scales under snout occasionally pigmented, neck with darker variegations evident and often forming loose longitudinal lines, ventral surface of tail tending to be more heavily marked than the rest of the body.

In spirit: Very similar to live colouration, except generally darker in appearance in older specimens.

VARIATION

Table 3 presents the range of values of the morphological characters measured. Although there was variation in some scalation characters, this was relatively small within *E. eos*. However, some adults showed clear wearing of the spines as evidenced by a flat edge at the tip; larger individuals also tended to have more broken spines. Juveniles have only a single central spine on the dorsal scales; the flanking spines elongate as individuals approach adult size. Colouration in preserved specimens ranged from a light greyish-yellow to a deeper yellowy brown. There was variation in the darkish variegations on the chin, ranging from scattered spots to longitudinal lines. The sutures between the enlarged chin scales also varied from unmarked to edged with dark brown. Two individuals (R60692, R98083) were unusual in that the transverse bars on the dorsum were present up to the level of the arms. Juveniles tended to be more heavily marked, especially the brown streak on the neck and the vertical bars on the sides.

HABITAT

Collection notes of three specimens report individuals being found ‘under large red granite rocks’ or ‘in rock crevice’. Three other notes mention ‘in mulga wood’ or simply ‘mulga flat’.

DISTRIBUTION

Eastern interior of Western Australia and extreme south-western Northern Territory (Figure 1). Most records are from the Warburton area but there are also two records from the Northern Territory near Mt Bowley in the Peterman Ranges. In addition, two specimens are recorded as being from Well 46 on the Canning Stock Route, over 250 km to the north of all other records. The sole specimen still extant (R4059) conforms in all aspects with other *E. eos* specimens.

ETYMOLOGY

eos (Latin) refers to dawn, alluding to their eastern distribution relative to the other members of the species-group and the yellowy-red colour of the sky in the morning that appears in the east. Used as a noun in apposition.

COMPARISON WITH OTHER SPECIES-GROUP MEMBERS

Egernia eos shares a similar background colouration to the two Pilbara species, but other morphological features are more similar to *E. depressa sensu stricto.*

The colouration mainly differs from the two Pilbara species by having a more conspicuous brown streak that runs between the tympanum to above the arm, similar to *E. depressa*. From *E. cygnitos* sp. nov. it differs by having a more yellowy background colour with the black transverse bands not usually extending to the arms. From *E. epsisolus* sp. nov. it differs by not having the black bands edged with white.

Morphologically, *E. eos* differs from *E. depressa* by having fewer MBSR (average of 32 v. 35), the parietal and other head scales have slightly raised posterior edges with a row of low spines (v. flat and lacking spines), palmar and plantar scales slightly rounded (v. flat), tail with rounded edges (v. flat) and most conspicuously by possessing short strong spines on the dorsum that project upwards (v. long thin spines that lie almost parallel to the body). Compared to the two Pilbara species (*E. cygnitos* sp. nov. and *E. epsisolus* sp. nov.), *E. eos* differs by possessing more supraciliaries (average of 5.6 v. 3.9 and 4.0) and in having an ear opening and head and limb sizes similar to *E. depressa* (i.e. large head and limbs). Further characters to separate *E. eos* from the Pilbara species are a completely divided nasal scale (v. incomplete in *E. epsisolus* sp. nov.) and moderately wide tail (v. narrow in *E. cygnitos* sp. nov.).

REMARKS

Morphologically, *E. eos* resembles *E. depressa* most closely, including the basic body proportions (large head and limbs, wide tail), numerous supraciliaries, large tympanum and also the brown streak on the neck. However, *E. eos* shares with the two Pilbara species the short, stout, upwards-projecting spines on the dorsum as well as the shorter, straighter spines on the edge of the tail. It is possible that *E. eos* has more recently moved to rock-dwelling habits from a log-dwelling ancestor shared with *E. depressa*. This would be true if body proportions were less evolutionarily labile than colour and scale characteristics. However, owing to the small number of evolutionary changes in rock v. log-dwelling habits within the *E. depressa* species-group and unknown polarity of the ancestral condition in *Egernia*, this idea is speculative, although consistent with the morphological and genetic patterns presented here. Another hypothesis is that *E. eos* makes use of crevices in both rocks and logs, and therefore shows adaptations to both habitats.

We recommend the conservation status of *E. eos* is listed as 'data deficient'. There have been few biological expeditions to the central ranges, so observations of individuals and potential threats are limited. Owing to the isolated records on the Canning Stock Route and in the Northern Territory it is likely that other widely-scattered populations exist. Further observations would be welcome to help understand this very remote and enigmatic species.

***Egernia cygnitos* sp. nov.**

Western Pilbara Spiny-tailed Skink

Figures 3–5, 8

MATERIAL EXAMINED

Holotype

Australia: *Western Australia*: R114257 (♀), Myaree Pool, 20°51'S, 116°36'E. Collected by M. Peterson and G. Shea on 8 July 1992.

Paratypes

Australia: *Western Australia*: R146626 (♀), 198 km S Port Hedland, 22°06'08"S, 118°59'24"E; R157599 (♂), 10 km NE Newman, 23°18'35"S, 119°47'51"E; R159890 (♀), 5 km E Whim Creek Hotel, 20°50'54"S, 117°51'16"E; R161012 (♂), 6 km SE Marda Pool, 21°04'11"S, 116°12'15"E; R165231 (♀), 3.5 km S Marda Pool, 21°03'55"S, 116°09'01"E; R170736 (♂), 13.5 km NNE Mount Rica, 21°52'17"S, 116°28'21"E.

DIAGNOSIS

A member of the *E. depressa* species-group, with a relatively small and flattened head, relatively short limbs, short and stout dorsal spines that project upwards, nasals in point to broad contact, divided nasal scale, few supraciliaries (3–4), posterior border of parietal and neighbouring head scales raised and with a row of moderately developed spines, ear opening small with lobules projecting from anterior border, 30–34 MBSR, subdigital lamellae on fourth fingers 10–13, toes 12–15, slightly round scales on palmar and plantar surfaces, tail narrow with relatively short stout spines that curve slightly forwards and projecting posteriorly at approximately 45°. Colouration a rich reddish-brown with dark brown to black irregular transverse bars (not edged with white) on posterior portion of body that usually extend to level of arms.

DESCRIPTION

Medium (to 102.5 mm SVL) body size, with robust habitus and extremely spiny scalation, especially on the flattened tail. Head triangular and robust, snout tapering to rounded tip when viewed laterally, slightly concave snout when viewed dorsally with brow protruding; upper labials 5–7, lower labials 4–7, loreals 2, presuboculars 2, supraciliaries 3–4, nasals in point to broad contact, postnarial groove strong, prefrontals in contact and forming broad suture; headscales raised posteriorly with a row of spines on posterior edge; ear opening small and round to oblong and oriented vertically, enlarged scales projecting into opening from anterior edge; no enlarged nuchal scales; neck only slightly narrower than widest part of head (above tympani); scales under chin enlarged to level between eye and ear, then abrupt shift to series of smaller scales that gradually enlarge on ventral surface of neck.

FIGURE 8 Holotype of *Egernia cygnitos* sp. nov. (WAM R114257), showing dorsal, lateral and ventral views. Scale bar = 1 cm.

Dorsal scales with a short stout central spine flanked by two smaller spines approximately two-thirds the length of the central spine, spines projecting upwards from scale and central spine projects slightly beyond posterior border of scale; body with 16–18 longitudinal rows of spines. On the upper lateral surfaces the spines are directed back towards midline; on lower lateral surfaces the spines gradually diminish in size to ventrolateral edge, scales in axillary region with at most diminutive spines. Ventral scales c. half the size of dorsal scales. Tail relatively narrow and dorsoventrally compressed, almost flat dorsally (edges are slightly rounded) but with ventral portion convex; dorsal surface with four longitudinal rows of spines with the outer rows following edge of tail half way along length after which the spines are enlarged to size of lateral spines; two rows of enlarged lateral spines, curved slightly forwards and projecting laterally approximately 45º, uppermost row terminating when outer dorsal row meets edge of tail; spines of ventrolateral row reduced to about one quarter the length of two lateral rows of spines; ventral surface smooth, tail tip terminating in a spine.

Limbs relatively short and robust; 3–5 rows of spines on upper portion of limbs with moderately long spines; spines not protruding on anterior, posterior and ventral surfaces of limbs. Palmar and plantar surfaces with slightly rounded scales; digits short and well-developed; finger length: 4>3>2>5>1, toe length: 4>3>5>2>1; smooth subdigital lamellae: fourth finger 10–13, fourth toe 12–15. Claws sharp and recurved.

Colouration

In life: Eyes red with black pupil. Background colour rich reddish-brown; blackish-brown short transverse bars or isolated blotches on tail, dorsum (usually to level of arms), sides and upper surfaces of limbs. Top of head browner than rest of dorsum; upper labials suffused with pale light red; transition from dorsal to ventral colouration on neck gradual, at most only a faint streak posterior to tympanum; sutures on snout and gular region unpigmented. Ventral surfaces yellowish white, with widely scattered dark blotches or flecks, ventral surface of tail tending to be more heavily marked.

In spirit: Similar to colouration in life, except older specimens tend to fade to a browner colour and upper labials whitish.

VARIATION

Table 3 presents the range of values of the morphological characters measured. Most individuals corresponded closely to the description above, with a few exceptions. Two specimens (R137876, R157599) had an undivided nasal scale, a character usually diagnostic for *E. epsisolus* sp. nov., indicating this condition can be present at low frequency. These individuals nevertheless had characteristics consistent with *E. cygnitos*. As for other members of the species-group, juveniles only had a single spine on the dorsal scales. Most of the variation apparent was in how far the transverse bands went up the body. In most individuals the bands went up to the level of the arms, but in many individuals these bands became diffuse or consisted of widely-spaced blotches (see Figure 4A). The specimen R129663 was distinctive in having very heavy dark markings compared to other individuals.

HABITAT

Observed to frequent rock crevices or large rock slabs among rocky outcrops. One specimen was recorded as occurring on a ‘detrital slope’ with *Triodia*.

DISTRIBUTION

Pilbara region of Western Australia, excluding most of the Chichester IBRA subregion (Thackway and Cresswell 1995) except for the southern Chichester Range bordering the Fortescue Marsh (Figure 1).

ETYMOLOGY

cygnitos (Greek) means resembling the red dwarf star 61 Cygni in the constellation Cygnus (over 11 light years from Earth), in reference to the reddish colouration of this species relative to the eastern Pilbara species. Used as a noun in apposition.

COMPARISON WITH OTHER SPECIES-GROUP MEMBERS

Egernia cygnitos is phenotypically similar to *E. eos* and *E. epsisolus* sp. nov. in having yellow- to reddish-brown colouration, few MBSR (~32), the spines on the dorsum are short, stout and project upwards and the spines on the tail are short and only slightly curved. In contrast to *E. depressa*, *E. cygnitos* has predominantly reddish-brown colouration, smaller head and limbs, narrower tail, fewer MBSR (v. ~35), fewer supraciliaries (average of 3.9 v. 5.4), fewer subdigital lamellae, headscales with raised posterior border with a row of spines, small ear opening with projecting spines, short and stout dorsal spines that point upwards and tail with rounded edges dorsally and shorter, straighter spines.

From *E. eos*, *E. cygnitos* differs by possessing a deeper reddish colouration, absence of brown streak on neck, the black transverse bars occur up to level of arms (v. usually restricted to tail and posterior dorsum), smaller head and limbs, longer and thinner tail, fewer supraciliaries (average of 3.9 v. 5.6), fewer subdigital lamellae, headscales raised at posterior edge with a row of moderately developed spines and small ear opening with projecting scales.

From *E. epsisolus* sp. nov., *E. cygnitos* differs by possessing more reddish colouration, the black transverse bars occur up to level of arms (v. usually restricted to tail and posterior dorsum) and are not edged with white, divided nasal (v. grooved only below

the nare), smaller head, dorsal spines stout (but not triangular) and a thinner tail.

REMARKS

Although Storr (1978) believed that Pilbara populations of *E. depressa* may have represented an undescribed subspecies, he hesitated owing to what he believed were intermediate individuals in the Ashburton–Jiggalong region to the south of the Pilbara. We now know that there is a mixture of both forms in the area near Newman (Figure 1), but the forms are quite distinct. The existence of a second Pilbara species revealed by skeletal (Hollenshead 2011), external morphology and genetic differences (this paper) likewise delayed our own resolution of the problem before the combined patterns of morphological and genetic variation were clear (see also Remarks below for *E. epsisolus* sp. nov.).

Egernia cygnitos shares with *E. eos* and *E. epsisolus* sp. nov. a suite of characters that appear to be adaptations for living in crevices in rocks. Unlike the spines of the log-dwelling *E. depressa sensu stricto*, the spines are short, stout and point upwards. The tail has evolved to be the thinnest within the species-group and the spines are relatively short and straight (Figure 4). It may be that the long thin spines of *E. depressa* are adaptations to lodging within a crevice within a log, whereas the short strong spines of *E. cygnitos* and the other rock-dwellers resist breakage and are designed to anchor the animal within a hard substrate (smooth rock) compared to the presumably more irregular surfaces and cavities inside fallen logs.

***Egernia epsisolus* sp. nov.**

Eastern Pilbara Spiny-tailed Skink

Figures 3–5, 9

MATERIAL EXAMINED

Holotype

Australia: *Western Australia*: R132848 (♀), 15 km E Mt Francisco, 21°24’05”S, 118°42’22”E. Collected by P.C. Withers and G.G. Thompson on 22 June 1998.

Paratypes

Australia: *Western Australia*: R16659 (♀), Mt Edgar, 21°19’S, 120°03’E; R108381 (♀), Nimingarra, 20°24’00”S, 120°01’08”E; R132846 (♂) and R132847 (♀), as for holotype; R145591 (♂), 69 km S Port Hedland, 20°54’36”S, 118°40’48”E; R170818 (♂), Old Pilga homestead, 21°29’S, 119°25’E.

DIAGNOSIS

A member of the *E. depressa* species-group, with a relatively small and flattened head, relatively short limbs, short triangular dorsal spines that project upwards, nasals in point contact, nasal scale incompletely divided (grooved below nare; ungrooved dorsally), posterior border of parietal and neighbouring head scales raised and with a row of moderately developed spines, few supraciliaries (3–5), ear opening small with scales projecting from anterior border, 30–34 MBSR, subdigital lamellae on fourth fingers 9–13, toes 11–14, slightly rounded scales on palmar and plantar surfaces, tail moderately thin with relatively short stout spines that curve slightly forward and projecting posteriorly at approximately 45°. Colouration a pale yellowy-brown with dark brown to black irregular transverse bars edged with white on tail and posterior half of body.

DESCRIPTION

Medium (to 110 mm SVL) body size, with robust habitus and extremely spiny scalation, especially on the flattened tail. Head triangular and robust, snout tapering to rounded tip when viewed laterally, slightly concave snout when viewed dorsally with brow protruding; upper labials 5–7, lower labials 4–6, loreals 2, presuboculars 2, supraciliaries 3–5, nasals in point contact, nasal scale incompletely divided (groove only present below and behind nare), prefrontals in contact and forming broad suture; posterior edge of head scales raised and with a moderately developed row of spines; tympanum small, round to oblong and oriented vertically, with enlarged scales projecting into opening from anterior edge; no enlarged nuchal scales; neck only slightly narrower than widest part of head (above tympani); scales under chin enlarged to level between eye and ear, then a shift to a series of smaller scales that gradually enlarge on ventral surface of neck.

Dorsal scales with a short triangular (in lateral view) central spine flanked by two smaller spines that are half to two-thirds the length of the central spine, spines projecting upwards from scale and central spine projects slightly beyond posterior border of scale; body with 16–20 longitudinal rows of spines. On the upper lateral surfaces the spines are directed back towards midline; on lower lateral surfaces the spines gradually diminish in size until ventrolateral edge, scales in axillary region with at most diminutive spines. Ventral scales c. half the size of dorsal scales. Tail moderately wide and dorsoventrally compressed, flat dorsally but with edges rounded, ventral portion convex; dorsal surface with four longitudinal rows of spines, outer rows following outline of tail halfway along length after which spines enlarged to size of lateral spines; two rows of enlarged lateral spines, curved slightly forwards and projecting laterally approximately 45º; upper lateral row terminating when outer dorsal row meets edge of tail half way along length; spines of ventrolateral row reduced to about a quarter of elongate lateral spines; ventral surface smooth, tail tip terminating in a spine.

Limbs relatively short and robust; 3–5 rows of spines on upper portion of limbs with moderately long spines; spines not protruding on anterior, posterior and ventral surfaces of limbs. Palmar and plantar surfaces with

FIGURE 9 Holotype of *Egernia epsisolus* sp. nov. (WAM R132848), showing dorsal, lateral and ventral views. Scale bar = 1 cm.

slightly rounded scales; digits short and well-developed; finger length: 4>3>2>5>1, toe length: 4>3>5>2>1; smooth subdigital lamellae: fourth finger 9–13, fourth toe 11–14. Claws sharp and recurved.

Colouration

In life: Eyes red with black pupil. Background colour pale yellowish-brown to light reddish-brown, with subtle darker patches sometimes present; blackish-brown short transverse bars on tail, posterior half of dorsum, sides, and upper surfaces of legs and usually arms; usually edged with white. Top of head slightly darker than rest of dorsum; upper labials pale, sutures edged brown; sometimes a faint narrow brownish streak posterior to tympanum with straight ventral border; sutures on snout and gular region usually unpigmented, although some signs of light variegations on the ventral portion of the neck are evident. Ventral surfaces yellowish white, with sparsely scattered dark flecks especially near distal edges, ventral surface of tail tending to be more heavily marked.

In spirit: Preserved specimens tend to appear browner than those in life. In addition, specimens in spirit show less reddish colouration and tend to be a yellowy-brown compared to live individuals. Otherwise, the colour patterns are similar to those of live individuals.

VARIATION

Table 3 presents the ranges of morphological variables recorded in our sample of *E. epsisolus*. Most specimens conformed reasonably well to the description above, although there were no juveniles in the collection for examination. Colour pattern varied slightly in that there were often variably expressed light brown transverse bands on the upper part of the body (Figure 4). The variegations on the neck showed a wide range of variation from none to loosely connected networks of lines that tended to run longitudinally.

HABITAT

Collection records indicate *E. epsisolus* most often occur on exfoliating granite outcrops, with a mixture of *Triodia* species present.

DISTRIBUTION

Chichester IBRA subregion of the Pilbara region, Western Australia. Replaced in the Chichester Range near the Fortescue River by *E. cygnitos*. Also a single outlying record from 80 km south of Telfer in the Little Sandy Desert.

ETYMOLOGY

epsisolus (Greek) means resembling the yellow dwarf star Epsilon Eridani in the constellation Eridani (10.4 light years from Earth), in reference to the more yellowy colouration of this species relative to the western Pilbara species. Used as a noun in apposition.

COMPARISON WITH OTHER SPECIES-GROUP MEMBERS

Egernia epsisolus is phenotypically similar to the other two rock-dwelling forms, *E. eos* and *E. cygnitos*, in having yellow- to reddish-brown colouration, posterior edge of headscales raised with a row of spines, rounded scales on plantar and palmar surfaces, few MBSR (~32), the spines on the dorsum are short, triangular and project upwards and the spines on the tail are short and only slightly curved. In contrast to *E. depressa*, *E. epsisolus* has yellowy-brown colouration (v. predominantly brownish-grey), divided nasal scale, rugose (v. flat) head scales, fewer MBSR (~32 v. 35), more supraciliaries (average of 4.0 v. 5.4), smaller limbs, fewer subdigital lamellae, short strong projecting spines on body and tail (v. long thin dorsal spines that lie almost parallel to body and longer, recurved spines on the tail).

From *E. eos*, *E. epsisolus* differs by having white edging on the black transverse bars, wide brown streak on the neck absent (although a thin faint streak is sometimes present), an incompletely divided nasal scale, narrower and less deep head, shorter legs, fewer supraciliaries, posterior edge of head scales raised higher and with taller spines, ear opening small with projecting scales and fewer subdigital lamellae.

From *E. cygnitos*, *E. epsisolus* differs by possessing more yellowish colouration, the black transverse bars are usually restricted to the tail and posterior dorsum and have white edging, the nasal scale is incompletely divided, the dorsal spines are triangular (v. merely stout) and the tail is slightly wider.

REMARKS

The existence of a second species in the Pilbara was surprising, given the phenotypic similarities between the two species. However, the genetic analysis clearly indicated that rather than being a closely-related sister species to *E. cygnitos*, *E. epsisolus* is a more ancient sister to all three of the other *E. depressa* species-group members (Table 2, Figure 2). However, further genetic sampling (e.g. sequencing nuclear genes) could change the pattern of relationships we recovered with the mitochondrial DNA and tRNA dataset. *Egernia epsisolus* is also the only member within the species-group to possess an incompletely divided nasal scale above the nare (below the nare it resembles the other three species in being deeply grooved; Figure 5). Another difference is the white-edged transverse bands (also occurring on *E. depressa*), but their significance is also unknown. Characters more obviously involved in evolving to a crevice-dwelling existence among rocks are the small head and limbs and the short strong spines on the body and tail (see also Hollenshead 2011).

Within the Chichester region and the Little Sandy Desert, populations of *E. epsisolus* seem to be secure, although no studies have been conducted. A conservative recommendation for conservation status would be simply to list it as ‘data deficient’ until studies are conducted.

ACKNOWLEDGEMENTS

We thank Brad Maryan, G. Gaikhorst and G. Johnston for images of living specimens, P. Campbell of the BMNH for access to specimens, C. Stevenson for preparing the specimen photographs and R. Foster and L. Wheaton for the nucleotide sequencing. CERF TRIN and Rio Tinto funded the molecular genetic work.

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MANUSCRIPT RECEIVED 21 JANUARY 2011; ACCEPTED 4 MAY 2011.

APPENDIX 1

Other material examined. ^{M}, mtDNA examined; ^{m}, examined mtDNA and morphologically; unmarked vouchers examined for morphology only. Numbers in bold indicate sites from which specimens had mtDNA sequenced and are also indicated on the map in Figure 1 and the phylogenetic tree in Figure 2. SA, South Australia; AMS, Australian Museum, Sydney; SAMA, SA Museum, Adelaide; NTM, Northern Territory Museum, Darwin. Unless otherwise stated, all locations are in Western Australia.

***Egernia depressa* (=southern group)** AMS: R102676^{M}, **27**, Menzies; SAMA: R22847^{M}, R29355^{M}, 6^{M}, 7^{M}, 8^{M}, 9^{M}, **21**, Overland Roadhouse, Shark Bay; R34037^{M}, **14**, Mount Phillip HS; R34043^{M}, **23**, Yoothapinna HS. WAM: R2700 (♂), Kojonup, Malvern, Orchid Valley, 25°08'S, 117°09'E; R12994 (♀), Cundeelee Mission, 30°44'S, 123°25'E; R17677 (♀), Mt Margaret Mission, 28°48'S, 112°11'E; R25666 (♂), Gnows Nest, 51 km S Yalgoo, 28°35'S, 116°52'E; R46229 (♂), 80 km NNW Sandstone, 27°22'S, 119°03'E; R60932 (♂), 9 km SW Paynes Find, 29°18'S, 117°38'E; R65717 (♀), R72755 (♂), 7.5 km NE Comet Vale, 29°53'40"S, 121°10'45"E; R67087 (♂), 1.5 km S Mt Jackson, 30°15'S, 119°15'E; R69236 (♀), R69237 (♀), Gum Well 13 km SE Banjawarn HS, 27°47'20"S, 121°42'00"E; R72655 (♂), R72656 (♀), 6.75 km NE Comet Vale, 29°54'00"S, 121°10'10"E; R74618 (♀), 3.5 km NE Comet Vale, 29°55'10"S, 121°08'30"E; R102776^{M}, **16**, Little Sandy Desert; R114256^{m} (♂), **19**, NW end of Mt Fraser, 25°35'S, 118°22'E; R120493^{m} (♂), **17**, 40 km SSE Carnarvon, 25°07'33"S, 113°49'22"E; R120631^{M}, **15**, 8.6k SE Mardathuna; R120863^{M}, R125781^{M}, **20**, 5.8k SE Old Woodleigh; R125553^{M}, **18**, Randall Well 210k NNE Meekatharra; R127598^{M} (♀), **26**, 21 km S Leonora, 29°04'S, 121°20'E; R129967^{M}, **24**, Mt Joel; R131497^{M}, **25**, Barwidgee; R132192 (♂), Duketon, 27°50'49"S, 122°15'49"E; R132503^{M}, **22**, Jundee; R134924 (♂), 5 km W Hampton Hill, 30°44'S, 121°42'E; R136630 (♂), Lake Mason Station, 27°35'13"S, 119°29'06"E; R145383 (♂), Goongarrie Station, 30°01'22"S, 121°02'40"E; R156171 (♂), Waldburg Station, 24°45'40"S, 117°11'25"E; R162910^{M}, 162911^{M}, **12**–**13**, NNE Boologooro; R167600^{M}, 167602^{M}, 167606^{M}, 167613^{M}, 167616^{M}, 167617^{M}, **11**, North West Coastal Highway, 147 km E Ningaloo.

***Egernia cygnitos* sp. nov. (=western Pilbara group)** SAMA: R22856^{M},7^{M},8^{M}, **7**, 0.5 km W Python Pool. WAM: R17690 (♀), Turee Creek Station, 23°37'S, 118°39'E; R29091 (♀), Mt Herbert, 21°20'S, 117°13'E; R114257 ^{m} (♀), R114258 (♂), **9**, Myaree pool, 20°51'S, 116°36'E; R114366^{M}–7^{M}, **8**, Cleaverville; R129633 (♀), 120 km NW Newman, 22°54'S, 119°00'E; R146626 (♀), 198 km S Port Hedland, 22°06'08"S, 118°59'24"E; R157511 (♀), Pack Saddle Range, 22°55'35"S, 118°49'39"E; R157599 (♂), 10 km NE Newman, 23°18'35"S, 119°47'51"E; R159827 (♂), 10 km S Mallina Homestead, 20°58'10"S, 118°02'54"E; R159890 (♀), 5 km E Whim Creek Hotel, 20°50'54"S, 117°51'16"E; R161012 (♂), R161039 (♀), 6 km SE Marda Pool, 21°04'11"S, 116°12'15"E; R161040 (♂), 3.5 km S Marda Pool, 21°03'55"S, 116°09'01"E; R162136 (♀), 12.5 km NW Mt Berry, 22°24'28"S, 116°22'18"E; R162162 (♂), 26 km WNW Mt Berry, 22°25'31"S, 116°12'55"E; R162907^{M}–8^{M}, **5**, North West Coastal Highway, 8km SW Mt Negri, Sherlock; R163138 (♀), 19.5 km SSW Mt

Amy, 22°25’09”S, 115°50’16”E; R163681 (♂), 12 km W Mt Bruce, 22°36’39”S, 118°01’21”E; R165230[M], R165231 (♀), **10**, 3.5 km S Marda Pool, 21°03’55”S, 116°09’01”E; R167650[M], **6**, Sherlock Station; R170736 (♂), 13.5 km NNE Mt Rica, 21°52’17”S, 116°28’21”E.

***Egernia eos* sp. nov. (=central group)** WAM: R14638 (♀), R22033 (♀), R22034 (♂), R22071 (♂), R22166 (♂), R22167 (♀), R22169 (♂), R22170 (♀), R31363 (♂), Warburton mission, 26°08’S, 126°35’E; R15697 (♀), R15699 (♀), R15701 (♀), R15732 (♂), R15733 (♂), R15734 (♀), 32 km E Warburton mission, 26°13’S, 126°52’E; R17784 (♀), R17785 (♀), Brown Range, 6 km S Warburton, 26°11’S, 126°35’E; R98077[m] (♂), R98078[m] (♂), **29**, Ainsley Gorge, 15.8 km ESE Warburton, 26°14’S, 126°42’E; R98082[M], R98083 (♂), **28**, 6 km N Mantamaru, 25°46’S, 127°43’E. NTM R36432 (formerly WAM R34201), 6 km N Mt Bowley, 25°06’S, 129°45’E.

***Egernia epsisolus* sp. nov. (=eastern Pilbara group)** WAM**:** R10793 (♀), R10794 (♂), R10795 (♀), R10796 (♀), Abydos, 21°25’S, 118°55’E; R16659 (♀), R16660 (♂), R16661 (♀), R16662 (♀), R16663 (♂), Mt Edgar, 21°19’S, 120°03’E; R90897[a,m] (♂), **2**, Woodstock Station; R94722 (♀), ca. 80 km S Telfer, 22°20’24”S, 122°04’21”E; R108381 (♀), Nimingarra, 20°24’00”S, 120°01’08”E; R132845[M], R132846[m] (♂), R132847[m] (♀), R132848 [m] (♀), **3**, 15 km E Mt Francisco, 21°24’05”S, 118°42’22”E; R137876 (♀), Balla Balla Creek, 20°47’S, 117°47’E; R139319 [m] (♂), R139323 [m] (♀), **1**, Meentheena, 21°21’04”S, 120°26’49”E; R145591 (♂), 69 km S Port Hedland, 20°54’36”S, 118°40’48”E; R164003 (♀), 13 km SSE Wodgina, 21°16’47”S, 118°41’56”E; R167653[M], R167656[M], R167658[M], R167660[M], R167662[M], R167663[M], R167664[M], **4**, Indee Station; R170818 (♂), Old Pilga homestead, 21°29’S, 119°25’E; R170905 (♀), 14.5 km S Dresser Mining Centre, 21°16’46”S, 118°24’43”E.

E. hosmeri NTM: R21300[M], Musselbrook Reservoir, Queensland

E. napoleonis SAMA: R23080[M], Denmark; R97546[M], Barrier Island, WA; WAM: R97547[M], Barrier Island; R97551[M], Taylor Island; R140501[M], ~15k WNW Cataby; R154034[M], Muchea Air Weapons Range.

E. kingii SAMA: R29444[M], Albany; WAM: R112794[M], R112801[M], Abrohlos; R141200[M], northern mainland.

E. richardi SAMA: R29217[M], 75k E SA/WA border, SA; R28383[M], 38k NE Minnipa, SA; WAM: R112656[M,] 7k SSW Ponier Rock; R156291[M], Forrestania area.

E. stokesii WAM: R112810[M], East Wallabi Island; R127654[A,M], Woodleigh HS; R131867[M], R132007[A,M], Baudin Island; R132048[M], R132750[A,M], Perenjori; R132101[M], Buntine Nature Reserve; R132102[M], Bowgada Nature Reserve; R135165[M], R135167[M], R151382[A,M], West Wallabi Island; R151372[M], Middle Island; R151375[M], R151376[M], Tattler Island; R152672[M], R152676[M], Murray Island; R152994[A,M], Redcliff Point, Peron Peninsula; R152995[M], near Monkey Mia, Peron Peninsula.

APPENDIX 2

GenBank accession numbers for mitochondrial *ND4* sequences.

Voucher Number	GenBank
***Egernia cygnitos* sp. nov.**	
WAM R114366	JF813026
WAM R165230	JF813027
WAM R114367	JF813028
WAM R114257	JF813029
SAMA R22856	JF813030
WAM R132192	JF813031
SAMA R22857	JF813032
SAMA R22858	JF813033
WAM R167650	JF813034
WAM R162907	JF813035
WAM R162908	JF813036
Egernia depressa	
WAM R167613	JF813037
WAM R167606	JF813038
WAM R167602	JF813039
WAM R167600	JF813040
WAM R167616	JF813041
WAM R167617	JF813042
WAM R120631	JF813043
WAM R125553	JF813044
WAM R102776	JF813045
WAM R129633	JF813046
WAM R129967	JF813047
WAM R132503	JF813048
WAM R131497	JF813049
AMS R102676	JF813050
WAM R127598	JF813051
WAM R120493	JF813052
SAMA R34043	JF813053
WAM R114256	JF813054
SAMA R34037	JF813055
WAM R125781	JF813056
WAM R162910	JF813057
WAM R162911	JF813058
WAM R120863	JF813059
SAMA R29356	JF813060
SAMA R22847	JF813061
SAMA R29357	JF813062
SAMA R29358	JF813063
SAMA R29359	JF813064
SAMA R29355	JF813065
Egernia eos sp. nov.	
WAM R98082	JF813023
WAM R98077	JF813024
WAM R98079	JF813025
Egernia epsisolus sp. nov.	
WAM R167658	JF813009
WAM R167653	JF813010
WAM R167660	JF813011

WAM R167656	JF813012
WAM R167663	JF813013
WAM R132847	JF813014
WAM R167664	JF813015
WAM R139319	JF813016
WAM R139323	JF813017
WAM R90897	JF813018
WAM R167662	JF813019
WAM R132846	JF813020
WAM R132845	JF813021
WAM R132848	JF813022
Egernia hosmeri	
NTM R21300	JF813076
Egernia kingii	
SAMA R29444	JF813005
WAM R141200	JF813006
WAM R112794	JF813007
WAM R112801	JF813008
Egernia richardi	
SAMA R28383	JF813066
SAMA R29217	JF813067
WAM R112656	JF813068
WAM R156291	JF813069
Egernia napoleonis	
WAM R97551	JF813070
WAM R97546	JF813071
WAM R97547	JF813072
SAMA R23080	JF813073
WAM R140501	JF813074
WAM R154034	JF813075
Egernia stokesii	
WAM R112810	JF813077
WAM R135165	JF813078
WAM R152672	JF813079
WAM R135167	JF813080
WAM R151376	JF813081
WAM R152676	JF813082
WAM R151375	JF813083
WAM R151382	JF813084
WAM R151372	JF813085
WAM R132007	JF813086
WAM R152995	JF813087
WAM R131867	JF813088
WAM R127654	JF813089
WAM R152994	JF813090
WAM R154800	JF813091
WAM R132102	JF813092
WAM R132048	JF813093
WAM R132750	JF813094
WAM R132101	JF813095