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Phylogenomics, taxonomy and conservation of the White's skink (Scincidae: *Liopholis whitii*) species complex in south-eastern Australia

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Abstract

White's Skinks, *Liopholis whitii* (Lacépède 1804) are widely distributed throughout rocky habitats of temperate south-eastern Australia, with a highly disjunct population occurring in Mutawintji National Park in arid far western New South Wales. Based on an analysis of genome-wide nuclear single-nucleotide polymorphisms (SNPs) and an assessment of variation in morphology, we provide an appraisal of the group's evolutionary history and re-evaluate the taxonomic status of candidate lineages. We reveal the presence of three major genetic lineages, including two lineages from temperate south-eastern Australia, and another representing the isolated arid population from Mutawintji National Park. We herein apply the name *Liopholis whitii* to the temperate "southern" lineage which occurs in South Australia, Victoria and Tasmania; resurrect the name *Liopholis compressicauda* (Quoy & Gaimard 1824) for the temperate "northern" lineage from southern Queensland, New South Wales, Australian Capital Territory and north-eastern Victoria; and describe the arid lineage from Mutawintji National Park as *Liopholis mutawintji* **sp. nov.** *Liopholis mutawintji* **sp. nov.** is of particular conservation concern and likely eligible for listing as Critically Endangered under multiple IUCN Red List Criteria.

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Key words: Australian arid zone, Broken Hill Complex bioregion, Mutawintji National Park, *Liopholis mutawintji* **sp. nov.**, paleoclimate

Introduction

The Australian endemic scincid lizard genus *Liopholis* Fitzinger 1843 comprises a group of small to moderately large viviparous species with distributions spanning areas of widely varying aridity across the continent; from the temperate and alpine zones of the south-east to the arid heartland of central Australia (Chapple & Keogh 2004; Wilson & Swan 2025). The group is characterised by two major ecologies—rock-dwelling or obligate burrowing habitat specialists (Chapple & Keogh 2004; Gardner *et al.* 2008). The 'rock-dwelling' subgroup currently includes seven species: the Central Ranges Rock Skink *Liopholis aputja* Farquhar, Mulder, Russell, Haines & Chapple 2024; Guthega Skink *L. guthega* (Donnellan, Hutchinson, Dempsey & Osborne 2002); MacDonnell Ranges Rock Skink *L. margaretae* (Storr 1968); Eastern Ranges Rock Skink *L. modesta* (Storr 1968); Mountain Skink *L. montana* (Donnellan, Hutchinson, Dempsey & Osborne 2002); Flinders Ranges Rock Skink *L. personata* (Storr 1968); and White's Skink *L. whitii* (Lacépède 1804).

Three rock-dwelling species, *Liopholis aputja*, *L. margaretae* and *L. personata*, occur entirely within the arid and semi-arid zone (Chapple & Keogh 2004; Farquhar *et al.* 2024), whereas two species with predominantly temperate distributions, *L. whitii* and *L. modesta*, have disjunct populations in arid and semi-arid western New South Wales (NSW) (Chapple & Keogh 2004; Chapple *et al.* 2005; Foster 1993; Sadlier *et al.* 2019; Sass & Swan 2010; Swan & Foster 2000; Swan & Foster 2005; Swan *et al.* 2022). Two populations of *L. modesta* occur in semi-arid rocky habitats near Collarenebri and in the Merrimerriwa Range of Yathong Nature Reserve, with the latter ~380 km from closest populations in eastern NSW. The highly disjunct *L. whitii* population occurs in the Bynguano Range of Mutawintji National Park, ~500 km from closest populations in South Australia (SA) and ~600 km from populations in eastern NSW. The disjunct distribution of these rock-dwelling species in the arid and semi-arid zone suggests that ancestral *Liopholis* populations were more widespread throughout inland Australia in the past. Relict populations are now constrained to relatively humid and climatically stable rocky uplands of the arid zone by an inability to tolerate water loss under dehydrating conditions (Chapple & Keogh 2004; Henzell 1972). This hypothesis is supported by phylogenetic divergence estimates suggesting a relatively rapid Miocene diversification between temperate and arid *Liopholis* taxa (Chapple & Keogh 2004; Brennan *et al.* 2024), coinciding with a period of intensifying aridification that drove a major transition in vegetation across inland areas of Australia (Byrne *et al.* 2008; Martin 2006; Pepper & Keogh 2021).

White's Skinks *Liopholis whitii* occur at low- to montane-elevations, with their widespread and fragmented distribution spanning predominantly rocky habitats of the temperate south-east, including SA, Victoria (VIC), Tasmania (TAS), NSW, Australian Capital Territory (ACT) and southern Queensland (QLD). Previous phylogenetic studies of *Liopholis whitii* have highlighted the complex evolutionary history of the group, indicating that taxonomic relationships are far from resolved (Chapple & Keogh 2004; Chapple *et al.* 2005). The *L. whitii* complex appears to have its origins in the late Tertiary, enabling an examination of the impact of both late Miocene-Pliocene and Pleistocene climatic events on the phylogenetic history of the group (Chapple *et al.* 2005). A deep phylogenetic break defining northern and southern lineages of *L. whitii* is estimated to have occurred during the late Miocene-early Pliocene (6.1–9.6 Mya). Further, substantial phylogenetic sub-structuring is evident within each of the northern and southern lineages, consistent with habitat fragmentation during glacial-interglacial cycles of the Plio-Pleistocene (~6–0.04 Mya) (Chapple & Keogh 2004; Chapple *et al.* 2005). Previous molecular investigations have found the isolated Mutawintji National Park population—hereafter referred to by its Wiimpatja parlku name Kungaka—grouped closely with the southern lineage of *L. whitii*, with divergence estimates suggesting the Kungaka became fragmented from southern populations of *L. whitii* relatively recently during the early Pleistocene (Chapple & Keogh 2004; Chapple *et al.* 2005). Uncertainty regarding the genetic status of this population warrants further molecular investigation to inform appropriate management. Monitoring surveys conducted since 2000 have indicated that the Kungaka population is extremely small, highly fragmented, declining, and at very high risk of extinction from multiple threatening processes (NSW National Parks & Wildlife Service 2000; Swan & Foster 2000; Swan & Foster 2005). Consequently, the Kungaka is listed as an 'Endangered Population' of *L. whitii* under the NSW Biodiversity Conservation Act 2016 (NSW Threatened Species Scientific Committee 2005a,b).

In this paper, we explore variation in nuclear genome-wide markers (SNPs) and morphology for the *Liopholis whitii* complex across its wide geographic distribution in south-eastern Australia to assess the systematic status of candidate lineages within the group, including the previously identified 'northern' and 'southern' lineages (Chapple & Keogh 2004; Chapple *et al.* 2005), and the Kungaka from Mutawintji National Park. We present an updated taxonomic framework and perform provisional conservation assessments for each taxon.

Materials and methods

Genetic sampling, DNA extraction and nuclear SNP genotyping

We obtained 115 tissues and DNA samples of *Liopholis whitii* complex individuals from 77 sites throughout their range in SA, VIC, TAS, ACT, QLD, and NSW, including 12 samples of the Kungaka. Tissue samples were obtained from the Australian Museum (AMS), Australian Biological Tissue Collection (ABTC) and Museums Victoria (NMV). For phylogenetic context, we included representative outgroup samples of rock-dwelling *Liopholis* species, including *L. guthega* ($n = 6$), *L. montana* ($n = 6$), *L. personata* ($n = 5$), *L. modesta* ($n = 7$; including 2 samples from the outlying semi-arid population in Yathong Nature Reserve, NSW), *L. aputja* ($n = 2$) and *L. margaretae* ($n = 4$). A map of genotyped samples is presented in Fig 1, with museum registration numbers and locality data for samples provided in Table A1 in the Appendix.

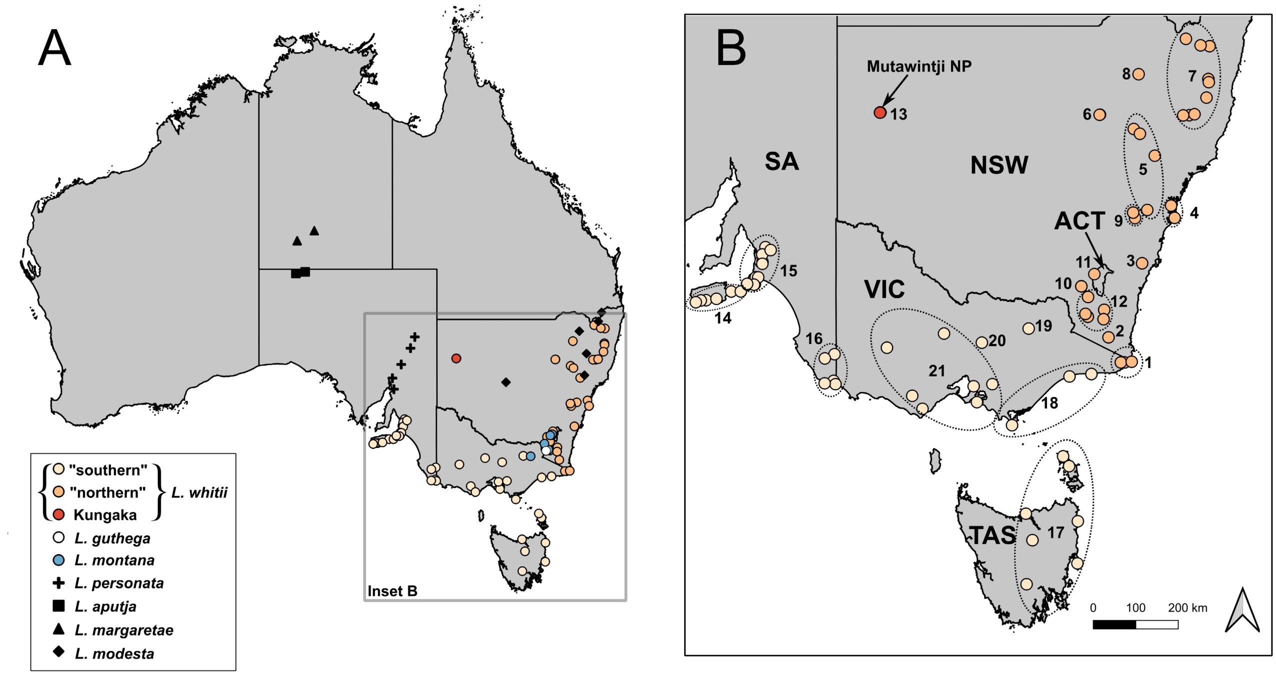

FIGURE 1. (**A**) Australia showing collection localities for the genotyped rock-dwelling *Liopholis* species examined in this study. (**B**) Map inset of samples included in the *Liopholis whitii* complex analysis. Numbers correspond to populations identified in the phylogenetic analysis (see Fig 2/B).

Genomic DNA was purified and extracted from tissue samples (muscle, liver) at the Australian Centre for Wildlife Genomics, Australian Museum, using a Bioline ISOLATE II Genomic DNA kit following the manufacturer's protocols for purification of genomic DNA from animal tissues.

DNA samples were submitted to Diversity Arrays Technology (DArT, Canberra) for DArT-seq^{TM} 1.0 medium-density sequencing to identify informative single-nucleotide polymorphisms (SNPs) from across the nuclear genome. DArT performed a genome-complexity reduction technique using double digestion of genomic DNA with two restriction endonucleases *PstI* (5'-CTGCA|G-3') and *SphI* (5'-GCATG|C-3'), and next-generation sequencing was carried out on an Illumina HiSeq2500. Sequences were processed using proprietary DArT analytical pipelines, with SNPs for the *L. whitii* complex "in-group" (i.e., with outgroup species removed) called and analysed as a separate report. Sequencing methods are described in more detail by Georges *et al.* (2018) and Kilian *et al.* (2012). We received data reports from DArT containing a matrix of SNP loci by individuals, with the contents stored as integers 0, homozygote; 1, heterozygote; and 2, homozygote for the alternate state. DNA sequences and statistics such as call rate, polymorphic information, heterozygosity, read depth and reproducibility for all loci and individuals were also reported.

SNP data filtering and analysis

The SNP reports, and associated specimen metadata, were read into a genlight object (Jombart *et al.* 2010) to facilitate filtering and analysis in R Studio using the 'dartRverse' package (Gruber *et al.* 2018). For the analysis of the total *Liopholis* dataset, including rock-dwelling outgroup species, a locus call rate of >90% and individual call rate of >70% were used. Reproducibility was filtered at >99% and average locus read-depth set from >5 to <30. We filtered out secondary SNPs where they occurred in a single sequence tag, retaining only one SNP from each tag at random. Any monomorphic loci arising from the removal of individuals were also deleted. Analysis of the *L. whitii* complex dataset used the same filtering methods but with a slightly more stringent locus call rate of >95% and minor allele frequency filter setting of 0.05. Given the low within-population sample sizes (n≤ 15), we did not filter loci for departures from Hardy-Weinberg equilibrium or linkage disequilibrium. Five samples of *L. whitii* were deleted due to not meeting the individual call rate of 70%, including the single QLD sample and four samples from TAS. After filtering, the total *Liopholis* species dataset retained 5,242 quality SNPs for 140 individuals, with 4.16% missing data scored as NA, and the *L. whitii* complex dataset retained 3,882 SNPs for 110 individuals with 2.37% missing data.

Phylogenetic analysis of the total *Liopholis* species dataset was carried out using two tree-building methods: maximum likelihood, implemented in IQ-TREE (Nguyen *et al.* 2015), and under the multispecies coalescent model with SVDquartets (Chifman and Kubatko 2014). The maximum likelihood analysis with IQ-TREE was conducted using the Lewis-type ascertainment bias correction, which considers that no invariant sites are included and helps reduce overestimation of tree lengths (Leaché *et al.* 2015). Heterozygous SNPs were recoded as the appropriate IUPAC ambiguity codes. The substitution model was determined with ModelFinder (Kalyaanamoorthy *et al.* 2017), with branch support assessed using 10,000 ultrafast bootstrap pseudo-replicates (Hoang *et al.* 2018). A species tree with SVDquartets was then generated in the program PAUP* version 4.0a build 168 (Swofford & Sullivan 2009). SVDquartets was run three times with 100,000 randomly sampled quartets, and branch support assessed using 10,000 bootstrap replicates.

We further explored broad patterns of genetic clustering among samples in the total *Liopholis* species dataset and *L. whitii* complex dataset using principal component analysis (PCA), implemented via the *gl.pcoa* and *gl.pcoa.plot* functions of the dartRverse package. We used a scree plot of the percentage of variation explained by each PC axis to determine the number of informative PCs to examine. Next, we used the Bayesian model-based clustering approach implemented in the program 'STRUCTURE' (Pritchard *et al.* 2000) to explore overall genetic structuring within the *L. whitii* in-group dataset. STRUCTURE assigns individuals to ancestral (*K*) populations based on allele frequencies, and is considered a robust method for evaluating genetic structure and hybridisation with SNPs (Stift *et al.* 2019). STRUCTURE runs were implemented using the uncorrelated allele frequency and admixture ancestry models to assess values of *K* from 1 to 10, performing three independent runs with 20,000 burn-in and then 100,000 MCMC iterations for each value of *K*. The preferred *K* value was determined using *L(K)* and the change in the second order of likelihood, *ΔK* (Evanno *et al.* 2005). We then summarised individual ancestry proportions across all runs in 'CLUMPAK' (Kopelman *et al.* 2015). Individuals were assigned to *K* populations based on ancestry proportions (*q*-values), with a *q*-value >90% indicating the sample was assigned to a single genetic population, and <90% indicating genetic admixture.

Further, we used two methods to estimate genetic divergence between *Liopholis* species and major *L. whitii* complex lineages identified in the PCA and STRUCTURE analysis. First, we calculated pairwise genomic differentiation ($G_{'st}$) via the *pairwise_Gst_Hedrick* function of the 'mmod' package (Winter 2012), obtaining significant *p* values for population pairs with the 'StAMPP' package (Pembleton *et al.* 2013). $G_{'st}$ is a standardized measure of genetic differentiation based on the fixation index (F_{st}) but is corrected for the number of populations being considered (Hedrick 2005). Second, we compared numbers of loci showing a fixed difference between species and lineages using the *gl.fixed.diff* function of dartRverse. Fixed difference at a locus occurs when two populations share no alleles. The accumulation of significant numbers of fixed differences between two populations is considered a robust indication of long-term reproductive isolation and may be considered a diagnosable characteristic between the populations compared (Gruber *et al.* 2018; Unmack *et al.* 2022). When many loci are examined, and sample sizes are finite, fixed differences will be observed through sampling error, so we used simulations implemented in dartRverse to estimate the expected false positive rate in pairwise comparisons, and used tloc = 0.05, meaning that SNP allele frequencies of 95,5 and 5,95 percent were regarded as fixed when comparing two populations at a locus. To minimise distortion of the genomic differentiation and fixed difference estimates (Unmack *et al.* 2022), populations showing evidence of genetic admixture in the STRUCTURE analysis (i.e., 'population 12', comprising localities in the NSW highlands: Jindabyne, Sawpit Creek, Cooma and lower Kosciuszko NP) were excluded from the analysis, resulting in a final dataset of 7,829 SNP loci for the comparisons.

Morphological sampling and analysis

To assess morphological variation between the three major *L. whitii* complex genetic lineages, we examined 119 specimens held in the Australian Museum, including 66 specimens from the "northern" lineage, 51 specimens from the "southern" lineage, and 2 Kungaka specimens. Additional measurements of snout-vent length (SVL) and original tail length (TL) were collected from 10 wild Kungaka captured and released in 2000–2001. The specimens represented a wide range of geographic localities; however, specimens from mainland SA and QLD were not available for examination. Museum registration numbers and collection locality data for specimens are listed in Table A1 in the Appendix, and a map of sampling locations is provided in Fig 7.

Specimens were assigned to prior groups based on genotype or proximity to genotyped samples. Sex of specimens was determined by the presence of everted hemipenes or internal examination of gonads. Measurements were collected for nine mensural body characters: SVL, TL, axilla-groin length (AGL), head length (HL), head depth (HD), head width (HW), snout length (SnL), antebrachium (forearm) length (AntL) and crus (lower hind limb) length (CrusL); and seven meristic scale counts: supralabials (SupLab), infralabials (InfLab), supraciliaries (SupCil), mid-body scale rows (MBSR), paravertebral scales (PVS), subdigital lamellae under the fourth finger (4FLam) and subdigital lamellae under the fourth toe (4TLam). Morphological measurements and meristic scale counts are defined further in Table A2 in the Appendix. All measurements were taken on the right side of the body, or from the left side if the right side was damaged. Additional notes were collected on colour-pattern variation, focusing on dorsal colour-pattern, and the presence/absence of dark calli on palmar and plantar scales of the hands and feet.

To evaluate the potential influence of sexual dimorphism on inter-lineage comparisons, we assessed morphological variation between sexes of each lineage independently. Sexual dimorphism was not assessed for the Kungaka due to a lack of females in the morphological dataset. Variation in four meristic scale counts (MBSR, PVS, 4FLam and 4TLam) was compared with one-way ANOVA, with variation in seven mensural variables (AGL, HL, SnL, HW, HD, AntL, and CrusL) compared with one-factor ANCOVA, using SVL as a covariate to control for age-related variation. SupLab, InfLab and SupCil counts were excluded from the statistical comparisons due to their low variability, and TL was also omitted due to the high proportion of specimens (~64%) with incomplete or regenerated tails.

For the inter-lineage univariate and multivariate comparisons, potentially confounding variation associated with differing body sizes and allometric growth was minimized by adjusting morphological variables to the values they would assume if they were of a mean body size for that sex using the allometric growth equation of Thorpe (1976): $Y_i^* = log_{10}Y_i – b(log_{10}SVL_i – log_{10}SVL_{mean})$, where Y_i^* is the adjusted value for character Y of the *i*th specimen; Y_i is the raw/unadjusted value for character Y; b is the mean of the regression coefficients for Y_i against SVL_i estimated independently for each taxon from logarithmically transformed values of Y_i and SVL_i; SVL_i is the measured snout-vent length (SVL) of the *i*th specimen; and SVL_{mean} is the pooled mean SVL. Data transformation was performed for seven mensural variables: AGL, HL, SnL, HW, HD, AntL, and CrusL. Following data transformation, each variable was assessed with bivariate plots to ensure there was no collinearity with SVL, then tested for conformance to a normal distribution with a Shapiro-Wilks test and for homoscedasticity with a Levene test. One-way ANOVA was used to test for significant differences between the northern and southern lineages in meristic scale counts, as well as the transformed and logged mensural variables. Kungaka specimens were excluded from the statistical comparisons due to the small number of preserved specimens available for morphometric data collection ($n = 2$).

We then compared overall morphological differences between lineages using a multivariate linear discriminant function analysis (LDA) using the *lda* function from v7.3-40 of the R package MASS (Venables & Ripley 2002).

Conservation assessments

Provisional conservation assessments were undertaken for each taxon based on the guidelines of the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2024). For a taxon to qualify for a specific threat category (Critically Endangered, Endangered or Vulnerable), only one of the criteria (A, B, C, D or E) needs to be met; however, it is recommended the taxon is assessed against as many criteria as available data permits. Geographic range size for each taxon was estimated under Criterion B based on calculations of Extent of Occurrence (EOO) and Area of Occupancy (AOO). EOO and AOO were estimated for each taxon using occurrence records obtained from the Atlas of Living Australia (ALA, www.ala.org.au), with the records assigned to a taxon based on their proximity to genotyped samples. Following the IUCN Red List guidelines, EOO was calculated as the area of a minimum convex polygon that encompasses all validated occurrence points. The AOO was calculated by overlaying a 2 x 2 km grid over the same occurrence points, with AOO defined as the total area of grid cells containing at least one record. Both metrics were calculated using the Geospatial Conservation Assessment Tool, GeoCAT (https://geocat.iucnredlist.org). Summary of the outcome of the conservation assessments are presented in the species profiles.

For the conservation assessment of the Kungaka, detailed survey data and relevant biology for the species were summarised from a series of fifteen unpublished monitoring reports jointly prepared by Mutawintji Wiimpatja Aboriginal Owners and ecologists between 2001–2025. A list of the monitoring reports is provided in Table A3 in the Appendix.

Results

SNP analyses

The phylogenetic and population structure analyses found strong support for three major genetic lineages/clusters within the *L. whitii* complex. In both the maximum-likelihood (Fig 2/B) and SVDquartets (Fig 2/A) phylogenetic analyses, samples of Kungaka from Mutawintji National Park formed a well-supported clade, sister to “northern” *L. whitii* populations from eastern NSW, ACT, far north-eastern VIC and likely QLD, although the single QLD sample in our dataset did not pass the initial SNP quality control filtering and was not included in the analysis. The third lineage, “southern” *L. whitii*, includes populations ranging from VIC, TAS and SA. The IQ-TREE analysis was based on 4,262 variable SNPs (following deletion of invariant sites) of which 3,454 were parsimony informative. The best-fit substitution model chosen according to the AIC and BIC criterion was TVM+F+ASC+G4.

The IQ-TREE analysis also detected substantial phylogeographic sub-structuring within the northern and southern *L. whitii* lineages. Divergence within the northern lineage was largely associated with population fragmentation across the Great Dividing Range. Notably, populations from the higher elevation Snowy Monaro region were relatively distantly related from proximal populations in lowland areas of southern NSW and north-eastern VIC. In the southern lineage, significant genetic breaks were identified between Kangaroo Island–mainland SA; across the Murray River Basin; and between populations in SA–VIC. Populations of *L. whitii* from eastern VIC grouped more closely with populations from TAS than western VIC, indicating more recent gene exchange between populations across Bass Strait, than within the VIC mainland.

The disjunct semi-arid population of *L. modesta* from the Merrimerriwa Range in Yathong Nature Reserve of western NSW was recovered as only a minor subclade in the maximum likelihood analysis, indicating relatively recent population isolation.

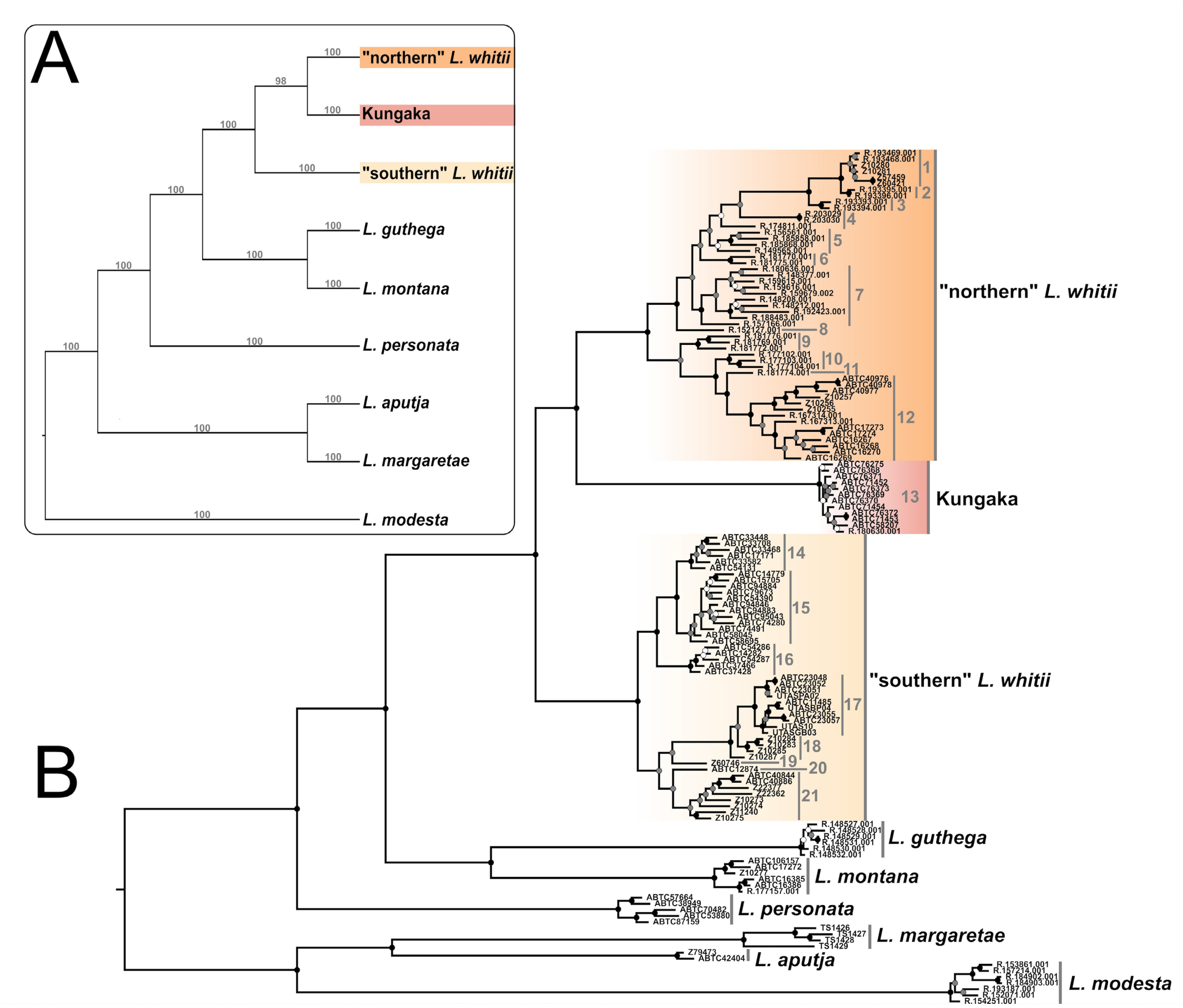

FIGURE 2. (**A**) SVDquartets SNP tree generated for the rock-dwelling *Liopholis* species group. Bootstrap support values indicated on branches. (**B**) Maximum likelihood SNP tree for the rock-dwelling *Liopholis* species group. Tree is rooted on the *L. modesta*, *L. margaretae* and *L. aputja* lineages based on the topology presented in Brennan *et al.* (2024) and Farquhar *et al.* (2024). Bootstrap support values indicated by circles at nodes: black circles = >95% support, grey circles = 70–95%, and white circles = <70%. Numbering of subclades within the northern and southern *L. whitii* complex lineages correspond to sampling localities in Figure 1/B.

The PCA of the total rock-dwelling *Liopholis* species dataset separated *L. whitii* samples from all other *Liopholis* species on the first PC axis, with the northern and southern *L. whitii* clusters separated on the second PC axis. Kungaka samples clustered more closely with northern *L. whitii* (Fig 3/A). The PCA performed on the *L. whitii* complex dataset (i.e., with outgroup species removed), demonstrated discrete clustering of the northern, southern and Kungaka samples (Fig 3/B).

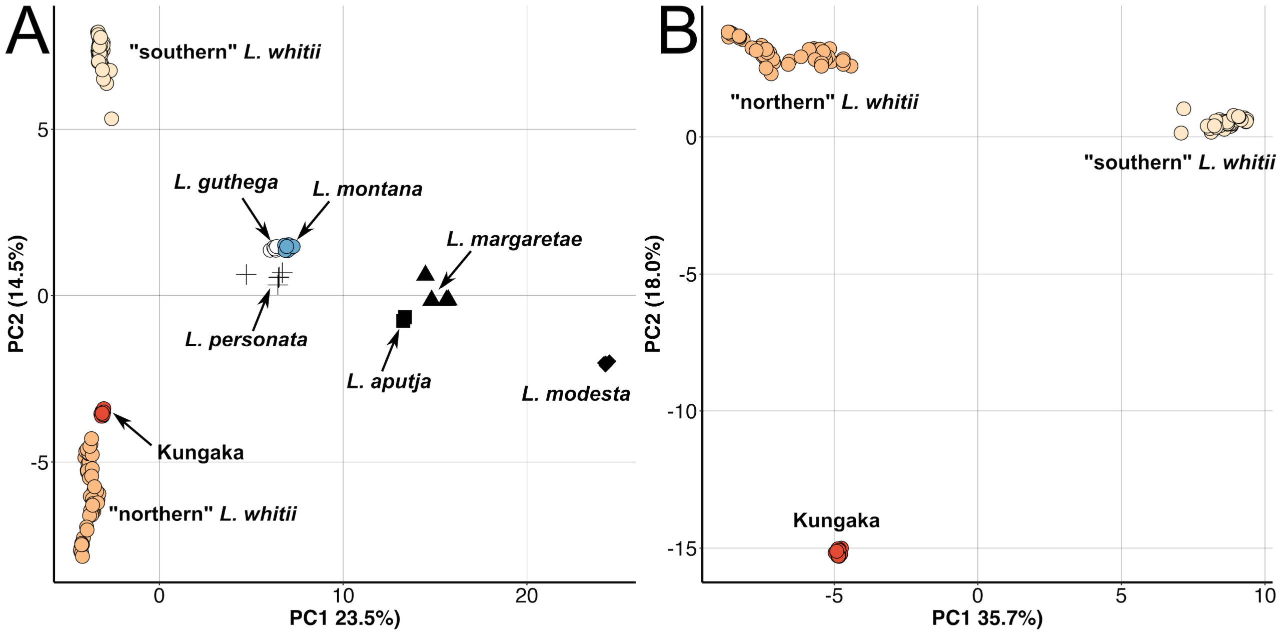

FIGURE 3. Principal component analysis (PCA) ordination plots of SNP diversity for: (**A**) the total rock-dwelling *Liopholis* species dataset, including outgroup species, and (**B**) the *Liopholis whitii* complex.

The plots of *L(K)* and *ΔK* for the STRUCTURE analysis found a consistent peak at $K = 2$, with a plateau from $K = 3$. In the $K = 3$ model, the three major clusters corresponded to the northern, southern, and Kungaka lineages (Fig 4). In the $K = 2$ model, Kungaka samples grouped with the northern cluster. Admixture was detected between the northern and southern *L. whitii* clusters where their ranges come into close proximity in the NSW highlands (i.e., 'population 12', Fig 1/B). One individual from lower Kosciuszko National Park (ABTC17274, Sawpit Creek, >1200 m elevation) was identified with significant genetic admixture between the northern and southern clusters (~20% *q*-values from the southern cluster), with a further 11 samples from the surrounding region recovered with slight levels of admixture (2–9% *q*-values from the southern cluster). All other samples in the *L. whitii* in-group dataset were identified with >99% *q*-values to a single genetic group.

Pairwise levels of genomic differentiation ($G_{'st}$) were high between *Liopholis* species and the major *L. whitii* lineages (Table 1), and significant numbers of fixed differences were detected between them (Table 2). Kungaka differed from *Liopholis* outgroup species by 0.89–0.97 $G_{'st}$, and by 0.74–0.80 $G_{'st}$ from the northern and southern *L. whitii* lineages respectively, with the northern and southern lineages differing by 0.60 $G_{'st}$. Among the *L. whitii* lineages, the Kungaka showed the highest number of fixed differences: 225–322 from the northern and southern lineages respectively, which showed 63 fixed differences from each other. The numbers of fixed differences detected between the *L. whitii* lineages were significantly higher than the expected count of false positives after simulation ($p < 0.01$), which ranged from 9–20 in the comparisons.

TABLE 1. Pairwise genomic differentiation ($G_{'st}$) between major *Liopholis whitii* lineages (in bold) and rock-dwelling *Liopholis* outgroup species. Comparisons based on 7,829 SNP loci. All comparisons returned significant *p* values.

	1	2	3	4	5	6	7	8	9
1. "southern" *L. whitii* (*n* = 47)	-								
2. "northern" *L. whitii* (*n* = 37)	**0.60**	-							
3. Kungaka (*n* = 12)	**0.80**	**0.74**	-						
4. *L. guthega* (*n* = 6)	0.88	0.86	0.95	-					
5. *L. montana* (*n* = 7)	0.84	0.83	0.92	0.89	-				
6. *L. personata* (*n* = 5)	0.82	0.80	0.90	0.90	0.88	-			
7. *L. margaretae* (*n* = 4)	0.88	0.87	0.93	0.93	0.91	0.88	-		
8. *L. aputja* (*n* = 2)	0.92	0.90	0.96	0.96	0.94	0.91	0.84	-	
9. *L. modesta* (*n* = 6)	0.93	0.93	0.97	0.97	0.95	0.93	0.91	0.93	-

TABLE 2. Count of fixed differences at nuclear SNP loci between the major *Liopholis whitii* lineages (in bold) and rock-dwelling *Liopholis* outgroup species. Lower left matrix is the observed count of fixed differences; upper right matrix is the expected count of false positives after simulation. Comparisons based on 5,459–7,829 loci. All comparisons returned significant *p* values after simulation.

	1	2	3	4	5	6	7	8	9
1. "southern" *L. whitii* (*n* = 47)	-	9	20	25	32	113	123	33	36
2. "northern" *L. whitii* (*n* = 37)	**63**	-	19	21	31	114	111	32	35
3. Kungaka (*n* = 12)	**322**	**225**	-	36	53	138	140	48	57
4. *L. guthega* (*n* = 6)	604	609	959	-	31	98	108	34	36
5. *L. montana* (*n* = 7)	541	535	874	552	-	105	117	66	74
6. *L. personata* (*n* = 5)	406	436	748	788	725	-	163	81	92
7. *L. margaretae* (*n* = 4)	880	899	1244	1147	1082	944	-	66	74
8. *L. aputja* (*n* = 2)	918	909	1215	1087	1029	892	539	-	37
9. *L. modesta* (*n* = 6)	1281	1254	1624	1491	1397	1241	998	840	-

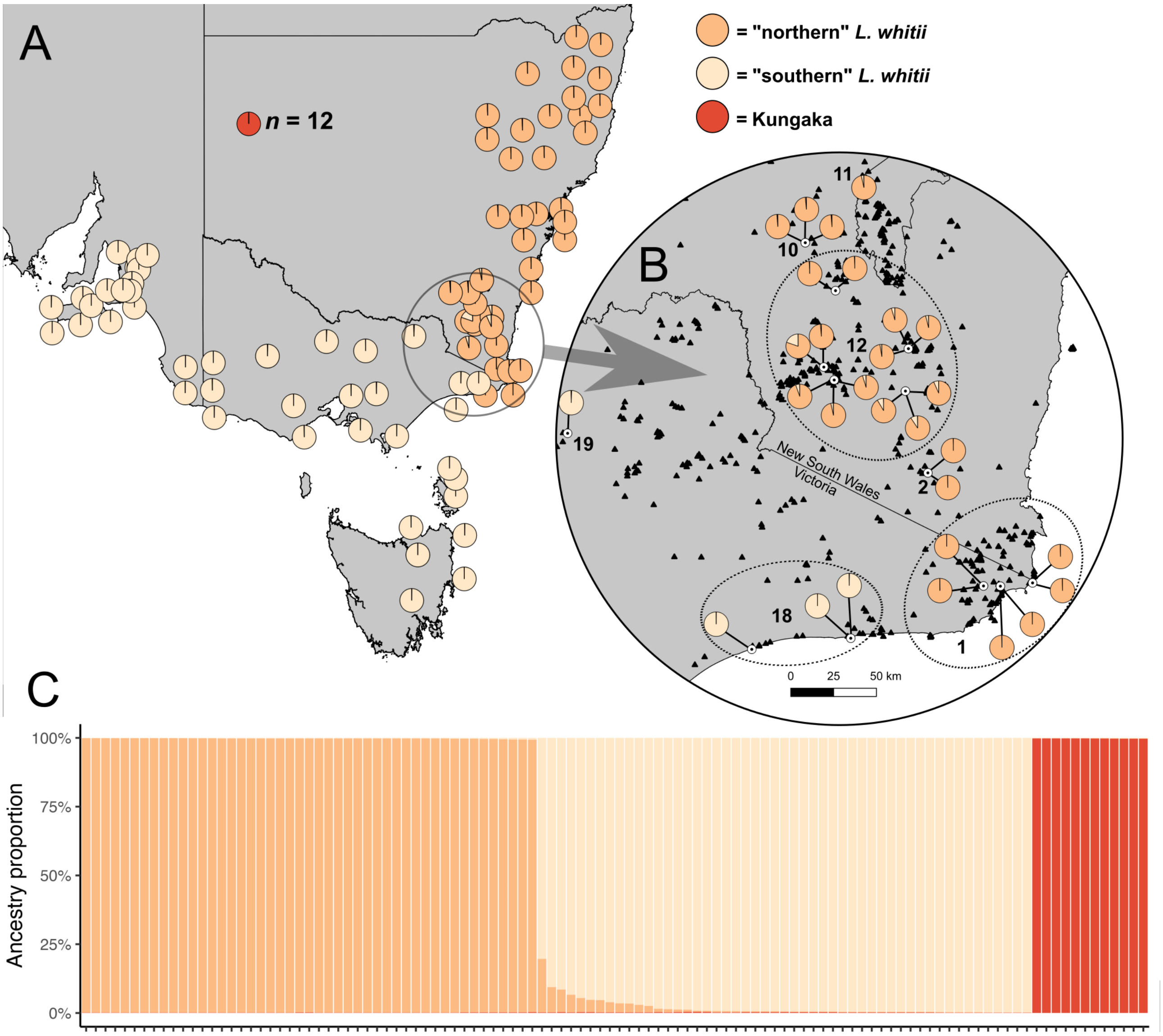

FIGURE 4. (**A**) South-eastern Australia showing pie charts of STRUCTURE ancestry proportions (K = 3 model) for individuals in the *Liopholis whitii* complex analysis. Pie charts are offset slightly from collection localities to aid with visualisation; (**B**) zoomed map of potential contact zone between the northern and southern lineages of L. whitii, across a distance of ~80–160 km. Small black triangles are *L. whitii* occurrence records downloaded from the Atlas of Living Australia (www.ala.org.au; accessed June 2025), numbers correspond to populations identified in Fig 1/B and Fig 2/B); (**C**) barplot of STRUCTURE ancestry proportions under the K = 3 model for all individuals in the *L. whitii* complex analysis.

Morphology

Significant sexual dimorphism was detected with one-factor ANCOVA for the northern lineage of *L. whitii* in six mensural character traits, including HL, SnL, HW, HD, AntL and CrusL, with mean values for males usually ~1 mm smaller than mean values for females. In contrast, no significant morphological differences were found between males and females of the southern lineage. Given sexual dimorphism was relatively slight overall, and non-existent in the southern lineage, sexes were pooled for the inter-lineage statistical comparisons

Despite overlap in morphological variables, one-way ANOVA found significant differences in the means between the northern and southern lineages in AGL, HL, HW, SnL, AntL, MBSR, PVS, 4Flam and 4TLam (Table 3). Statistical comparisons were not performed between Kungaka and other lineages due to the small number of museum specimens available for morphometric examination (*n* = 2); however, visual inspection of box plots revealed clear differences in mean values and character distributions among lineages for the unadjusted measurements of SVL and TL as a proportion of SVL (Fig 5). The northern lineage had the largest mean and maximum SVL, the southern lineage the smallest, and the Kungaka intermediate in size. When tail length was expressed as a proportion of SVL, Kungaka exhibited the longest tails, followed by the northern and then the southern lineage.

TABLE 3. Summary statistics (mean ± SD; range in parentheses) for unadjusted measurements (mm) and meristic scale counts for males and females of each major lineage within *Liopholis whitii*. Only 2 male Kungaka specimens were available for morphological examination, but SVL and TL are based on additional wild specimens which were captured and released (see footnote for sample sizes). TL measurements were taken from specimens with original tails only (see footnote for sample sizes). Statistical tests were performed between the northern and southern lineages using the SVL-transformed and logged data, with sexes pooled for the comparison. Except for SVL and TL, Kungaka specimens were excluded from the statistical tests due to low sample sizes. Significance levels of *p*-values: * < 0.05, ** < 0.01, *** < 0.001.

Character	Kungaka (m)	"northern" *L. whitii* (f)	"northern" *L. whitii* (m)	"southern" *L. whitii* (f)	"southern" *L. whitii* (m)	ANOVA *p*-value
	n = 2	*n* = 40	*n* = 26	*n* = 27	*n* = 24	
SVL	84.4±5.2[†]	89.4±11.0	93.6±8.5	76.0±6.5	76.0±7.1	***
	(72–93)	(72–112)	(79–108)	(64–93)	(63–90)	
TL	143±7.0[†]	138.3±19.2[†]	154.9±15.6[†]	102.5±8.3[†]	107.8±8.4[†]	***
	(136–150)	(96–166)	(121–172)	(91–121)	(94–115)	
AGL	40.1±3.5	46.0±6.3	46.4±4.8	40.0±4.8	39.0±4.9	***
	(37.6–42.6)	(34.9–58.9)	(38.3–54.4)	(32.9–54.1)	(28.3–47.1)	
HL	17.5±0.4	19.2±1.8	20.6±1.5	16.5±1.0	16.7±1.4	***
	(17.2–17.8)	(16.5–23.4)	(17.7–23.1)	(14.6–18.5)	(14.4–18.9)	
HW	11.6±0.4	13.3±1.9	14.2±1.8	10.9±1.0	11.2±1.2	**
	(11.3–11.8)	(10.4–18.5)	(10.7–17.9)	(8.8–12.8)	(9–13.3)	
HD	8.9±0.1	11.0±1.3	12.0±1.7	9.9±1.3	9.7±1.3	NS
	(8.8–8.9)	(8.2–13.9)	(9.2–15.0)	(7.2–12.9)	(7.8–12.5)	
SnL	7.4±0.1	7.7±0.8	8.4±0.8	6.4±0.5	6.6±0.7	***
	(7.3–7.4)	(6.4–9.3)	(7.1–10.0)	(5.3–7.6)	(5.3–7.7)	
AntL	8.5±0.5	8.8±1.1	9.6±1.2	7.6±0.7	7.6±0.8	**
	(8.1–8.8)	(7.0–11.2)	(7.4–11.4)	(6.0–8.9)	(6.3–9.2)	
CrusL	10.7±0.3	11.6±1.5	12.6±1.5	10.0±0.8	10.1±1.0	NS
	(10.5–10.9)	(9.8–14.6)	(9.9–15.5)	(8.5–11.5)	(7.9–12.0)	
MBSR	36	39.5±1.9	40.0±1.7	36.6±2.0	36.6±2.3	***
	(36)	(36–44)	(37–44)	(33–42)	(33–41)	
PVS	52.0±2.8	57.5±4.4	58.9±4.5	54.2±2.9	53.5±2.4	***
	(50–54)	(51–68)	(52–69)	(50–60)	(51–61)	

......continued on the next page

TABLE 3. (Continued)

Character	Kungaka (m)	"northern" *L. whitii* (f)	"northern" *L. whitii* (m)	"southern" *L. whitii* (f)	"southern" *L. whitii* (m)	ANOVA *p*-value
4FLam	13.5±0.7	16.5±1.9	17.0±1.2	14.4±1.0	14.6±1.2	***
	(13–14)	(13–21)	(15–19)	(12–16)	(13–17)	
4TLam	21.0±1.4	24.4±2.5	24.7±2.4	22.3±1.5	22.0±1.9	***
	(20–22)	(20–30)	(21–29)	(20–25)	(20–26)	

[†]Sample sizes: Kungaka SVL = 6f/4m; Kungaka TL = 2f/1m; northern (f) TL = 17; northern (m) TL = 8; southern (f) TL = 13; southern (m) TL = 5.

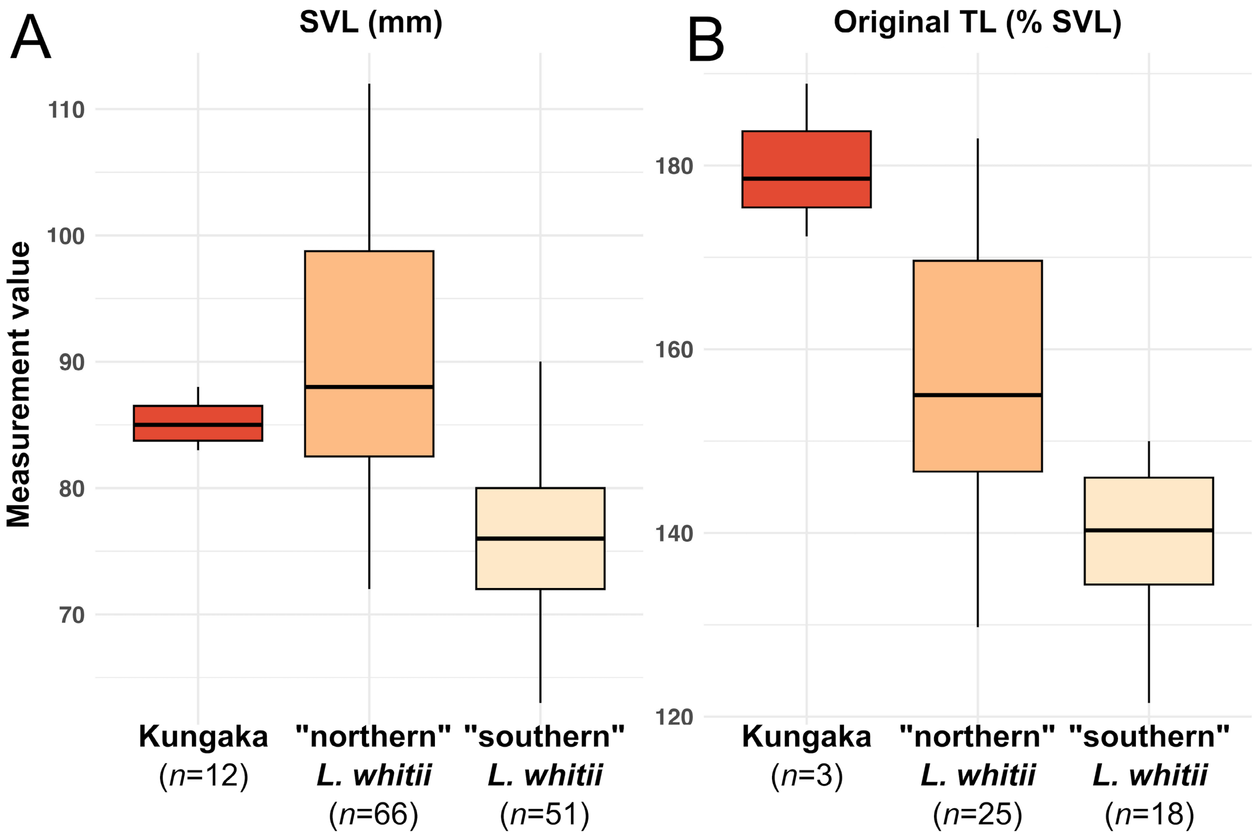

FIGURE 5. (**A**) Comparison of snout-vent length (SVL), and (**B**) original tail length (TL) as a proportion of SVL between the three major *Liopholis whitii* complex lineages.

Overall, colour-pattern was similar between the major lineages, with dorsal pattern falling into three broad categories: (1) patterned, (2) patternless, and (3) plain-back with patterned lateral surfaces. The patterned morph was the most prevalent form among all lineages, representing 77% of northern specimens, 92% of southern, and 81% of Kungaka; the plain-back morph was present in 17% of northern individuals; 2% of southern; and 11% of Kungaka; and patternless form represented 6% of northern individuals, 6% of southern, and 7% of Kungaka. Specimens from all lineages have dark calli on subdigital lamellae of the fingers and toes. Kungaka specimens have dark calli on palmar and plantar scales of the hands and feet (Fig 6), whereas specimens from the northern and southern lineages have plain palmar and plantar surfaces (sometimes weakly callused in the northern lineage).

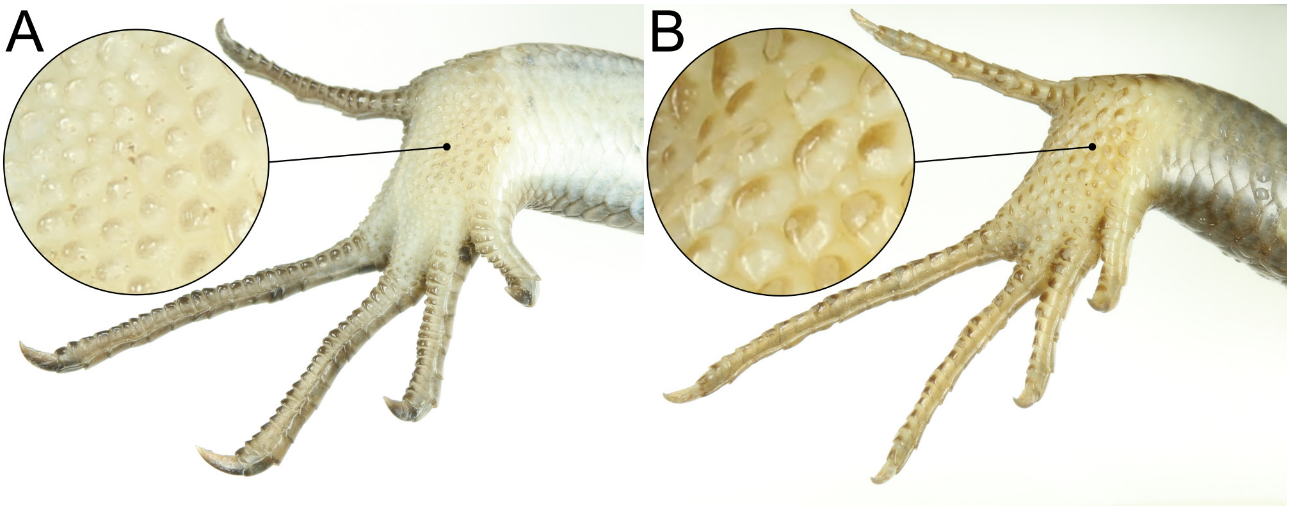

FIGURE 6. Comparison of the hind feet of: (**A**) the "northern" lineage of *Liopholis whitii* (AMS R.203029, Malabar Headland National Park, NSW), and (**B**) the Kungaka (AMS R.147150, Mutawintji National Park, NSW) showing diagnostic dark callusing on plantar scales.

In the linear discriminant function analysis (Fig 7), based on eight adjusted mensural variables (SVL, AGL, HL, SnL, HW, HD, AntL and CrusL) and four meristic scale counts (MBSR, PVS, 4Flam and 4TLam), the model correctly assigned 88.8% of specimens to their prior assumed groups during posterior classification and following jack-knifing. Characters which contributed the highest coefficients of linear discrimination for LD1 were HL, SnL, PVS, and AntL, and for LD2 was AntL, SnL, and 4TLam.

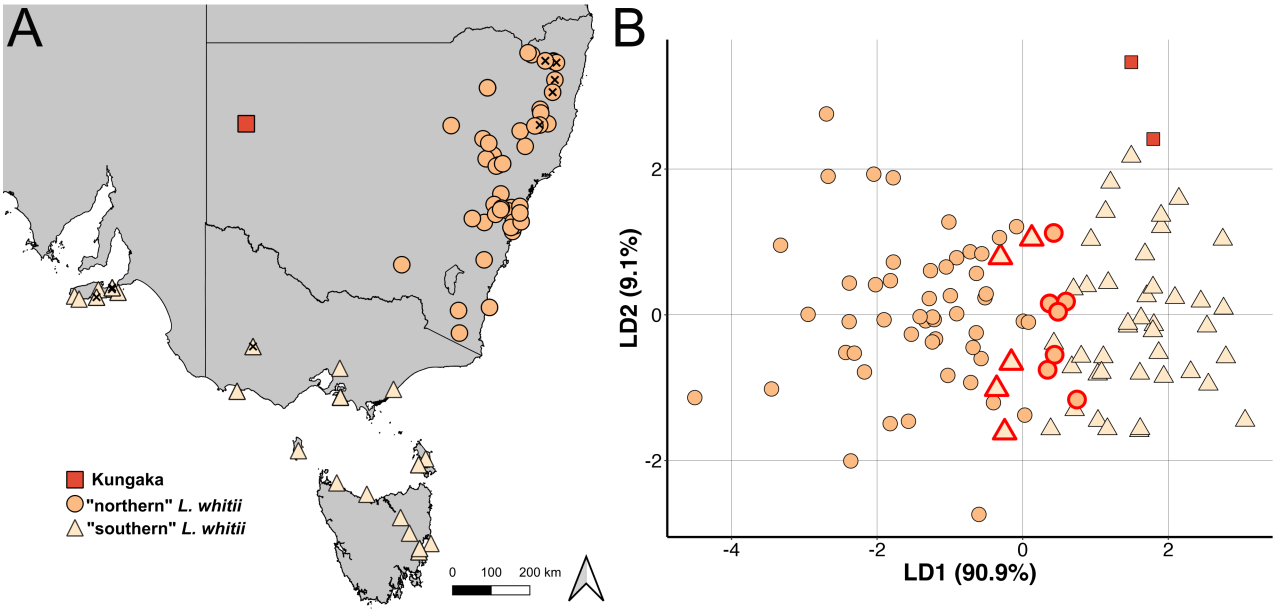

FIGURE 7. (**A**) South-eastern Australia showing sampling locations for the *Liopholis whitii* complex specimens examined in the morphological analysis. Samples marked with an X were individuals incorrectly classified by the linear discriminant function analysis (LDA); (**B**) Plot of the results of the LDA based on the SVL-adjusted and log transformed morphological measurements for the three major *Liopholis whitii* complex lineages. Samples outlined in red were incorrectly classified by the LDA model.

Taxonomic conclusions

Our analyses of range-wide variation in nuclear genome-wide SNPs revealed the presence of three deeply divergent and monophyletic lineages within the *Liopholis whitii* complex, corresponding to "northern" and "southern" populations, and the isolated Kungaka from Mutawintji National Park in arid far western NSW. The three major lineages (particularly the Kungaka) showed levels of genomic differentiation comparable to other well-recognised taxa within *Liopholis*, and the lineages have accumulated significant numbers of fixed differences at nuclear SNP loci, which is evidence for long-term geographic or reproductive isolation. Contact between the northern and southern lineages appears likely based on genetic admixture detected where the lineages come into closest proximity in the southern NSW highlands; however, further genetic sampling from the ~80–160 km distributional gap between the two lineages is required to determine the extent of genetic isolation between them.

Morphometric divergence between the lineages is subtle but multivariate and univariate statistical comparisons demonstrated the lineages differ in body proportions, with 88.8% of individuals correctly classified in the linear discriminant function analysis. The Kungaka further differs from the northern and southern lineages by the presence of dark palmar and plantar calli, and by having longer tails proportionate to SVL. Specimens from the southern lineage differ from the northern lineage by their smaller SVL, shorter TL relative to SVL, and by slight, yet statistically significant differences in mean body proportions.

Our conceptualisation of a 'species' follows the unified species concept (*sensu* de Queiroz 1998; 2007), wherein a species is viewed as a separately evolving population lineage. We interpret divergence between the three major lineages of *L. whitii* as of evolutionary significance and at a scale indicating speciation.

Nomenclature

The nomenclatural history of the group was reviewed in detail by Donnellan *et al.* (2002) and forms the basis of our interpretation of naming conventions for the group, although we provide some expansions and corrections of their conclusions. The earliest name available for the species group is *Scincus whitii* Lacépède, 1804, described from material obtained by the French naturalists François Péron and Charles-Alexandre Lesueur, during the Baudin scientific expedition to Australia between 1800–1804. Two of these are held in the Muséum National d'Histoire Naturelle (MNHN) in Paris, with the larger of the two specimens designated as the lectotype by Wells & Wellington (1985). Donnellan *et al.* (2002) identified this specimen as MNHN 2988A. The original publication did not give a type locality for the specimens, instead reporting on the collection of specimens received from the Baudin Expedition under the broad locality Nouvelle Hollande (=Australia); however, registration data for the specimens (Cogger *et al.* 1983; Brygoo 1985) indicate they were collected from Île Decrès (= Kangaroo Island, South Australia). We therefore apply the species name *Liopholis whitii* to the 'southern' lineage, which includes topotypic populations from Kangaroo Island. An additional name, *Tiliqua leucopsis* Gray, 1838, was based on specimens in the British Museum of Natural History (BMNH), of which BMNH xv.17a was designated the lectotype by Donnellan *et al.* (2002). Those authors used the variation in number of ear lobules provided by Gray (1838) to suggest that Gray may have had more than one specimen in front of him. The later listing of specimens of *Egernia whitii* in the BMNH collection by Gray (1845) listed 19 specimens representing nine donation events. Of these, only two specimens, a (xv.17a, Kangaroo Island, donated by the Paris Museum), and b (xv.17b, from Swan River, donated by W. Buchanan, who is known to have donated reptile specimens to the British Museum in January and March 1838) would have been available to Gray in 1838. From the locality, the latter specimen may represent a different species, either *L. pulchra* or *L. multiscutata*. Given the provenance of xv.17a from Kangaroo Island through the Paris Museum, which is likely to also make it one of the original type series for *Scincus whitii*, we consider this name a junior synonym of *Liopholis whitii*.

Condon (1941) described a new subspecies, *Egernia whitei tenebrosa*, from Kangaroo Island (holotype: SAMA R.2161) presumably based on the belief that the type locality for *whitii* was somewhere in mainland Australia. The type locality identifies this name as belonging to the southern lineage.

Quoy & Gaimard (1824a,b) described *Scincus compressicauda* without specific reference to type specimens but based on material collected during the 1817–1820 voyage of the *Uranie*, under Louis de Freycinet, with Jean René Quoy and Joseph-Paul Gaimard as naturalists. In the first description of the species, a report to the Societe d'Histoire naturelle de Paris on 7 November 1823, but published in the first issue of the first volume of Baron André Étienne Justin Pascal Joseph François d'Audebert de Férussac's new journal, the Bulletin des Sciences Naturelles et de Géologie, which would have been the January issue for 1824 (that journal initially published three volumes a year, each with four issues, giving 12 issues a year, presumed to be released monthly), there is a short description with the locality "La Nouvelle-Galles du sud, au-delà des montagnes Bleues" (beyond the Blue Mountains of New South Wales). Quoy travelled across the Blue Mountains, reaching Bathurst, between 27 November and 7 December 1819 (de Freycinet 1839).

The more extended description, accompanied by a plate, was published in the Zoologie volume of the expedition report (Quoy & Gaimard 1824b) and gives the locality as "le Port-Jackson" (Port Jackson, presumably near Neutral Bay, where the expedition was moored during its Sydney sojourn). This second description, on pp. 180–181, was published as part of the fourth livraison of that volume, on 18 September 1824 (Sherborn & Woodward 1901). No indication was provided as to the number of specimens on which these descriptions were based, but the earlier description gives measurements of snout-vent length 3 po[uces]. 2 lignes, and a tail length of 6 po[ouces] 9 lignes, while the second description gives a total length of "onze pouces de longueur, sur lesquels la queue en prend sept" [Eleven inches, of which the tail takes up seven]. The French pouce (inch) is equivalent to 27.1 mm in current metric definitions, and was divided into 12 lignes [lines], giving each ligne a length of 2.26 mm (Jacobs & Koch, 2021). While the differences between the two sets of measurements are marked, the measurements provided by Quoy & Gaimard (1824a) would give a ratio of tail length/SVL of 213%, well beyond that in any lineage of *L. whitii*, while the measurements provided by the second description (Quoy & Gaimard 1824b) would give a ratio of tail length/SVL of 175%, within the range for the northern lineage. Hence, we assume that the second account is more accurate, and that there is an error in the first account (likely to be of the measurement of SVL). There are no other indications that more than one specimen was obtained by the expedition. Guibé (1954) and Cogger *et al.* (1983) were unable to identify a type specimen, but Brygoo (1985) identified a single specimen in the MNHN collection, MNHN 2989, as collected by Quoy & Gaimard, which he tentatively considered to be the holotype. He reported the total length of the specimen as 288 mm and tail length as 188 mm, giving an SVL of 100 mm, a reasonable approximation of the measurements provided by Quoy & Gaimard (1824b), which would give a snout-vent length of 108 mm and a tail length of 190 mm.

Donnellan *et al.* (2002) designated MNHN 2989 as the lectotype, though it is more likely simply the holotype. We therefore apply the species name *Liopholis compressicauda* to the "northern" lineage which includes topotypic populations from the Sydney and Blue Mountains areas.

Duméril & Bibron (1839) described *Gongylus* (*Lygosoma*) *moniligera*, a name they attribute to an Achille Valenciennes manuscript in the Paris collection, from a series of specimens in the MNHN. As originally construed by them, this species consisted of two varieties. Variety A, which represents the patterned-back morph, was represented by the types of both *Scincus whitii* and *Scincus compressicauda*, as well as two later specimens also obtained by Quoy & Gaimard, from their second visit to Australia as part of the voyage of the *Astrolabe* and led by Jules-Sébastien-César Dumont d'Urville, between 1826 and 1829: MNHN 7123 and 7123A (Brygoo 1985). While these latter specimens just bear the locality Australie (although Cogger *et al.* 1983, reported the locality Hobart), the *Astrolabe* expedition landed in Australia at five places: King George Sound (7–25 October 1826), Westernport (12–19 November 1826), Jervis Bay (26–29 November 1826), Sydney (2–17 December 1826) and Hobart (16 December 1827–5 January 1828) (Duyker 2014).

Variety B, which represents the plain-backed morph, was represented by two specimens obtained by Péron and Lesueur during the Baudin Expedition, with locality Terre de Leeuwin (= SW Western Australia, between about Swan River and Walpole): MNHN 2992 and 2992A (Brygoo 1985). This area is only inhabited by *L. pulchra*, so either the locality or the identification of these two specimens are in doubt. While these specimens were collected on the same expedition as the types of *S. whitii*, they cannot be considered part of the type series of that species, as they do not agree with the diagnosis of that species provided by Lacépède (1804), which clearly states "quatre raies noires et tachées de blanc, sur le dos" (four black stripes spotted with white on the back).

Loveridge (1934) and Cogger *et al.* (1983) also suggest that MCZ 2133, a specimen bearing just the locality Australia but donated to the MCZ collection by Auguste Duméril in 1865, may be a syntype of *Gongylus moniligera*. However, in the absence of any clear evidence that this specimen was in the Paris collection prior to 1839, this would not appear to be able to be confirmed.

The combination of specimens of both the northern and southern lineages in the type series of *Gongylus* *moniligera* was resolved by the designation of the holotype of *Scincus compressicauda* (MNHN 2989) as lectotype of *moniligera* by Donnellan *et al.* (2002), fixing that name as a junior objective synonym of *compressicauda*.

Gongylus moniligera is the type species of *Liopholis* Fitzinger 1843.

Wells & Wellington (1985) also named *Liopholis coplandi* from a series of specimens collected from Cooma, New South Wales, considering that this taxon was most closely related to Sydney populations, to which they restricted the name *L. compressicauda* (incorrectly spelt as *compressicaudus*, evidently erroneously considering the epithet as an adjective), but differentiating it from *compressicauda* solely on habitat preferences (*coplandi* from "cool temperate (granite) habitats of the southern highlands" and *compressicauda* from "sandstone habitats and associated heathlands" of the Sydney Basin), and citation of Cogger (1983), who does not provide any such statement differentiating the two populations. In the absence of any specific character state of morphology or genetics in the original description, it may be that *Liopholis coplandi* is a *nomen nudum*. We included genetic samples from the Cooma area and our analysis confirms these populations are conspecific with *Liopholis compressicauda*.

There are no existing scientific names available for the Kungaka, and so in agreement with Mutawintji Wiimpatja Aboriginal Owners, represented by the Board of Management and the local Wiimpatja that have been involved in looking after the kungaka since 2001, we hereby apply the name *Liopholis mutawintji* **sp. nov.** to this taxon.

Systematics and taxonomy

Family Scincidae Oppel 1811

Subfamily Lygosominae Gray 1845

Tribe Tiliquini Gray 1845

Genus *Liopholis* Fitzinger 1843

Type species: *Gongylus (Lygosoma) moniligera* Duméril & Bibron 1839, by monotypy = *L. compressicauda*

Diagnosis: (from Gardner *et al.* 2008; and Aplin *et al.* 2024): A genus of relatively small to medium-sized tiliquin skinks (adult SVL 75–200 mm); head and body squarish in cross-section; midbody scales in 34–52 rows, the dorsals smooth (keeled in *L. pulchra*); nasal scale without postnarial groove; subocular scale row incomplete; eyes relatively large, the eyelids usually with distinct cream margins, easily differentiated from adjacent scales. Terrestrial; mainly diurnal with some species crepuscular to nocturnal; viviparous.

Includes 17 species: *aputja* Farquhar, Mulder, Russell, Haines & Chapple 2024; *compressicauda* (Quoy & Gaimard 1824); *inornata* (Rosén 1905); *guthega* (Donnellan, Hutchinson, Dempsey & Osborne 2002); *kintorei* (Stirling & Zietz 1893); *margaretae* (Storr 1968); *modesta* (Storr 1968); *montana* (Donnellan, Hutchinson, Dempsey & Osborne 2002); *multiscutata* (Mitchell & Behrndt 1949); *parva* Aplin, Maryan, Armstrong, Pavey & Donnellan 2024; *personata* (Storr 1968); *pulchra* (Werner 1910); *purnululu* Aplin, Maryan, Armstrong, Pavey & Donnellan 2024; *slateri* (Storr 1968); *striata* (Sternfeld 1919); *whitii* (Lacépède 1804), and *mutawintji* **sp. nov.** (this work).

Liopholis whitii (Lacépède 1804)

Southern White's Skink

(Fig 8)

Lectotype. MNHN 2988A (designated by Wells & Wellington 1985; identified by registration number by Donnellan *et al.* 2002). Collection locality published as Nouvelle Hollande (=Australia), collected by François Péron and Charles-Alexandre Lesueur, during the Baudin scientific expedition to Australia between 1800–1804; however, the registration entry and jar labels for the two syntypes indicate they were collected from Île Decrès (= Kangaroo Island, South Australia), which was visited by the Baudin expedition between 6–31 January, 1803. Morphological details of MNHN 2988A are presented in Donnellan *et al.* (2002): SVL of 89 mm, the tail is broken off, leaving a 9 mm stump, the midbody scales are smooth and in 36 longitudinal rows, the 25 subdigital lamellae are smooth, the lateral markings are in the form of black-bordered ocelli and there is a complex dorsal pattern including a pair of dorsolateral stripes, each bearing a series of white spots. *Paralectotypes*: MNHN 2988 (no suffix, smaller of the two specimens in the series); BMNH xv.17a, Kangaroo Island, donated by Paris Museum prior to 1838).

Synonymy

Scincus taeniolatus quadrilineatus Merrem 1820: 72 [replacement name for *Scincus whitii*].
Tiliqua leucopsis Gray 1838: 291. Syntypes in British Museum from New Holland. Lectotype BMNH xv.17a, Kangaroo Island, South Australia, donated by Paris Museum (designated by Donnellan *et al.* 2002).
Hinulia whitei Gray 1845: 79 [incorrect subsequent spelling of *whitii*].
Lygosoma whitei Peters 1863: 230.
Egernia whitii Boulenger 1887: 135.
Egernia whitei tenebrosa Condon 1941: 111. Holotype: SAMA R.02161, Flinders Chase, Kangaroo Island, South Australia, collected by Tate Society, University of Adelaide.

Diagnosis. A relatively small to medium-sized skink (SVL up to 93 mm; $\bar{x}$ = 76 mm), with smooth dorsal scales, a pointed snout and original tail length 130–142% of SVL ($\bar{x}$ = 139.6%). Head length 19–24% of SVL ($\bar{x}$ = 21.9%), mid-body scale rows 33–42 ($\bar{x}$ = 37), and paravertebral scales 50–61 ($\bar{x}$ = 54). Subdigital lamellae number 12–17 under fourth finger (mode = 15) and 20–26 under fourth toe (mode = 21), each with dark calluses restricted to the free edge of lamellae. Plantar scales on hands and feet are plain and lack dark calluses. Supralabials 7–9 (mode = 7), infralabials 6–9 (mode = 7), and supraciliaries 6–8 (mode = 7). Antebrachium length 8–12% of SVL; crus length 12–15% of SVL.

FIGURE 8. Southern White's Skinks (*Liopholis whitii*). (**A**) Paddys Ranges, VIC; (**B**) Glenelg Plain, VIC; (**C**) Mount Buangor State Park, VIC; (**D**) Grampians National Park, VIC; (**E**) Budj Bim National Park, VIC; (**F**) Korobeit, VIC; (**G**) Freycinet Peninsula, TAS; (**H–I**) Chatsworth, VIC. Photographs A–E: Jules Farquhar; F–I: Ray Lloyd.

Comparison with similar species. Distinguished from *L. compressicauda* by its smaller size (SVL to 93 mm [$\bar{x}$ = 76 mm] versus SVL to 112 mm [$\bar{x}$ = 91 mm]), proportionately shorter original tail length (TL = 130–142% of SVL [$\bar{x}$ = 139.6%] versus 130–183% [$\bar{x}$ = 157.7%]). Distinguished from *L. mutawintji* **sp. nov.** by its consistently plain palmar and plantar scales (versus dark callused palmar and plantar scales), and proportionately shorter TL (130–142% of SVL [$\bar{x}$ = 139.6%] versus 172–189%).

Description. Morphometric summary statistics for males and females are provided in Table 3. Snout-vent length (SVL) for males 63–90 mm ($\bar{x}$ = 76 mm, *n* = 24) and females 64–93 mm ($\bar{x}$ = 76 mm, *n* = 27), original tail length (TL) for males 94–115 mm ($\bar{x}$ = 107.8 mm, *n* = 5) and females 91–121 mm ($\bar{x}$ = 102.5 mm, *n* = 13), with TL for males and females equal to 130–142% of SVL ($\bar{x}$ = 139.6%). Axilla-groin length (AGL) of males and females 28.3–54.1 mm (= 41–58% of SVL, $\bar{x}$ = 51.9%). Snout relatively pointed, head length (HL) for males and females 14.4–18.9 mm (= 19–24% of SVL, $\bar{x}$ = 21.9%), head width (HW) 8.8–13.3 mm (= 59–80% of HL, $\bar{x}$ = 66.5%), head depth (HD) 7.2–12.9 mm (= 49–70% of HL, $\bar{x}$ = 58.9%), snout length (SnL) 5.3–7.7 mm (= 34–45% of HL, $\bar{x}$ = 38.8%). Palmar and plantar scales on palms of hands and feet plain, lacking dark calli. Subdigital lamellae under fourth finger number 12–17 (mode 15), and 20–26 (mode 21) under fourth toe, both with dark calli on free edge of lamellae. Antebrachium length (AntL) 6.0–9.2 mm (= 8–12% of SVL, $\bar{x}$ = 10%), crus length (CrusL) 7.9–12.0 mm (= 12–15% of SVL, $\bar{x}$ = 13.2%). Supralabial scales numbering 7–9 (mode 7), infralabials 6–9 (mode 7), supraciliaries 6–8 (mode 7), mid-body scale rows 33–42 ($\bar{x}$ = 37), paravertebral scales 50–61 ($\bar{x}$ = 54).

Colour-pattern. Light grey to rusty grey-brown dorsal surface with grey to brown lateral surface, and plain grey to cream ventral surface, sometimes with an orange flush under the hind limbs and tail. Lateral patterns typically comprise variable dark mottling overlaid with cream ocelli bordered by an irregular ring of black. A faint to prominent cream-coloured streak usually present on the upper labials. Three colour-pattern morphs occur, including patterned, plain-back and patternless. The patterned morph occurs most frequently, followed by the plain-back morph, with patternless individuals rarely observed. Patterned morph individuals typically have a complex and variable pattern consisting of brown to black dorsolateral stripes and spots, with longitudinally aligned series of dark or pale cream to yellow stripes, dashes and spots.

Distribution and habitat. Widely distributed in temperate areas of south-eastern Australia, including SA, VIC and TAS. In SA, the species has a disjunct distribution, with isolated populations in Kangaroo Island; Fleurieu Peninsula and Mount Lofty Ranges; and in the south-eastern corner of the state. In VIC, the species is distributed widely through coastal to montane elevations across the state. In TAS, the species occurs in the north-west, central and eastern sections of the state but is absent from the south-west region. Insular populations occur on Greenly, Neptune, Wedge and Lady Julia Percy Islands, as well as numerous islands in Bass Strait, including King, Flinders and Chappell Islands. Occupies a range of predominantly rocky and sandy habitats, including open eucalypt forest, dry woodland, coastal heathland, and open tussock grasslands.

Ecology. Reaches maturity at 3 to 4 years and ~72–78 mm SVL, based on study populations in TAS (Chapple 2005; While *et al.* 2009). Reproduction typically occurs annually, with mating recorded in October and parturition in January and February. Litter size ranges from one to five. The species typically lives in stable social groups comprising a long-term monogamous adult pair and single cohort of offspring. Most offspring are sired by the social male; however, approximately 30% of offspring are sired by extra-pair males (Halliwell *et al.*, 2017; While *et al.*, 2009). Diet consists of insects, other invertebrates and small amounts of plant material (Chapple 2003).

Conservation status. *Liopholis whitii* does not currently qualify for a specific threat category under the IUCN Red List Criteria. There is no evidence for a ≥30% population size reduction to qualify the taxon under Criteria A. Geographic range size, based on an estimation of EOO and AOO, exceeds the threshold under Criterion B (EOO <20,000 km^2; AOO <2,000 km^2). Total population size undoubtedly exceeds 10,000 mature individuals, meaning the species does not qualify under Criteria C or D. Further, we did not undertake a quantitative analysis under Criteria E; however, the species is not considered likely to meet any of the extinction risk thresholds. Based on this provisional conservation assessment, a conservation status of Least Concern is deemed appropriate for the species.

Liopholis compressicauda (Quoy & Gaimard 1824)

Northern White's Skink
(Fig 9)

Lectotype. MNHN 2989 (designated by Donnellan *et al.* 2002). Collection locality given as "La Nouvelle-Galles du sud, au-delà des montagnes Bleues" (beyond the Blue Mountains of New South Wales) in Quoy & Gaimard (1824a) and "le Port-Jackson" (Port Jackson, presumably near Neutral Bay) in the extended description by Quoy & Gaimard (1824b). Collected by French naturalists Joseph-Paul Gaimard and Jean René Constant Quoy, during the voyage of the *Uranie* between 1817–1820.

FIGURE 9. Northern White's Skinks (*Liopholis compressicauda*). All individuals photographed in New South Wales: (**A**) Warrumbungle National Park; (**B**) Ebor Falls; (**C**) Mount Canobolas; (**D**) Mount Kaputar National Park; (**E**) Hawkesbury Sandstone region; (**F**) Malabar Headland National Park; (**G**) Bombala; (**H–I**) Tianjara. Photographs A–C: Mark Sanders (EcoSmart Ecology); D–E: Jules Farquhar; F: Dane Trembath; G–I: Tom Parkin.

Synonymy

Gongylus (*Lygosoma*) *moniligera* Duméril & Bibron 1839: 736. Holotype (designated as lectotype by Donnellan *et al.* 2002): MNHN 2989, Nouvelle Hollande.
Liopholis moniligera Fitzinger 1843: 22.
Egernia whitii moniligera Cogger 1975: 290.
Liopholis coplandi Wells & Wellington 1985: 32. Holotype: AMS R.76863 (formerly AM field series 14610), Cooma Airstrip, 17 km S of Cooma, NSW; R. Wells, R. Sadlier, K. Kennerson, 4.x.1978. Paratypes AMS R.76662-75 and R. 76864, same data.
Liopholis compressicaudus Wells & Wellington 1985: 32 (incorrect subsequent spelling of *compressicauda*).
Liopholis whitii compressicaudus Wells & Wellington 1988: 6
Liopholis whitii coplandi Wells & Wellington 1988: 6.

Diagnosis. A medium to large skink (SVL up to 112 mm; $\bar{x}$ = 91 mm), with smooth dorsal scales, a pointed snout and original tail length 130–183% of SVL ($\bar{x}$ = 157.7%). Head length 19–24% of SVL ($\bar{x}$ = 21%), mid-body scale rows 36–44 ($\bar{x}$ = 40), and paravertebral scales 51–69 ($\bar{x}$ = 58). Subdigital lamellae number 13–21 under fourth finger (mode = 16) and 20–30 under fourth toe (mode = 26), both with a prominent dark callus on the free edge. Palmar and plantar scales usually plain, but faint dark calli present in ~10% of individuals. Supralabials 7–8 (mode = 7), infralabials 7–8 (mode = 7), and supraciliaries 6–9 (mode = 7). Antebrachium length 9–12% of SVL; crus length 11–15% of SVL.

Comparison with similar species. Distinguished from *L. whitii* by its larger size (SVL to 112 mm [$\bar{x}$ = 91 mm] versus SVL to 93 mm [$\bar{x}$ = 76 mm]), and proportionately longer original tail length (TL = 130–183% of SVL [$\bar{x}$ = 157.7%] versus 130–142% [$\bar{x}$ = 139.6%]). Distinguished from *L. mutawintji* **sp. nov.** by its usually plain palmar and plantar scales (versus dark callused palmar and plantar scales), and proportionately shorter original tail length (TL = 130–183% of SVL [$\bar{x}$ = 157.7%] versus 172–189%).

Description. Morphometric summary statistics for males and females are provided in Table 3. Snout-vent length (SVL) for males 79–108 mm ($\bar{x}$ = 93.6 mm, *n* = 26) and females 72–112 mm ($\bar{x}$ = 89.4 mm, *n* = 40), original tail length (TL) for males 121–172 mm ($\bar{x}$ = 154.9 mm, *n* = 8) and females 96–166 mm ($\bar{x}$ = 138.3, *n* = 17), with TL for males and females equal to 130–183% of SVL ($\bar{x}$ = 157.7%). Axilla-groin length (AGL) of males and females 38.9–58.9 mm (= 47–53% of SVL, $\bar{x}$ = 50.7%). Snout relatively pointed, head length (HL) for males and females 16.5–23.4 mm (= 19–24% of SVL, $\bar{x}$ = 21%), head width (HW) 10.4–18.5 mm (= 58–79% of HL, $\bar{x}$ = 68.9%), head depth (HD) 8.2–15.0 mm (= 49–67% of HL, $\bar{x}$ = 57.5%), snout length (SnL) 6.4–10.0 mm (= 37–45% of HL, $\bar{x}$ = 40.3%). Palmar and plantar scales on palms of hands and feet usually plain and lacking dark calli, although dark calli were weakly present in ~10% of specimens examined. Subdigital lamellae under fourth finger number 13–21 (mode 16), and 20–30 (mode 26) under fourth toe, both with a prominent dark callus on the free edge of lamellae. Antebrachium length (AntL) 7.0–11.4 mm (= 9–12% of SVL, $\bar{x}$ = 10%), crus length (CrusL) 9.8–15.5 mm (= 11–15% of SVL, $\bar{x}$ = 13.2%). Supralabial scales numbering 7–8 (mode 7), infralabials 7–8 (mode 7), supraciliaries 6–9 (mode 7), mid-body scale rows 36–44 ($\bar{x}$ = 40), paravertebral scales 51–69 ($\bar{x}$ = 58).

Colour-pattern. Light grey to rusty grey-brown dorsal surface with grey to brown lateral surface, and plain grey to cream ventral surface. Lateral patterns typically comprise variable dark mottling overlaid with cream ocelli bordered by an irregular ring of black. A prominent cream-coloured streak usually present on the upper labials. Three colour-pattern morphs occur, including patterned, plain-back and patternless. The patterned morph occurs most frequently, followed by the plain-back morph, with patternless individuals rarely observed. Patterned morph individuals typically have a complex and variable pattern consisting of brown to black dorsolateral stripes and spots, with longitudinally aligned series of dark or pale cream to yellow stripes, dashes and spots.

Distribution and habitat. Found in mostly temperate areas of eastern Australia, including south-eastern QLD, eastern NSW, ACT and north-eastern VIC, typically associated with rocky habitats of the Great Dividing Range (GDR). In QLD, the species is restricted to the south-east, including Mount Barney and Girraween National Parks. In NSW, the species' distribution encompasses a wide range of elevations from coastal lowlands to the montane uplands, with several outlier populations west of the GDR, including Warrumbungle and Goobang National Park. An insular population occurs on Barunguba Montague Island off the South Coast. In the ACT, the species is found in mid to montane elevations at Namadgi National Park and Bimberi Nature Reserve. In VIC, the species is restricted to the north-eastern corner of the state, in the coastal lowlands of the East Gippsland region. Occupies a range of primarily rocky habitats, including open eucalypt forest, dry woodland, coastal heathland, and open tussock grasslands.

Ecology. Life history and reproductive ecology is summarised by Chapple (2005) based on study populations in Namadgi National Park, ACT and Amiens, QLD, the latter studied by Milton (1987). The species reaches maturity at 2–3 years and ~75–85 mm SVL for both sexes. Reproduction typically occurs annually, with mating in September–October and parturition in January–February. Litter size ranges from one to five. The species lives in small but stable social groups, with a mating system that consists of both polygyny and monogamy (Chapple & Keogh 2005; 2006). Diet consists of insects, other invertebrates and small amounts of plant material (Chapple 2003).

Conservation status. *Liopholis compressicauda* does not currently qualify for a specific threat category under the IUCN Red List Criteria. There is no evidence for a ≥30% population size reduction to qualify the taxon under Criteria A. Geographic range size, based on an estimation of EOO and AOO, exceeds the threshold under Criterion B (EOO <20,000 km^2; AOO <2,000 km^2). Total population size undoubtedly exceeds 10,000 mature individuals, meaning the species does not qualify under Criteria C or D. Further, we did not undertake a quantitative analysis under Criteria E; however, the species is not considered likely to meet any of the extinction risk thresholds. Based on this provisional conservation assessment, a conservation status of Least Concern is deemed appropriate for the species.

Liopholis mutawintji sp. nov

Kungaka

(Figs 10, 11)

Holotype. AMS R.147150 (formerly SAMA R.45513), adult male, collected from Bynguano Range, Mutawintji National Park, NSW, on the 13th April 1995 by members of the Australian Herpetological Society (AHS) and South Australian Herpetological Group (SAHG). Holotype details: SVL 83 mm, TL (original) 143 mm, AGL 42.6 mm, HL 17.2 mm, SnL 7.4 mm, HW 11.3 mm, HD 8.8 mm, AntL 8.1 mm, CrusL 10.9 mm, supralabials 7, infralabials 7, supraciliaries 7, mid-body scale rows 36, paravertebral scales 50, subdigital lamellae 13 (fingers) and 20 (toes), patterned morph.

Paratype. AMS R.146257, adult male, plain-back morph, Bynguano Range, Mutawintji National Park, NSW. Collected on the 25th October 1994 by members of the AHS and SAHG.

FIGURE 10. Kungaka, *Liopholis mutawintji* **sp. nov.** type specimens collected from the Bynguano Range, Mutawintji National Park. Holotype (top specimen), male, patterned morph, AMS R.147150; Paratype (bottom), male, plain-back morph, AMS R.146257.

Diagnosis. A medium-sized skink (SVL 72–93 mm; $\bar{x}$ = 84.5 mm), with smooth dorsal scales, a pointed snout and long original tail length (172–189% of SVL). Head length 21–23% of SVL, mid-body scale rows 36, and paravertebral scales 50–54. Subdigital lamellae number 13–14 under fourth finger and 20–22 under fourth toe, both bearing prominent dark calli. Palmar and plantar scales of the hands and feet exhibit prominent dark calli. Supralabials number 7–8, infralabials 7, and supraciliaries 7. Antebrachium length 8–11% of SVL; crus length 13–14% of SVL.

Comparison with similar species. Distinguished from *L. whitii* and *L. compressicauda* by its prominent dark palmar and plantar calli (versus plain in *L. whitii* and typically plain in *L. compressicauda*, although faint dark calli present in ~10% of specimens) and proportionately longer TL (172–189% of SVL versus 130–142% [$\bar{x}$ of 139.6%] for *L. whitii* and 130–183% [$\bar{x}$ of 157.7%] for *L. compressicauda*).

Description. Morphometric summary statistics are provided in Table 3. Snout-to-vent-length (SVL) for males 79–88 mm ($\bar{x}$ = 84.7 mm, *n* = 6), and females 72–93 mm ($\bar{x}$ = 84.2 mm, *n* = 6), original tail length (TL) 136–150 mm (=172–189% of SVL, *n* = 3), weight 8.2–18.8 g ($\bar{x}$ = 15.6 g, *n* = 10). Axilla-groin length (AGL) 37.6–42.6 mm (= 48–51% of SVL). Snout relatively pointed, head length (HL) 17.2–17.8 mm (= 21–23% of SVL), head width (HW) 11.3–11.8 mm (= 66% of HL), and head depth (HD) 8.8–8.9 mm (= 50–51% of HL). Antebrachium length (AntL) 8.1–8.8 mm (= 8–11% of SVL), crus length (CrusL) 10.5–10.9 mm (= 13–14% of SVL). Palmar and plantar scales on palms of hands and feet with prominent dark calli. Subdigital lamellae under fourth finger number 13–14, and 20–22 under fourth toe, both with a prominent dark callus on the free edge of lamellae. Supralabial scales numbering 7–8, infralabials 7, supraciliaries 7, mid-body scale rows 36, paravertebral scales 50–54.

Colour-pattern. Grey to rusty brown dorsal and lateral surface, with blueish grey to cream ventral surface, sometimes with dark edged scales forming a reticulated pattern. Juveniles have a distinctive, blue-tinged dorsal and ventral colouration (Fig 11/I). Lateral patterns typically comprise variable dark mottling overlaid with cream spots or ocelli bordered by a faint ring of black. A rusty orange-red flush often present on the lower jaws and throat, varying in intensity between specimens. A prominent cream-coloured streak usually present on the upper labials, and a single cream spot typically behind the ear opening. Three colour-pattern morphs occur, including patterned (i.e., Fig 11/A/C/D), plain-back (i.e., Fig 11/B/E) and patternless (i.e., Fig 11/G/H). The patterned morph occurs most frequently, followed by the plain-back and patternless morphs. Patterned morph individuals typically have a complex and variable pattern consisting of brown to black dorsolateral stripes and spots, with longitudinally aligned series of dark or pale cream to yellow stripes, dashes and spots. Juveniles have a distinctive, blue-tinged dorsal and ventral colouration (Fig 11/G/H/I).

Etymology. The species name reflects the distribution of *Liopholis mutawintji* **sp. nov.** occurring entirely within Mutawintji National Park. The place name *Mutawintji* is given by Wiimpatja Aboriginal Owners of the area and means *place of green grass and waterholes*. The common name *Kungaka* (pronounced 'kung-aka') means *the hidden one* in Wiimpatja parlku and is in reference to the species habit of remaining hidden in rocky crevices and burrows.

Distribution and habitat. The Kungaka is endemic to NSW, where it is restricted to the Bynguano Range of Mutawintji National Park in the Broken Hill Complex bioregion of the state's arid Far West region. Kungaka occur in eastern facing, mid to lower slopes in relatively sheltered areas adjacent to ephemeral creeks (Table A3). Key habitat sites comprise red sandstone rock and soil complexes (rather than rock-on-rock), with a groundcover of primarily Rock Sida (*Sida petrophila*) and native grasses, and moderate tree coverage of mulga (*Acacia aneura*) and *Callitris* (Table A3). Burrows are typically excavated in soil beneath rocks and within crevices. Moderate shade and groundcover vegetation appear to be important habitat features, with shade likely reducing site temperatures, and groundcover vegetation providing shelter from predators while Kungaka forage (Table A3).

Ecology. Reproductive ecology and life-history of the Kungaka is relatively unknown. Gravid females have been observed in October and November, with juveniles sighted in February and March (Table A3). Lifespan, age and size at maturity unknown. Monitoring surveys indicate Kungaka are largely solitary or semi-colonial. Most sightings consist of a single individual; however, the species appears to live in population 'clusters', with individuals often observed in close proximity (within ~10 m) of one another (Table A3). Direct social behaviour has been observed on one occasion when a sub-adult Kungaka was seen sharing a crevice with an adult, possibly suggesting that offspring are tolerated by the parents in some instances (Table A3). Based on repeat sightings of individuals during monitoring surveys, Kungaka home ranges appear to be small with individuals demonstrating a high level of site fidelity. Individual Kungaka have been observed to use the same or nearby sheltering sites across multiple days and survey periods, with movements of up to 42 m recorded between individual sightings (Table A3). Territorial marking behaviour such as 'scat-piling' has not been observed, despite being a common behaviour among members of the tribe Tiliquini (Chapple 2003). Kungaka feed opportunistically on insects and other invertebrates. Individuals have been observed eating crickets, ants and flies (Table A3). Stomach contents of a museum specimen contained unidentified larvae and fragments of a beetle. It is unknown whether plant material forms part of the diet.

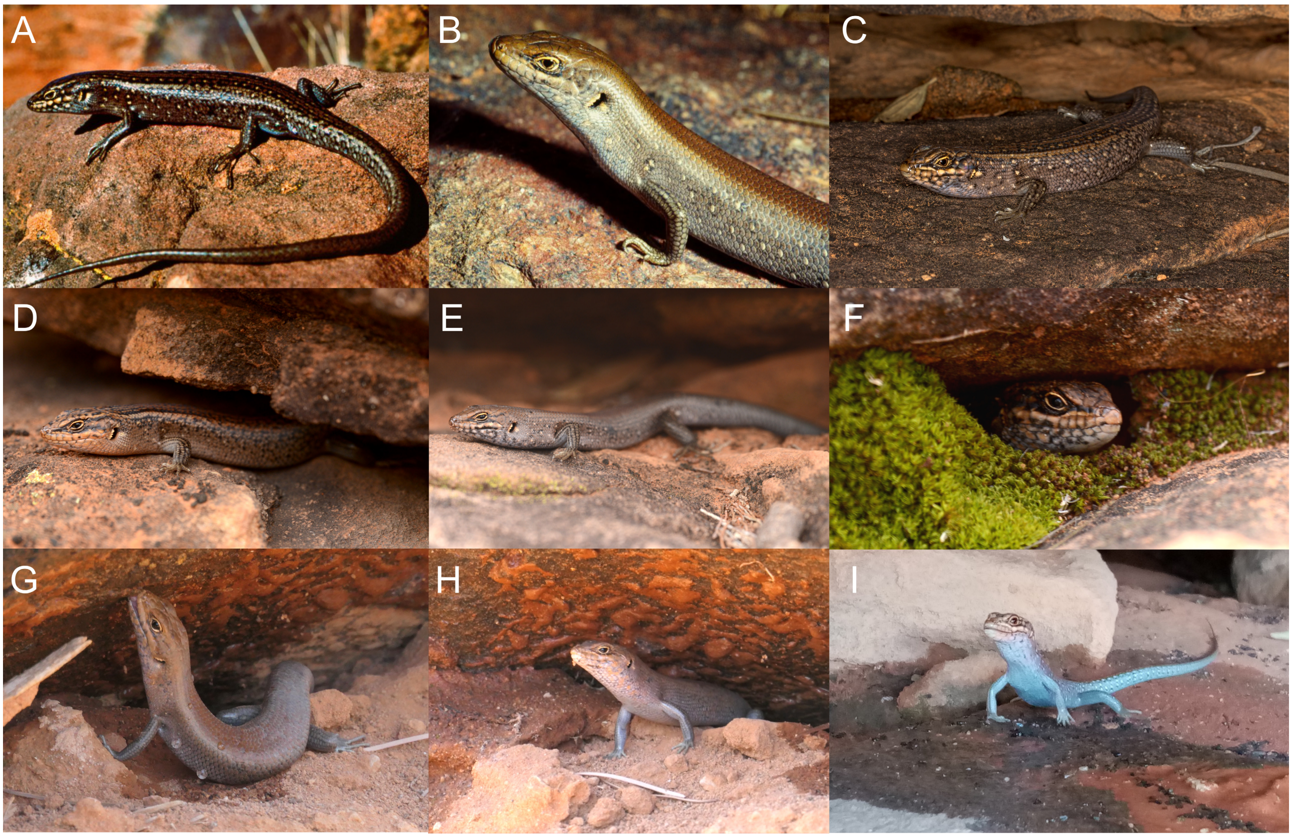

FIGURE 11. Kungaka (*Liopholis mutawintji* **sp. nov.**). All individuals photographed in the Bynguano Range, Mutawintji National Park, New South Wales. Photographs A–B: Gerry Swan; C: Ray Lloyd; D–F: Tom Parkin; G–H: Lyndy Marshall; I (juvenile): Keanu Garni Bates.

Conservation status. Based on population monitoring survey data collected over the past 25 years (Table A3), the Kungaka was found to be eligible for listing as Critically Endangered under multiple IUCN Red List criteria, including: B1ab(i,ii,iii,v), B2ab(i,ii,iii,v), C1, C2a(i) and D1; and as Endangered under Criterion A2bce. The primary justifications for the species' eligibility were a restricted geographic distribution, small population size, extremely low number of mature individuals, and observed and inferred declines in geographic range, population size, and extent and quality of habitat, resulting primarily from habitat degradation by feral goats (*Capra hircus*) and increasingly from climate change, such as the unprecedented drought conditions of 2017–2019 (Bureau of Meteorology 2025). Additional projected threats include predation by feral cats (*Felis catus*), predation by feral foxes (*Vulpes vulpes*), habitat degradation and predation by feral pigs (*Sus scrofa*), loss of genetic diversity due to small and fragmented populations, and human interference from habitat alteration and poaching. A summary of the conservation assessment for the Kungaka against IUCN Red List criteria is provided below.

Criterion A (Population size reduction)—*Outcome*: Endangered under A2bce. *Justification*: Population reduction was inferred under Criterion A2 because the causes of reduction (i.e., habitat degradation by feral goats and climate change) do not appear to have ceased, are not fully understood, and may not be reversible. Population reduction was inferred under subcriterion (b) based on a 72.9% reduction in the mean number of Kungaka observed per survey over 24 years; under subcriterion (c) based on a 72.1% decline in EOO over 13 years; and under subcriterion (e) due to the effects of introduced taxa, namely feral goats, which occur in high densities in Mutawintji National Park and surrounding regions, and have caused severe degradation and fragmentation of Kungaka habitat through trampling and overgrazing of ground cover vegetation, shade trees and shrubs, and displacement of sheltering rocks (Table A3).

Criterion B (Geographic range in the form of AOO and EOO)—*Outcome*: Critically Endangered under B1ab(i,ii,iii,v) and B2ab(i,ii,iii,v). *Justification*: For the assessment of B1, EOO was estimated at 0.493 km^2 based on a minimum convex hull enclosing all validated records for the species dating back to 1992. For B2, AOO was estimated at 8 km^2, based on 2 x 2 km grid cells. The IUCN guidelines state that *if EOO is less than AOO, EOO should be changed to make it equal to AOO to ensure consistent with the definition of AOO as an area within EOO*. Therefore, EOO was scaled up to 8 km^2 to be equal to AOO. Calculations of both EOO and AOO met the distributional thresholds for Critically Endangered under Criterion B1 (<100 km^2) and B2 (<10 km^2). Further, two of the three additional conditions were met: (a) severely fragmented or number locations = 1 (Critically Endangered); and (b) an observed or inferred continuing decline in: (i) EOO, (ii) AOO, (iii) area, extent, and/or quality of habitat, and (v) number of mature individuals, resulting from current and ongoing threats such as feral goats and climate change (Critically Endangered).

Criterion C (Small population size and decline)—*Outcome*: Critically Endangered under C1 and C2a(i). *Justification*: Recent monitoring surveys using individual photograph-identification methods have identified 14 individuals in total, 12 of which are mature, which is well below the threshold of <250 individuals to qualify the taxon for Critically Endangered (Table A3). Subcriterion C1 was met as a continuing decline has been observed based on a 27% decline in the number of mature individuals counted in the population over the past 18 years, meeting the threshold for Critically Endangered. The species also met the conditions for Critically Endangered under sub-criterion C2, based on an observed and inferred continuing decline in EOO, number of mature individuals, and extent and quality of habitat. Further, condition (a)(i) was met given the number of mature individuals in each subpopulation is estimated to be <50.

Criterion D (Very small or restricted population)—*Outcome*: Critically Endangered under D1. *Justification*: Recent monitoring surveys utilising individual photograph identification methods have identified 14 individuals in total, 12 of which are mature, which is well below the threshold of ≤50 mature individuals to qualify the species as Critically Endangered (Table A3).

Criterion E (Quantitative analysis)—*Outcome*: Given the species qualified as Critically Endangered against multiple other criteria, we did not conduct a quantitative analysis under Criteria E.

Discussion

This study presents a comprehensive phylogenetic and morphological assessment of the *Liopholis whitii* species complex, finding strong evidence for taxonomic recognition of three evolutionarily significant lineages. These include *L. compressicauda* and *L. whitii*, which occur in predominantly temperate rocky habitats of south-eastern Australia, and *Liopholis mutawintji* **sp. nov.** which is restricted to rocky habitats of Mutawintji National Park in the arid far western division of NSW. These findings of deep phylogeographic structure further emphasise the role of paleoclimatic changes in shaping present-day diversity within the group, which we discuss further herein.

Historic population isolation of *Liopholis whitii* and *L. compressicauda*

Our findings corroborate those of previous studies which revealed a deep phylogenetic break between southern (*L. whitii*) and northern (*L. compressicauda*) populations of the *L. whitii* complex across the Gippsland Basin in eastern Victoria (Chapple & Keogh 2004; Chapple *et al.* 2005). Based on a rough calibration of 1.3–2.0% mitochondrial sequence divergence per million years, Chapple *et al.* (2005) estimated the split between *L. whitii* and *L. compressicauda* to have occurred during the late Miocene (6.1–9.6 Mya), consistent with a period of heightened global sea levels and marine incursion of the Gippsland Basin. The location of the genetic break between these taxa is concordant with other organisms, such as the frogs *Limnodynastes peronii* (Schauble & Moritz 2001) and *Crinia signifera* (Symula *et al.* 2008), and the skink *Lampropholis guichenoti* (Chapple *et al.* 2011), although only the genetic break in *Liopholis* is reflected in current taxonomy. The Gippsland Basin is a low-lying sandy coastal plain that has been subject to repeated marine incursions since the mid-Tertiary, and it represents one of the major sedimentary basins in southern Australia (Holdgate *et al.* 2014). Inundation of the Gippsland Basin would likely have presented a significant historic barrier to dispersal and gene flow between lowland organisms, as it is bordered to the north and west by the highlands of the Great Dividing Range (GDR). While inundation of coastal habitats in the Gippsland region likely fragmented ancestral populations, contact between *L. whitii* and *L. compressicauda* remains a possibility in the Gippsland coastal strip today; however, the species appear to be patchily distributed and generally uncommon across the region, presumably owing to a lack of typical rocky habitat. Contact in mid to montane elevation areas of the GDR in NSW and VIC also appears possible based on our findings of genetic admixture in the region, although the mountainous topography and presence of multiple major river drainage systems in the region likely present enduring barriers to contemporary dispersal between the taxa.

Plio-Pleistocene sub-structuring within *Liopholis whitii* and *L. compressicauda*

Between the late Pliocene to Pleistocene (~6–0.04 Mya), climatic oscillations fluctuated rapidly between the cool-dry conditions of glacial periods to the warm-wet conditions of interglacials (Bryant & Krosch 2016; Byrne *et al.* 2008; Hewitt 2000, 2004; Pepper & Keogh 2021). These climatic shifts caused major fluctuations in sea levels, resulting in cyclic inundation and exposure of low-lying coastal areas such as the Murray River and Gippsland Basins, and terrestrial land bridges connecting continental Australia with its island territories, such as Tasmania and Kangaroo Island (Lambeck & Chappell 2001; Bryant & Krosch 2016). Further, glacial-interglacial cycles drove repeated expansion, contraction and fragmentation of temperate habitats, isolating taxa during glacial periods and providing opportunities for population expansion and secondary contact during interglacials (Bryant & Krosch 2016; Byrne 2008; Moritz *et al.* 2009). Although full glacial conditions were present only in the most elevated sections of the GDR, periglacial conditions existed throughout most environments above 1000 m elevation during glacial maxima (Barrows *et al.* 2001; Bryant & Krosch 2016).

Our findings of significant phylogeographic sub-structuring within *L. whitii* and *L. compressicauda* are largely consistent with previous studies (Chapple & Keogh 2004; Chapple *et al.*, 2005), and provide further evidence for the impact of glacial-interglacial cycles of the Plio-Pleistocene on historic population fragmentation within the group. We found that sub-structuring within the northern lineage (*L. compressicauda*) was largely associated with fragmentation across the GDR, comparable to Chapple *et al.* (2005), with separate inland and coastal clades, particularly in southern NSW. Inland clades were generally confined to elevated regions along and west of the GDR, suggesting the GDR has been an important biogeographic barrier and possibly amplified the effects of habitat fragmentation during glacial cycles. Our data also aligns with Chapple *et al.* (2005), finding complex sub-structuring in the southern lineage (*L. whitii*). Populations from the South Australian mainland (Adelaide/Mount Lofty Ranges), Kangaroo Island and south-eastern South Australia formed distinct subclades across known biogeographic barriers, including the Murray River Basin and “Backstairs Passage” separating Kangaroo Island from the mainland. Significant phylogenetic breaks across these barriers are reflected in several other organisms across the region, including the frogs: *Crinia signifera* (Symula *et al.* 2008) and *Rawlinsonia* (Parkin *et al.* 2024); skinks: *Acritoscincus duperreyi* (Dubey & Shine 2010; Dissanayake *et al.*, 2022), *Tiliqua rugosa* (Ansari *et al.* 2018), and *Lampropholis guichenoti* (Chapple *et al.* 2011); marsupial dunnart: *Sminthopsis crassicaudata* (Cooper *et al.* 2000); and grasshopper: *Vandiemenella viatica* (Kawakami *et al.* 2009). In addition, eastern Victorian populations formed a subclade with eastern Tasmanian populations, suggesting more recent dispersal and gene flow between populations across Bass Strait during periods of low sea levels, than between mainland populations in eastern and western Victoria.

Isolation of temperate-adapted *Liopholis* in arid and semi-arid western New South Wales

It is well-established that a pattern of intensifying aridity since the mid to late Miocene (~15 Mya) has strongly influenced the biogeographic history of organisms across the Australian arid zone (Byrne *et al.* 2008; Chapple & Keogh 2004; Pepper & Keogh 2021). Many arid zone organisms show phylogenetic signals of mid to late Miocene and early Pliocene (20–2.5 Mya) radiation and diversification consistent with widespread contraction of temperate vegetation from inland areas (Byrne *et al.* 2008; Martin 2006; Pepper & Keogh 2021). Although the timing of aridification was not uniform across the arid zone, a broad drying trend commenced in the Miocene and was followed by an abrupt return to warm and wet conditions in the early Pliocene (~5–3 Mya), with aridification intensifying even further during glacial-interglacial cycling of the Pleistocene, ~800 Kya (Byrne *et al.* 2008; Pepper & Keogh 2021; Sniderman *et al.* 2016). During the Cenozoic era, the vegetation of inland Australia consisted of extensive tracts of warm temperate to subtropical rainforest; however, by the late Miocene, rainforests had been largely replaced by dry open woodlands and chenopod shrublands (Byrne *et al.* 2008; Martin 2006; Pepper & Keogh 2021). Phylogenetic studies have also highlighted the rocky uplands of the arid zone as containing significantly higher levels of endemism and diversity than the surrounding lowlands, suggesting they have provided relatively stable climatic refugia during periods of extreme aridity (Byrne *et al.* 2008; Chapple & Keogh 2004; Farquhar *et al.* 2024; Pepper & Keogh 2021).

The persistence of several temperate-adapted *Liopholis* species in disjunct, relatively mesic rocky refugia of the arid zone is evidence that ancestral populations of these taxa were more widespread in the past, with their distributions likely tracking the retreat of temperate vegetation across the continent (Chapple & Keogh 2004; Farquhar *et al.* 2024). Our analysis of nuclear SNP diversity found the Kungaka (*Liopholis mutawintji* **sp. nov.**) to represent a deeply divergent population lineage, with its origins appearing to pre-date the Pleistocene as previously suggested based on mitochondrial gene markers (Chapple & Keogh 2004; Chapple *et al.* 2005). Based on relative levels of divergence in nuclear SNP markers, we consider it plausible that ancestral populations of Kungaka became isolated in rocky outcrops of the Bynguano Range with the onset of widescale aridification across the region between the late Miocene-early Pliocene; however, we do not provide a formal molecular clock analysis and so the precise timing of the population's vicariance remains unresolved.

Our finding that the disjunct population of *L. modesta* from Yathong Nature Reserve in the semi-arid zone of western New South Wales was nested among the other samples of *L. modesta* from the GDR (Fig 2/B), suggests a more recent history of population fragmentation compared to the Kungaka. The semi-arid margins of the arid zone are thought to have been subject to more highly variable climate fluctuations than areas further inland, which likely provided additional, more recent opportunities for population expansion and fragmentation during the Pleistocene (Pepper & Keogh 2021).

Conservation priorities for the Kungaka, *Liopholis mutawintji* sp. nov.

The Kungaka is currently listed as an 'Endangered Population' of *L. whitii* under the NSW Biodiversity Conservation Act 2016 (NSW Threatened Species Scientific Committee 2005a,b) and is not listed under the Environment Protection and Biodiversity Conservation Act 1999. Formal taxonomic recognition as a distinct species now qualifies the Kungaka for reassessment under both state and federal legislation, with a higher priority status of Critically Endangered supported by our provisional conservation assessment.

Field surveys indicate the Kungaka has a highly restricted geographic distribution (EOO—0.493 km^2; AOO—8 km^2) within a single location in the Bynguano Range, Mutawintji National Park (NSW National Parks & Wildlife Service 2000; Swan & Foster 2000; Swan & Foster 2005; Table A3). Mark-recapture surveys suggest the Kungaka is among the most threatened reptile species in Australia, with recent photograph-identification surveys detecting only fourteen individuals in total (twelve mature) since October 2024 (Table A3). Further, monitoring surveys over the past 25 years have documented significant observed and inferred declines in geographic range, population size, and extent and quality of habitat (Table A3).

The primary threat faced by the Kungaka is habitat loss and degradation from overgrazing and trampling of vegetation and sheltering sites by feral goats, which occur in high densities in Mutawintji National Park and more broadly across western NSW (NSW National Parks & Wildlife Service 2000; Table A3). Additional significant threats include predation by feral cats, foxes, habitat degradation and predation by feral pigs, loss of genetic diversity due to small and fragmented populations, and human interference from habitat alteration and poaching (NSW National Parks & Wildlife Service 2000; Table A3). Climate change remains a significant long-term threat due to the species' highly restricted range, low dispersal capability and preference for relatively sheltered rocky habitat in an otherwise hot and dry landscape. Climate change projections for far western New South Wales forecast temperature increases of 1.4°C by 2090 under a low emissions scenario, and up to 4.2°C under a high emissions scenario. The numbers of hot days may increase by 19.6–30.4 days each year. Rainfall will decrease by 15–20%. The warmest year on record (in both average and maximum temperature) for far western NSW was 2019, which was 1.1°C above the 1990–2009 average (Department of Climate Change, Energy, the Environment and Water 2024). In addition, the three years of drought from 2017–2019 were the driest on record for far western NSW (Bureau of Meteorology 2025). A climate change vulnerability assessment of Australian skinks found arid zone species to be especially vulnerable to current and future climate impacts (Cabrelli & Hughes 2015). Increases in temperature and decreases in rainfall are expected to affect species with narrow thermal and water tolerances, compromising their ability to maintain body temperatures in their preferred range, likely resulting in physiological stress, poorer body condition and reduced rates of reproduction and survival (Cabrelli & Hughes 2015). Behavioural responses of species, such as excavating deeper burrows and changing daily and seasonal activity patterns, may buffer some impacts of climate change; however, increased time spent sheltering from temperature extremes may result in a reduction in time spent foraging (Cabrelli & Hughes 2015).

Considering these significant and compounding threats, a coordinated conservation response is required to prevent further decline and potential extinction of the Kungaka. Priority actions include: (1) nomination of the Kungaka for priority listing as Critically Endangered under both state and federal legislation; (2) ongoing monitoring of known populations to assess trends in population size, distribution and recruitment; (3) targeted surveys to detect any additional extant populations within Mutawintji National Park and surrounding regions; (4) mitigation of key threatening processes, particularly feral goats, through active management and control programs; and (5) consideration of *ex situ* conservation options, including establishment of a captive or semi-wild insurance population for potential future reintroductions.

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Data availability/supplementary materials

SNP data report is available from the corresponding author on reasonable request.

Supplementary Table S1: Morphological data (unadjusted, and logged-transformed), LDA results—uploaded to www.zenodo.org; doi: 10.5281/zenodo.18324928.

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Appendix

TABLE A1. Collection locality data for genotyped *Liopholis* samples examined in this study. Source museum/university codes: ABTC—Australian Biological Tissue Collection; AMS—Australian Museum; NMV—Museums Victoria; MAGNT—Museum and Art Gallery of the Northern Territory; UTAS—University of Tasmania. Locality abbreviations: NP—National Park; APY—Anangu Pitjantjatjara Yankunytjatjara; SF—State Forest; IPA—Indigenous Protected Area; CP—Conservation Park; NR—Nature Reserve. Latitude and longitude data is not included for threatened species.

Source	RegNum	Locality	State	Population	Latitude	Longitude
***Liopholis mutawintji* sp. nov.**						
ABTC	ABTC58207	Bynguano Range, Mutawintji NP	NSW	13	-	-
ABTC	ABTC71452	Bynguano Range, Mutawintji NP	NSW	13	-	-
ABTC	ABTC71453	Bynguano Range, Mutawintji NP	NSW	13	-	-
ABTC	ABTC71454	Bynguano Range, Mutawintji NP	NSW	13	-	-
ABTC	ABTC76275	Bynguano Range, Mutawintji NP	NSW	13	-	-
ABTC	ABTC76368	Bynguano Range, Mutawintji NP	NSW	13	-	-
ABTC	ABTC76369	Bynguano Range, Mutawintji NP	NSW	13	-	-
ABTC	ABTC76370	Bynguano Range, Mutawintji NP	NSW	13	-	-
ABTC	ABTC76371	Bynguano Range, Mutawintji NP	NSW	13	-	-
ABTC	ABTC76372	Bynguano Range, Mutawintji NP	NSW	13	-	-
ABTC	ABTC76373	Bynguano Range, Mutawintji NP	NSW	13	-	-
AMS	R.180630.001	Bynguano Range, Mutawintji NP	NSW	13	-	-
Liopholis aputja						
ABTC	ABTC42404	Amata, APY Lands	SA	-	-26.256	131.493
NMV	Z79473	Alalkanya Gorge, Musgrave Ranges	SA	-	-26.163	132.117
Liopholis compressicauda						
ABTC	ABTC16267	Jindabyne	NSW	12	-36.42	148.62
ABTC	ABTC16268	Jindabyne	NSW	12	-36.42	148.62
ABTC	ABTC16269	Jindabyne	NSW	12	-36.42	148.62
ABTC	ABTC16270	Jindabyne	NSW	12	-36.42	148.62
ABTC	ABTC17273	Sawpit Creek	NSW	12	-36.35	148.55
ABTC	ABTC17274	Sawpit Creek	NSW	12	-36.35	148.55
ABTC	ABTC40976	Cooma	NSW	12	-36.25	149.12
ABTC	ABTC40977	Cooma	NSW	12	-36.25	149.12
ABTC	ABTC40978	Cooma	NSW	12	-36.25	149.12
AMS	R.148208.001	Riamukka SF	NSW	7	-31.34	151.708
AMS	R.148212.001	Walcha	NSW	7	-31.345	151.521
AMS	R.148377.001	Gibraltar Range NP	NSW	7	-29.533	152.324
AMS	R.149565.001	Blue Mountains NP	NSW	5	-33.767	150.429
AMS	R.152127.001	Mt Kaputar NP	NSW	8	-30.271	150.166
AMS	R.156561.001	Denman	NSW	5	-32.386	150.658
AMS	R.157166.001	Emmaville	NSW	7	-29.338	151.604

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TABLE A1. (Continued)

Source	RegNum	Locality	State	Population	Latitude	Longitude
AMS	R.159615.001	Ebor	NSW	7	-30.397	152.287
AMS	R.159616.001	Ebor	NSW	7	-30.397	152.287
AMS	R.159679.002	Glen Innes	NSW	7	-29.511	152.049
AMS	R.167313.001	Kosciuszko NP	NSW	12	-35.934	148.629
AMS	R.167314.001	Kosciuszko NP	NSW	12	-35.934	148.629
AMS	R.174811.001	Ku-ring-gai Chase NP	NSW	4	-33.656	151.154
AMS	R.177102.001	Kosciuszko NP	NSW	10	-35.673	148.425
AMS	R.177103.001	Kosciuszko NP	NSW	10	-35.673	148.425
AMS	R.177104.001	Kosciuszko NP	NSW	10	-35.673	148.425
AMS	R.180636.001	Ebor	NSW	7	-30.48	152.3
AMS	R.181769.001	Kanangra-Boyd NP	NSW	9	-33.971	150.056
AMS	R.181770.001	Warrumbungle NP	NSW	6	-31.326	148.992
AMS	R.181772.001	Kanangra-Boyd NP	NSW	9	-33.832	150
AMS	R.181774.001	Brindabella Ranges	ACT	11	-35.37	148.82
AMS	R.181775.001	Warrumbungle NP	NSW	6	-31.33	148.98
AMS	R.181776.001	Kanangra-Boyd NP	NSW	9	-33.832	150
AMS	R.185858.001	Coolah Tops NP	NSW	5	-31.697	150.018
AMS	R.185868.001	Coolah Tops NP	NSW	5	-31.821	150.205
AMS	R.188483.001	Mummel Gulf NP	NSW	7	-31.315	151.866
AMS	R.192423.001	Carrai Plateau NP	NSW	7	-30.883	152.23
AMS	R.193393.001	Tianjara	NSW	3	-35.102	150.272
AMS	R.193394.001	Tianjara	NSW	3	-35.102	150.272
AMS	R.193395.001	Bombala	NSW	2	-36.922	149.251
AMS	R.193396.001	Bombala	NSW	2	-36.922	149.251
AMS	R.193468.001	Mallacoota	VIC	1	-37.529	149.74
AMS	R.193469.001	Mallacoota	VIC	1	-37.529	149.74
AMS	R.203029.001	Malabar Headland NP	NSW	4	-33.966	151.261
AMS	R.203030.001	Malabar Headland NP	NSW	4	-33.966	151.261
NMV	Z10255	Cooma	NSW	12	-36.48	149.1
NMV	Z10256	Cooma	NSW	12	-36.48	149.1
NMV	Z10257	Cooma	NSW	12	-36.48	149.1
NMV	Z10280	Genoa	VIC	1	-37.528	149.626
NMV	Z10281	Genoa	VIC	1	-37.528	149.626
NMV	Z57459	East Gippsland	VIC	1	-37.512	149.957
NMV	Z60421	East Gippsland	VIC	1	-37.512	149.957
Liopholis guthega						
AMS	R.148527.001	Kosciuszko NP	NSW	-	-	-
AMS	R.148528.001	Kosciuszko NP	NSW	-	-	-
AMS	R.148529.001	Kosciuszko NP	NSW	-	-	-
AMS	R.148530.001	Kosciuszko NP	NSW	-	-	-
AMS	R.148531.001	Kosciuszko NP	NSW	-	-	-
AMS	R.148532.001	Kosciuszko NP	NSW	-	-	-

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TABLE A1. (Continued)

Source	RegNum	Locality	State	Population	Latitude	Longitude
Liopholis margaretae						
MAGNT	TS1426	Kings Canyon, Watarrka NP	NT	-	-24.256	131.579
MAGNT	TS1427	Kings Canyon, Watarrka NP	NT	-	-24.256	131.578
MAGNT	TS1428	Kings Canyon, Watarrka NP	NT	-	-24.256	131.579
MAGNT	TS1429	Ormiston Gorge, Tjoritja/West Macdonnell NP	NT	-	-23.635	132.732
Liopholis modesta						
AMS	R.152071.001	Moonbi Lookout, Moonbi Ranges	NSW	-	-30.993	151.083
AMS	R.153861.001	9.9 km N Liston	NSW	-	-28.585	152.1
AMS	R.154251.001	Warialda SF	NSW	-	-29.691	150.602
AMS	R.157214.001	Tenterfield	NSW	-	-29.116	151.887
AMS	R.184902.001	Merrimerriwa Range, Yathong NR	NSW	-	-32.637	145.657
AMS	R.184903.001	Merrimerriwa Range, Yathong NR	NSW	-	-32.629	145.659
AMS	R.193187.001	Muswellbrook	NSW	-	-32.234	150.952
Liopholis montana						
ABTC	ABTC106157	Mount Bogong, Alpine NP	VIC	-	-	-
ABTC	ABTC16385	Mount Gingera, Namadgi NP	ACT	-	-	-
ABTC	ABTC16386	Mount Ginini, Namadgi NP	ACT	-	-	-
ABTC	ABTC17272	Rennex Gap, Kosciuszko NP	NSW	-	-	-
AMS	R.177157.001	High Plains, Kosciuszko NP	NSW	-	-	-
NMV	Z10277	Jagumba Range, Kosciuszko NP	NSW	-	-	-
Liopholis personata						
ABTC	ABTC38949	Mount Fitton, northern Flinders Ranges	SA	-	-30.028	139.511
ABTC	ABTC53880	Devils Peak, southern Flinders Ranges	SA	-	-32.4	138
ABTC	ABTC57664	Moro Gorge, Nantawarrina IPA	SA	-	-30.68	139.22
ABTC	ABTC70482	Telowie Gorge	SA	-	-33.026	138.102
ABTC	ABTC87159	Wilpena Pound, Flinders Ranges	SA	-	-31.619	138.593
Liopholis whitii						
ABTC	ABTC11485	Freycinet Peninsula	TAS	17	-42.21	148.305
ABTC	ABTC12874	Highlands	VIC	20	-37.05	145.4
ABTC	ABTC14282	Penola SF	SA	16	-37.33	140.92
ABTC	ABTC14779	Cherry Gardens	SA	15	-35.07	138.67
ABTC	ABTC15705	Mylor	SA	15	-35.07	138.73
ABTC	ABTC17171	Kangaroo Island	SA	14	-36.015	137.014
ABTC	ABTC23048	Flinders Island	TAS	17	-39.984	148.053
ABTC	ABTC23051	Flinders Island	TAS	17	-39.984	148.053
ABTC	ABTC23052	Flinders Island	TAS	17	-39.984	148.053
ABTC	ABTC23055	4 km S Bracknell	TAS	17	-41.686	146.939
ABTC	ABTC23057	4 km S Bracknell	TAS	17	-41.686	146.939

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TABLE A1. (Continued)

Source	RegNum	Locality	State	Population	Latitude	Longitude
ABTC	ABTC33448	Kelly Hill CP, Kangaroo Island	SA	14	-36.021	136.856
ABTC	ABTC33468	Flinders Chase NP, Kangaroo Island	SA	14	-36.065	136.703
ABTC	ABTC33582	Kangaroo Island	SA	14	-35.801	137.782
ABTC	ABTC33708	Kangaroo Island	SA	14	-35.98	137.33
ABTC	ABTC37428	Penambol CP	SA	16	-37.972	140.893
ABTC	ABTC37466	Wattle Range	SA	16	-37.431	140.625
ABTC	ABTC40844	Stonyford	VIC	21	-38.328	143.283
ABTC	ABTC40886	Beech Forest	VIC	21	-38.638	143.595
ABTC	ABTC54131	Kangaroo Island	SA	14	-35.8	138.07
ABTC	ABTC54286	Piccanninie Ponds CP	SA	16	-38.05	140.95
ABTC	ABTC54287	Blanche Bay	SA	16	-38.03	140.62
ABTC	ABTC54390	Humbug Scrub	SA	15	-34.7	138.82
ABTC	ABTC58045	Deep Creek CP	SA	15	-35.632	138.276
ABTC	ABTC58695	Newland Head CP	SA	15	-35.62	138.5
ABTC	ABTC74280	Black Hill CP	SA	15	-34.882	138.724
ABTC	ABTC74491	Echunga	SA	15	-35.114	138.726
ABTC	ABTC79673	Cromer CP	SA	15	-34.774	138.979
ABTC	ABTC94846	Spring Mount CP	SA	15	-35.448	138.527
ABTC	ABTC94883	Mount Billy	SA	15	-35.45	138.601
ABTC	ABTC94884	Waitpinga Hill	SA	15	-35.633	138.473
ABTC	ABTC95043	Deep Creek CP	SA	15	-35.611	138.265
UTAS	BP04	Bushy Park	TAS	17	-42.678	146.76
UTAS	GB03	Greens Beach	TAS	17	-41.082	146.738
UTAS	PA02	Palana, Flinders Island	TAS	17	-39.756	147.871
UTAS	UTAS10	Binnalong Bay	TAS	17	-41.255	148.319
NMV	Z10273	Phillip Island	VIC	21	-38.48	145.25
NMV	Z10274	Mandurang SF	VIC	21	-36.83	144.25
NMV	Z10275	Cannibal Creek Reserve, West Gippsland	VIC	21	-38.05	145.72
NMV	Z10283	Sunset Peak, Cape Conran CP	VIC	18	-37.807	148.732
NMV	Z10284	Sunset Peak, Cape Conran CP	VIC	18	-37.807	148.732
NMV	Z10285	Lake Tyers Beach	VIC	18	-37.866	148.065
NMV	Z10287	Wilsons Promontory NP	VIC	18	-39.025	146.318
NMV	Z11240	Seaford	VIC	21	-38.1	145.15
NMV	Z22362	Grampians NP	VIC	21	-37.172	142.515
NMV	Z22377	Grampians NP	VIC	21	-37.172	142.515
NMV	Z60746	Mount Buffalo	VIC	19	-36.708	146.824

TABLE A2. Definitions of the morphological measurements and scale counts used in this study. All measurements taken with digital vernier callipers to 0.1 mm accuracy unless otherwise stated.

Character	Definition
SVL	Snout-to-vent length; from tip of snout to posterior edge of cloacal scale. Measured by flattening the specimen straight against a flat ruler. Measured to 1 mm accuracy.
TL	Tail length; from posterior edge of cloacal scale to tip of tail. Only measured for complete original tails. Measured by straightening tail against a flat ruler. Measured to 1 mm accuracy.
AGL	Axilla-groin length; from anterior crease of hindlimb to posterior crease of the forelimb, with the limbs held at right angles to the body axis.
HL	Head length; from anterior edge of ear opening to tip of snout.
HW	Head width; distance across the temporal region, level with the centre of the ear opening.
HD	Head depth; distance from the top of the head to bottom of the lower jaw, measured level with centre of the ear opening, with the mouth held closed if preserved in an open position.
SnL	Snout length; from tip of snout to anterior canthus of the eyelids.
AntL	Antebrachium (forearm) length; measured from the base of the wrist (defined by the termination of palmar scales) to the posterior edge of the elbow when held at a right angle.
CrusL	Crus (lower hind limb) length; measured from the posterior edge of the foot to the posterior edge of the knee when held at a right angle.
MBSR	Mid-body scale rows; counted diagonally at halfway point between the axilla and groin around the entire circumference of the body.
PVS	Paravertebral scales; counted in one line from the posterior margin of the parietals to the beginning of the hindlegs.
SupLab	Supralabials; count of scales bordering the upper lip, counted as a series beginning at the scale adjoining the rostral to the last scale above the commissure of the mouth when closed.
InfLab	Infralabials; count of scales bordering the lower lip, counted as a series beginning at the scale adjoining the mental to the last scale below the commissure of the mouth when closed.
SupCil	Supraciliaries; count of scales, beginning with the scale adjoining the prefrontal and loreal and ending with the scale still contacting ciliaries and last supraocular.
4FLam	Subdigital lamellae under the fourth finger, beginning with the scale adjoining the claw and extending to the last large scale distinguishable from the palmar scales.
4TLam	Subdigital lamellae under the fourth toe, beginning with the scale adjoining the claw and extending to the last large scale distinguishable from the plantar scales.

TABLE A3. Kungaka (*Liopholis mutawintji* **sp. nov.**) survey and monitoring reports (unpublished).

Authors/surveyors	**Year**	**Report title**
Bonnett, M. & Swan, G.	2001	Survey for the Centralian Ranges Rock-Skink (*Egernia margaretae*) in Western New South Wales. Unpublished report. Cygnet Surveys and Consultancy, St Ives, NSW.
Swan, G. & Marshall, L.	2019	White's Skink (*Liopholis whitii*) at Mutawintji National Park: April 2019. Unpublished report. Cygnet Surveys and Consultancy, St Ives, NSW.
Swan, G. & Marshall, L.	2019	White's Skink (*Liopholis whitii*) at Mutawintji National Park: October 2019. Unpublished report. Cygnet Surveys and Consultancy, St Ives, NSW.
Swan, G. & Marshall, L.	2020	White's Skink (*Liopholis whitii*) at Mutawintji National Park: February-May 2020. Unpublished report. Cygnet Surveys and Consultancy, St Ives, NSW.
Swan, G., Marshall, L. & Bates, K.	2020	White's Skink (*Liopholis whitii*) at Mutawintji National Park: October-November 2020. Unpublished report. Cygnet Surveys and Consultancy, St Ives, NSW.
Swan, G., Marshall, L. & Bates, K.	2021	White's Skink (*Liopholis whitii*) searches at Mutawintji National Park: March 2021. Unpublished report. Cygnet Surveys and Consultancy, St Ives, NSW.

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TABLE A3. (Continued)

Authors/surveyors	**Year**	**Report title**
Swan, G., Marshall, L. & Bates, K.	2022	Kungaka (*Liopholis whitii*) at Mutawintji National Park: February 2022. Unpublished report. Cygnet Surveys and Consultancy, St Ives, NSW.
Bates, K., Hunter, R. & Marshall, L.	2023	Kungaka, (*Liopholis whitii*) at Mutawintji National Park: March 2023. Unpublished report.
Bates, K. & Marshall, L.	2024	Kungaka (*Liopholis sp.*) at Mutawintji National Park: May 2024. Unpublished report.
Bates, K., Hunter, R., Swan, G., Parkin, T., Parkin, B., Thompson, N. & Marshall, L.	2024	Kungaka (*Liopholis spp*.) at Mutawintji National Park: October 2024. Unpublished report.
Hunter, R., Imisides, Z. & Marshall, L.	2024	Kungaka (*Liopholis spp.*) surveys at Mutawintji National Park: November 2024. Unpublished report.
Hunter, R., Imisides, Z., Bates, K., Thomas, G. & Marshall, L.	2024	Kungaka (*Liopholis spp*.) surveys at Mutawintji National Park: December 2024. Unpublished report.
Hunter, R. & Marshall, L.	2025	Kungaka (*Liopholis spp*.) surveys at Mutawintji National Park: January 2025. Unpublished report.
Hunter, R., Bates, K., Imisides, Z. & Marshall, L.	2025	Kungaka (*Liopholis spp*.) surveys at Mutawintji National Park: February 2025. Unpublished report.
Marshall, L.	2025	Kungaka (*Liopholis spp.*) at Mutawintji National Park: October 2024–May 2025. Unpublished report.