Zootaxa 5437 (3): 336–362
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5437.3.2
http://zoobank.org/urn:lsid:zoobank.org:pub:49565730-9EA2-4231-B974-89A0321D6200

Morphological and genetic data challenge species and subspecies in the *Lerista microtis* group (Squamata: Scincidae)

JULES E. FARQUHAR[1,4*], IVAN PRATES[2,5], PAUL DOUGHTY[3], DANIEL L. RABOSKY[2,6] & DAVID G. CHAPPLE[1,7]

[1]*School of Biological Sciences, Monash University, Clayton, Victoria, Australia.*
[2]*Museum of Zoology & Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor MI USA.*
[3]*Collections & Research, Western Australian Museum, Welshpool, WA 6106, Australia.*
paul.doughty@museum.wa.gov.au; https://orcid.org/0000-0003-0631-0571
[4] *jules.farquhar@monash.edu; https://orcid.org/0000-0002-1894-7580*
[5] *ivanprates@gmail.com; https://orcid.org/0000-0001-6314-8852*
[6] *drabosky@umich.edu; https://orcid.org/0000-0002-7499-8251*
[7] *david.chapple@monash.edu; https://orcid.org/0000-0002-7720-6280*
**Corresponding author*

Abstract

The subspecies rank has been widely applied by taxonomists to capture infraspecific variation within the Linnaean classification system. Many subspecies described throughout the 20th century were recognised largely based on perceived variation in single morphological characters yet have since been found not to correspond to separately evolving population lineages, thus requiring synonymy or elevation to full species under lineage-based views of species. These modern lineage-based taxonomic resolutions have resulted from a combination of new molecular genetic techniques, improved geographical sampling of specimens, and more sophisticated analyses of morphological variation (e.g., statistical assessments rather than solely univariate descriptive ones). Here, we revisit the current taxonomic arrangement of species-level and subspecific taxa in the *Lerista microtis* (Gray) group, which is distributed along a narrow ~2000 km strip on the southern coast of Australia. From specimens of the *L. microtis* group, an additional species (*Lerista arenicola*) and two additional subspecies (*L. m. intermedia* and *L. m. schwaneri*) were described. We collected data on mensural, meristic, and colour pattern characters to explore morpho-spatial relationships among these taxa. Although our morphological analyses revealed some distinctiveness among specimens from locations assigned to each taxon, this variation is continuous along Australia's southern coastline, assuming the form of a geographic cline rather than discrete forms. For many characters, however, spatial patterns were inconsistent with the original descriptions, particularly of the subspecies. Moreover, analysis of genome wide restriction-associated DNA loci revealed multiple instances of paraphyly among taxa, with phylogenetic clustering of specimens assigned to distinct species and subspecies. These emerging patterns provide no support for *L. arenicola* as a species evolving separately from *L. microtis*. Additionally, our findings challenge the presumed distinctiveness and coherence of the three subspecies of *L. microtis*. We thus synonymise *L. arenicola* and the *L. microtis* subspecies with *L. microtis* and provide a redescription of a single yet morphologically variable species—an arrangement that best reflects evolutionary history and the continuous nature of morphological variation across space.

Key words: Australia, clinal variation, colour pattern, mitochondrial and nuclear DNA, Reptilia, south-coast five-toed slider, subspecies, taxonomy

Introduction

Evolutionary proccesses tend to create continuous variation (Darwin 1859), which presents difficulties for those attempting to fit categorical classification schemes to organisms (de Queiroz 1998; Remsen 2010). Occasional or ongoing introgression between lineages is now known to be common, and hence the condition of complete reproductive separation among lineages is not as ubiquitous as once thought under the biological species concept (Jackson *et al*. 2017; Wang *et al*. 2019; de Queiroz 2020; Pulido-Santacruz *et al*. 2020). While modern biologists

 Accepted by A. Datta-Roy: 20 Mar. 2024; published: 15 Apr. 2024

have increasingly found consensus in the broad concept that species are segments of population-level evolutionary lineages, the existence of incomplete lineage separation creates 'gray zones' in speciation. As a result, there is considerable debate regarding where the limits between species should be drawn (de Queiroz 1998; Burbrink *et al*. 2022).

Within species, phenotypically distinct populations in different geographic regions are common, especially in widespread species. As a means of capturing this variation in the taxonomic classification system, researchers have sometimes applied the rank of subspecies (Smith & White 1956; Mayr 1965, 1982; Patten 2015). Some authors have noted, however, that subspecies are typically recognised based solely on one or few conspicuous yet arbitrary phenotypic characters that, under integrative analyses of phenotypic and genetic variation, have been often found to be uncorrelated to evolutionary lineage divergence (Zink 2004; Bradby *et al*. 2012; de Queiroz 2020; Prates *et al*. 2022). Furthermore, the conceptual definitions of subspecies are numerous and inconsistent (Reydon & Kunz 2021; Burbrink *et al*. 2022), and the criteria for delimiting the boundaries between subspecies are usually subjective (Wilson & Brown 1953; Bradby *et al*. 2012). As such, there has been extensive debate over the utility of the subspecies rank in recent years (e.g., Hillis 2019, 2020, 2021, 2022; de Queiroz 2020, 2021; Padial & De la Riva 2020; Hillis & Wüster 2021; Burbrink *et al*. 2022). Some researchers assert that, by being population-level lineages, subspecies and species are the same thing (de Queiroz 2020; Burbrink *et al*. 2022). In this view, there may be no meaningful reason to recognise subspecies in taxonomy, with the species rank occupying the lowest rung of the taxonomic hierarchy. In turn, some authors hold that morphologically diagnosed subspecies need not correspond to evolutionary lineages (Patton & Conroy 2017), or that subspecies should be recognised because doing so affords conservation attention to phenotypically unique or threatened populations (Haig *et al*. 2006; Bradby *et al*. 2012).

Despite the apparent decreasing popularity of the subspecies category at least in certain taxonomic groups (de Queiroz 2020; Burbrink *et al*. 2022), there still exists a large number of recognised trinomial names. For example, of the world's 11,940 reptile species, 936 have a total of 2,158 recognised subspecific names (Uetz *et al*. 2022). It remains unclear how many of these subspecies actually correspond to evolutionary lineages, given that many have been described based on somewhat arbitrary divisions of single morphological character clines in the past (Zink 2004). Defining subspecies based on the congruence of both morphological and molecular distinctiveness offers a more comprehensive means of testing the evolutionary coherence of populations presently recognised as taxa (Zink 2004; Patten *et al*. 2015). Despite the subjectivity of the criteria used in traditional subspecies delimitations, subspecies in the historical literature can be seen as taxonomic hypotheses about inferred evolutionary relationships, which modern researchers can test using more comprehensive datasets and methods. Indeed, contemporary genetic analyses have revealed that many traditionally defined subspecies—which were described based largely on their morphological distinctiveness—either: (1) do not constitute phylogenetic lineages, hence requiring invalidation under views of subspecies as evolutionary coherent units (e.g., Brenneman *et al*. 2016; Prates *et al*. 2022), or (2) *do* constitute phylogenetic lineages, and thus would require elevation to full species (e.g., Kealley *et al*. 2020). However, in the case of populations that are not phylogenetically independent, but which are morphologically *and* geographically distinct, some authors would give such entities nomenclatural and taxonomic recognition. For example, the Carnarvon Basin dwarf skink *Menetia surda creswelli* (Aplin & Adams 1998) and the western stone gecko *Diplodactylus granariensis rex* (Hutchinson *et al.* 2009) from Australia are both recognised as subspecific taxa based on geographic and morphological distinctiveness.

By the end of his career, the late Glen M. Storr (1921–1990), curator of ornithology and herpetology at the Western Australia Museum, had described 180 species and 50 subspecies of reptiles (Smith 1991), ranking him as one of the world's most prolific describers of reptile taxa (Uetz & Stylianou 2018). His research included many taxonomic works on Australian scincid lizards, including those of Australia's second-most speciose genus of skinks, *Lerista* Bell, 1833 (currently 97 species). Many of these descriptions were based on the limited numbers of specimens and geographic locations available at the time, and often emphasized differences in scalation or colour pattern that now appear minute based on increased sampling (e.g., Storr 1972, 1978, 1991a,b,c). Recent analyses of some taxa described by Storr have failed to recover their presumed morphological coherence and distinctiveness partly as a result of unclear and inconsistent character differences between populations (Prates *et al.* 2002; Maryan *et al.* 2020; Nankivell *et al.* 2023). Arguably, lack or inconclusive evidence of morphological distinction is more problematic for subspecies than for species taxa. "Cryptic species" can show little to no differences in morphology but still be supported as divergent evolutionary lineages based on genetic evidence (de Queiroz 1998). By contrast, subspecies cannot be morphologically cryptic, as the fundamental role of traditional subspecies is to denote morphologically

distinctive populations (Prates *et al.* 2022). As such, a combined reassessment of morphological and genetic variation might be necessary to confirm the scenario of concomitant morphological divergence and genetic interdependence required to justify recognizing subspecific taxa.

Previous authors have mostly used an apparent spatial clustering in morphological characters to justify partitioning populations into subspecies. However, these supposedly distinct populations often appear to reflect incompleteness of spatial sampling rather than discrete morphological distinctiveness (Kealley *et al*. 2020; Prates *et al*. 2022). Using an integrative taxonomic approach, we combine new genetic data with detailed quantitative morphological analyses to test the distinctiveness of currently recognized species- and subspecies-level taxa in the *Lerista microtis* group (Fig. 1). Our working definition of species understands them to be population lineages that are genetically distinct and separately evolving, with or without morphological distinction. Under this definition, individuals may look similar morphologically yet belong to different species based on genomic evidence of their evolutionary divergence. Morphological distinctions among species may be treated as helpful diagnostic markers once evolutionary relationships are known, but they should not be interpreted as primary evidence of evolutionary differences when deliminating species. In turn, we understand subspecies to correspond to populations that are not phylogenetically divergent but which may warrant nomenclatural and taxonomic recognition given evidence of spatially segregated morphological distinction. We emphasise the dual condition of morphological and geographic distinction because this is the criterion implicitly or explicitly captured by most decisions to recognize subspecies. Under this view, a morphologically distinct population that is nevertheless contained within a spatial pattern of clinal variation and overlaps significantly with neighbouring morphs should not be considered a subspecies, as such continuous variation cannot be objectively partitioned within a classification system (Mayr 1963; Owen 1963a, b; Wilson & Brown 1953; Hillis 2022; Prates *et al*. 2022).

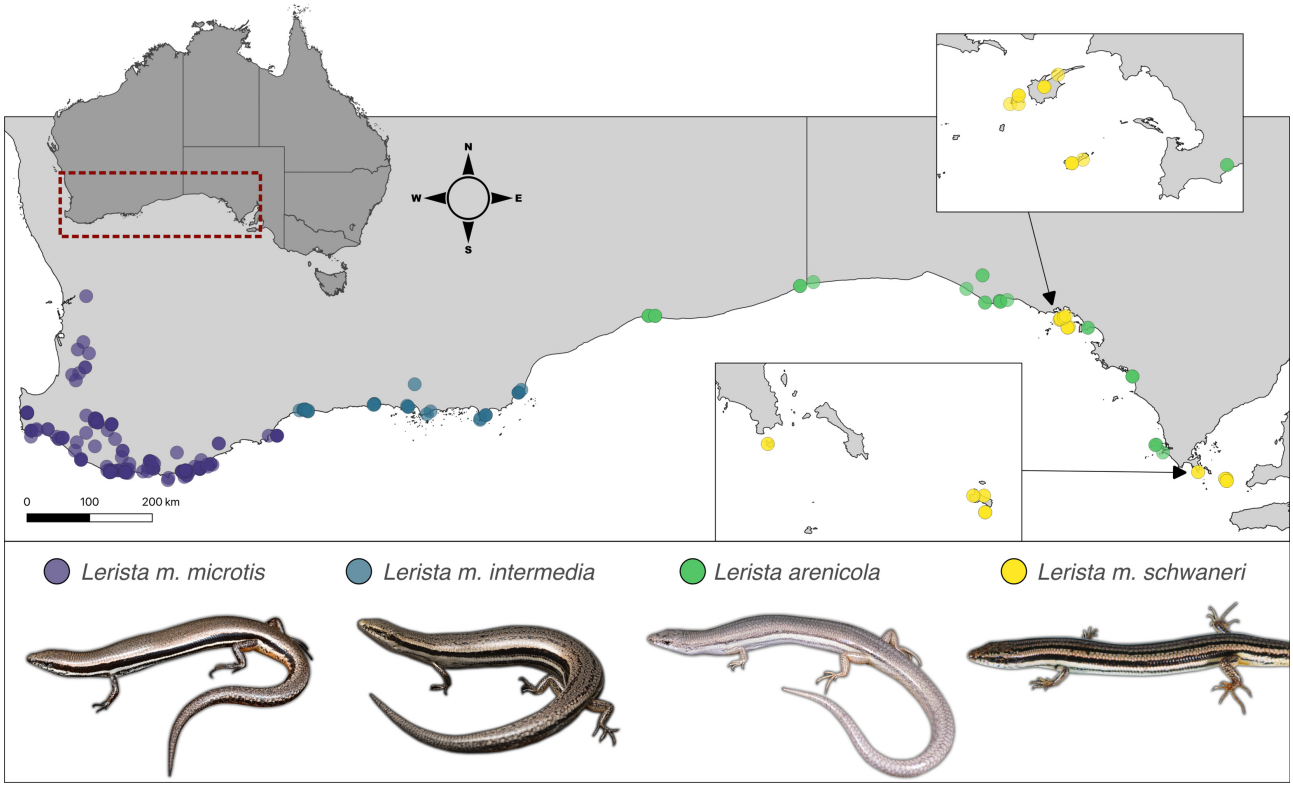

FIGURE 1. Distribution of currently recognized *Lerista microtis* subspecies and *Lerista arenicola.* Taxon assignment reflects that of the original museum records and the purported distribution as described in the literature (e.g., Storr 1991a; Wilson & Swan 2021). Note that all confirmed records of *L. m. schwaneri* are confined to islands near the SA mainland. Photographs of live specimens as follows: *L. m. microtis* (green)—Anders Zimny; *L. m. intermedia* (blue)—Jordan Vos; *Lerista arenicola* (red)—Brad Maryan; *L. m. schwaneri* (yellow)—Trevor Peters. Record colours are made slightly transparent to show overlapping records better, with more saturated colours indicating greater density of records.

Materials and Methods

Subspecific taxonomy and distribution of *Lerista microtis*

Gray (1845) described the species *Mocoa microtis* from south-west Australia, which was then transferred to the genus *Lerista* by Greer (1967). Storr (1971) partitioned *L. microtis* into two subspecies, *L. m. microtis* and *L. m. arenicola.* Under this arrangement, the name *L. m. microtis* applied to specimens from south-west Western Australia (WA), while *L. m. arenicola* applied to those from the Nullarbor coastline along the southern coast. Based on many more specimens 20 years later, Storr (1991a) revised the *L. microtis* group, in which he elevated *L. m. arenicola* to full species (*L. arenicola*) and erected two new subspecies: *L. m. intermedia* and *L. m. schwaneri*.

According to Storr (1991a), *L. m. microtis* occurs from Dwellingup State Forest east to Bremer Bay (WA), *L. m. intermedia* from East Mount Barren east to Israelite Bay (WA), and *L. m. schwaneri* is likely restricted to islands of the Nuyts Archipelago (SA) (see Fig. M). Storr (1991a) considered *L. arenicola* as occurring from Twilight Cove (WA) east to Fowlers Bay (SA). Since Storr's latest revision, more specimens have been collected, extending the known distribution of the proposed taxa. In particular, additional SA specimens of *L. arenicola* have been recorded on OzCam (Wallis 2006; available at https://ozcam.org.au) from Edrilpa, Thalia Caves, and Coffin Bay, suggesting this taxon also extends down the western coast of the Eyre Peninsula. Of note, there are no confirmed occurrences of *L. arenicola* on islands; based on our assessment of a 2006 specimen (SAMA_R61932) from St Peter Island, identified on OzCam as *L. arenicola*, we believe this specimen is instead consistent with the *L. m. schwaneri* morphotype (based on the diagnostic characters of Storr [1991a]). In contrast to *L. arenicola*, *L. m. schwaneri* is apparently restricted to islands. Additional specimens lodged as *L. m. schwaneri* have been recorded from islands off the south-eastern coast of the Eyre Peninsula (Williams Island and Wedge Island). Importantly, the collection locality of the only mainland *L. m. schwaneri* specimen is unconfirmed; Storr (1991a) speculated that one paratype specimen (SAMA_R1599) was from the 'west coast' of SA, given that the specimen was donated in 1930 by someone who lived in Fowlers Bay (i.e., on the mainland). However, we view that the location where the collector lives cannot be presumed as the collection locality. Owing to the unsubstantiated provenance of specimen R1599, we exclude it from our distribution mapping of taxa. Hence, all confirmed records of *L. arenicola* are from the mainland, whereas all confirmed records of *L. m. schwaneri* are from islands. Any morphological distinctiveness among specimens assigned to these taxa (explored herein) should thus be interpreted in light of the oceanic allopatry between *L. arenicola* and *L. m. schwaneri* specimens. We emphasise these points because Storr speculated on whether *L. arenicola* and *L. microtis* were sympatric on the mainland, and although he did not assume that they were, he evidently used this possible sympatry as partial justification for elevating *L. arenicola* to full species (in addition to morphological differences).

Assessment of morphological distinctiveness

To assess the morphological distinctiveness of *Lerista arenicola* and *L. microtis* (including its three subspecies), we examined 45 specimens from the Western Australian Museum, Perth (WAM), the South Australian Museum, Adelaide (SAMA) and Museums Victoria, Melbourne (NMV). We made a deliberate effort to sample relatively evenly across the proposed taxon ranges. This sampling strategy was designed to provide a representative cross-section of the species' distribution. We focused on measuring characters that Storr (1991a) used to distinguish the putative taxa, such as lateral and dorsal patterning, number of mid-body scale rows, nasal scale contact/separation, and size (Table 1). However, for a more comprehensive exploration of group structure, we also obtained a range of other potentially important characters from three classes of morphological data: mensural (linear morphometrics), meristic (scale counts), and qualitative characters (colour pattern). Details of specimens examined are provided in Table A1, appendix.

Mensural characters were: snout–vent length (***SVL***); head length (***HL***, from snout to anterior margin of ear opening); head width (***HW***, widest point of head); axilla–groin distance (***AGD***, between the posterior insertion of forelimb and anterior insertion of hindlimb); forelimb length (***Forelimb***, distance from the attachment of the limb to the body to the terminus of the fourth finger, including the claw); hindlimb length (***Hindlimb***, distance from the attachment of the limb to the body, to the terminus of the fourth toe). For SVL, specimens were straightened out

against a flat surfaced ruler, which ensures the long body is kept straight during measurements. All other mensural characters were measured with digital callipers to 0.1 mm precision. For limb measurements, limbs were held at right angles to the body wall, and the measurement was taken from the tip of the longest digit to the posterior insertion of the limb into the body.

Meristic characters were: number of mid-body scale rows (***MSR***); number of subdigital lamellae under the fourth toe of left foot (***SubDig***); number of nuchal scales on the left side (***Nuchals***).

Qualitative characters (e.g., Figure 2) were: dorsal patterning (***DP***), upper lateral stripe boldness (***ULSB***), upper lateral stripe width (***ULSW***), mid-lateral stripe width (***MLSW***), and nasal scale separation (***NSS***) (Table 1).

TABLE 1. Variables used in statistical analysis. Justification is provided for why each variable was included in our study. For variables that were key diagnostic characters used by Storr (1991a), we state the degree of evidential support (consistent or weak) for the reliability of such diagnostics, as revealed by our study.

Variable	Unit	Justification for use in present study (e.g., presumed differences)	Evidence
SVL	mm	**L. m. schwaneri* is larger than *L. m. microtis* and *L. m. intermedia*	Consistent
HL	mm	Typically used in lizard taxonomy	-
HW	mm	Typically used in lizard taxonomy	-
AGD	mm	Typically used in lizard taxonomy	-
Forelimb	mm	**L. m. microtis* has short limbs, while *L. m. schwaneri* has long limbs.	Consistent
Hindlimb	mm	As for Forelimb justification	Consistent
MSR	Counts	**L. m. schwaneri* and *L. arenicola* typically have two more MSR than *L. m. microtis* and *L. m. intermedia*	Consistent
SubDig	Counts	Typically used in lizard taxonomy	-
Nuchals	Counts	Typically used in lizard taxonomy	-
DP	0: Absent 1: Faint traces of broken stripes	**L. m. microtis* have few dorsal markings, whereas *L. m. intermedia* tend to have indistinct dorsal stripes	Weak
	2: Indistinct continuous stripes 3: Bold continuous stripes	**L. m. schwaneri* has more complex dorsal pattern than that of *L. m. microtis*	Weak
ULSB	1: Indistinct edges 2: Bold edges	*Indistinct in *L. arenicola*, bold in *L. microtis*	Consistent
ULSW	1: Narrow	*Narrow in *L. arenicola*, wide in *L. microtis*	Consistent
	2: Wide	*Narrower in *L. m. intermedia* than that of *L. m. microtis*	Weak
MLSW	1: Narrower than upper lateral 2: Wider than upper lateral	Considered relevant given our prior observation that *L. arenicola* tend to have wider mid-lateral stripes than that of *L. microtis*	-
NSS	0: Wide separation 1: Narrowly separated 2: Just touching 3: Short contact 4: Broad contact	Typically used in lizard taxonomy	-

* Denotes important diagnostic claims made by Storr (1991a).

Statistical analysis of morphology

Univariate and multivariate analyses were used to determine whether morpho-spatial variation could form the basis of detectable group structure among the *Lerista* taxa posited by Storr (1991a), namely *L. arenicola* and the subspecies of *L. microtis*.

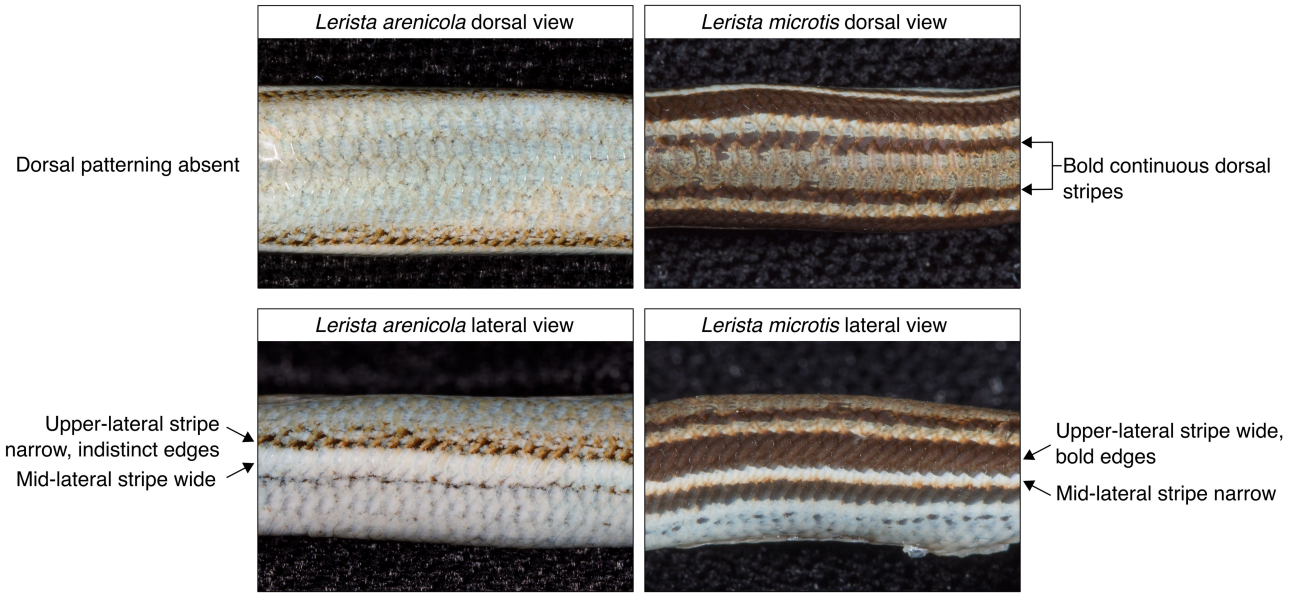

FIGURE 2. Examples of variation in colour pattern characters in the *Lerista microtis* group: upper row—dorsal view; lower row—lateral view. Storr (1991a) proposed that the black upper lateral stripe of *L. arenicola* (left) is narrow with indistinct edges, whereas that of *microtis* (right) is wide and boldly edged, thereby distinguishing it from *L. arenicola.*

Size correction of mensural data

To remove potential bias caused by ontogenetic variation, juvenile specimens (n = 3, assessed based on their very small size compared to adult specimens) were excluded from mensural analyses, and adult size variation in mensural characters was normalised using a modification of the Thorpe (1975) allometric growth equation: $X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$, where X_{adj} = size corrected value; X = measured trait value; β = unstandardized regression coefficient for each taxon; and SVL_{mean} = the mean SVL of each taxon (different SVL_{mean} calculated for each taxon) (Thorpe 1975, 1983; Turan 1999; Lleonart *et al*. 2000; Chan & Grismer 2022). There is no inter-lineage conflation of variation, given that mensural character adjustments were conducted separately on each taxon (Reist 1985; McCoy *et al*. 2006). Logarithmic transformations were performed at base 10. This allometric correction was implemented with the '*allom()*' function in the *GroupStruct* package (v0.1.0; Chan & Grismer 2022). All downstream mensural character analyses were performed on these adjusted values. No size adjustments were made to meristic data because scale characters do not change during ontogeny (Chang *et al*. 2009).

Univariate analysis

Given that many specimens (35%) had incomplete tails (i.e., regenerated, broken, or missing), tail length was excluded from analyses. One-way analyses of variance (ANOVA) were performed on the mensural characters to test for the presence of statistically significant ($p<0.05$) mean inter-taxon differences. Tukey HSD *post hoc* tests were used to determine which taxon pairs had significantly different mean values for each character, after adjusting for multiple comparisons. For characters that did not meet the parametric assumption of normality (Shapiro-Wilk test $p<0.05$) or equal variance across groups (i.e., Levene's test $p<0.05$), we used Welch's F-test and Games-Howell *post hoc* test. Meristic characters (i.e., positive integer count data) were analysed using generalised linear models (GLMs) to explore significant differences among lineages. Tests for over-dispersion of meristic variables, using the

'*dispersiontest*' function in the *AER* package (v1.2-10; Kleiber & Zeileis 2008), revealed that all meristic traits were under-dispersed, hence we used Quasi-Poisson errors for all GLMs. To visualise the distribution of trait variation across taxa, we produced violin plots with embedded boxplots for the mensural (continuous) characters, and boxplots for the meristic (discrete) characters.

Multivariate analysis

For mensural characters, we first created low-dimensional representations of variation in the data, achieved by performing principal component analyses (PCA) implemented with the packages *FactorMineR* (v2.4; Lê *et al*. 2008) and *factoextra* (v1.0.7; Kassambara & Mundt 2017). Eigenvalues >1 were retained according to Kaiser's criterion (Kaiser 1960), resulting in the first PC retained. To visualise multivariate group structure among taxa in qualitative characters (plus MSR), we employed non-metric multidimensional scaling (MDS) using the *'metaMDS()'* function of the *vegan* package (v2.6–5; Oksanen *et al*. 2020). We then tested whether longitude predicts morphological variation by performing linear regression of longitude against major axes of morphological variation (i.e. PC1, nMDS1, nMDS2).

Separately for the mensural character dataset and the qualitative character (plus MSR) dataset, we used the *'adonis2()'* function of the *vegan* package (v2.6–5; Oksanen *et al*. 2020) to perform non-metric permutation multivariate analysis of variance (PERMANOVA) to determine if the centroid locations of each taxon are statistically different from one another. PERMANOVAs were based on the calculation of a Euclidean (dis)similarity matrix using 5,000 permutations for each dataset. The *'pairwise.adonis()'* function of the *pairwiseAdonis* package (v0.4; Martinez 2017) was used to generate summary statistics of *post hoc* pairwise comparison tests between lineages, providing a pseudo-F statistic, R^2 value, *p*-value, and adjusted *p*-value for each comparison. Significant *p*-values ($p<0.05$) indicate segregation of taxon pairs, the strength of which is denoted by larger pseudo-F statistics. All morphological analyses were performed and visualized in R (v4.1.2, R Core Team 2022).

Sampling of genetic data

To assess the genetic coherence and distinctiveness of currently recognized taxa in the *L. microtis* complex, we inferred evolutionary relationships based on both mitochondrial and genome-wide nuclear loci. Our genetic analyses incorporated data from 15 ingroup individuals, namely *L. arenicola* (N = 3), *L. m. intermedia* (3), *L. m. microtis* (8), and *L. m. schwaneri* (1). To provide a reference of levels of intra-taxon divergence across *Lerista*, we also incorporated data from 94 individuals representing 22 taxa from other major *Lerista* clades, namely *L. allochira* (3), *L. apoda* (3), *L. baynesi* (3), *L. borealis* (5), *L. christinae* (4), *L. dorsalis* (5), *L. flammicauda* (5), *L. greeri* (5), *L. griffini* (5), *L. kalumburu* (4), *L. kendricki* (3), *L. neander* (4), *L. nichollsi* (4), *L. onsloviana* (4), *L. petersoni* (6), *L. picturata* (4), *L. planiventralis* (5), *L. praepedita* (8), *L. taeniata* (3), *L. tridactyla* (4), *L. viduata* (3), and *L. walkeri* (4). These selected taxa appear to correspond to separately evolving species lineages based on previous investigations incorporating genome-wide data (Singhal *et al*. 2017, 2018). As outgroups, we included two representatives of each of three species of *Ctenotus*, the sister group of *Lerista*, namely *C. atlas*, *C. pantherinus* and *C. schomburgkii*. We have also included two samples of each of two species of *Eremiascincus*, a more distantly related genus yet still within the Sphenomorphini tribe, namely *E. fasciolatus* and *E. musivus*. In total, our genetic sampling included 119 sampled specimens.

To infer evolutionary relationships based on the nuclear genome, we incorporated double-digest restriction site-associated data (ddRAD) generated by broad-scale evolutionary investigations of Australian sphenomorphin skinks (Singhal *et al.* 2017, 2018; Prates *et al.* 2022) and available in the Sequence Read Archive (BioProjects PRJNA755251 and PRJNA382545). Briefly, DNA extractions were digested with the restriction enzymes EcoRI and MspI, tagged with individual barcodes, PCR-amplified, multiplexed, and sequenced on an Illumina platform. We then used the *ipyrad* v. 0.9.71 pipeline (Eaton & Overcast 2020) to de-multiplex and assign reads to individuals based on sequence barcodes (allowing no nucleotide mismatches from individual barcodes), perform *de novo* read assembly (minimum clustering similarity threshold = 0.90), align reads into loci, and call single nucleotide polymorphisms (SNPs) while enforcing a minimum Phred quality score (= 33), minimum sequence coverage (=

6x), minimum read length (= 35 bp), and maximum proportion of heterozygous sites per locus (= 0.5), and ensuring that variable sites had no more than two alleles within an individual (i.e., a diploid genome). The final dataset was composed of 133,163 base pairs (19,647 being single nucleotide polymorphisms) across 940 loci, with each locus present in at least 30% of the sampled individuals.

To infer evolutionary relationships based on the mitochondrial genome, we PCR-amplified, sequenced, edited, and aligned a 1,143 base pair fragment of the *cytochrome B* gene following standard protocols described in Rabosky *et al*. (2009). Newly generated mitochondrial sequences were uploaded to GenBank (OR026697-OR026711).

Inferring evolutionary coherence and distinctiveness

To infer evolutionary relationships, we analysed the nuclear and mitochondrial datasets separately. In each case, we used an individual-based approach for phylogenetic inference under Maximum Likelihood, allowing us to assess whether individuals assigned to the same taxon (at the level of species or subspecies) are phylogenetically clustered. To this goal, we used RaxML-HPC v. 8.2.12 (Stamatakis 2014) through the CIPRES Science Gateway (Miller *et al.* 2010) using the GTRCAT model of nucleotide evolution and estimating node support based on 1,000 bootstrap replicates. All phylogenetic analyses included both variant and invariant sites.

Results

Mapping morphological characters in geographic space

There is evidence of geographical partitioning in some morphological characters, but not others (Figure 3). The main geographical distinction is in the colour pattern characters that Storr (1991a) used to distinguish *L. arenicola* from *L. microtis*. Specifically, we found that mainland specimens from the Eyre Peninsula and the Nullarbor tend to have wide white midlateral stripes and narrow black upper lateral stripes with indistinct edges; these typically were specimens that had been assigned to *L. arenicola* (Figure 3). Dorsal patterning was largely inconsistent across southern Australia; for example, within the supposed region of *L. m. intermedia*, specimens may have bold continuous stripes, indistinct continuous stripes, or no dorsal patterning (Figure 3). Storr (1991a) distinguished *L. m. schwaneri* from the other two *L. microtis* subspecies by its higher number of mid-body scale rows. We found support for this, however, *L. arenicola*—which is geographically closer to *L. m. schwaneri*—also has a similarly higher mid-body scale count compared to the western taxa, suggesting a geographical cline in this character, albeit with some within-region variation. Thus, it is not always possible to confidently assign a given specimen to a taxon in this group, although the morphological characters of *L. arenicola* specimens were the most consistent.

Statistical analysis of morphology

Univariate results

Summary statistics for each taxon are shown in Table 2. While there is extensive overlap among groups in all traits, ANOVA results revealed numerous statistically significant differences between proposed *L. microtis* taxa, including in 6 of 6 mensural characters and in 1 of 3 meristic characters (Figure 4; Table 3). The fewest number of differences are between *L. arenicola* and *L. m. intermedia*, with *L. arenicola* having significantly more mid-body scale rows and longer forelimbs. The greatest number of differences occur between *L. m. microtis* and *L. m. schwaneri* (i.e., the two most geographically separated subspecies, ~1400 km), which differed significantly in all traits except subdigital lamellae and nuchal scales. Specimens of *L. m. schwaneri* have significantly longer limbs, and longer and wider heads, than all other taxa. The axilla–groin distance of *L. m. schwaneri* is shorter than other taxa, but not significantly shorter than that of *L. m. intermedia*. The range of mid-body scale rows are similar between *L. arenicola* and *L. m. schwaneri*, whereas both taxa had significantly more mid-body scale rows than *L. m. microtis* and *L. m. intermedia*. Subdigital lamellae and nuchal scales did not differ significantly between any group.

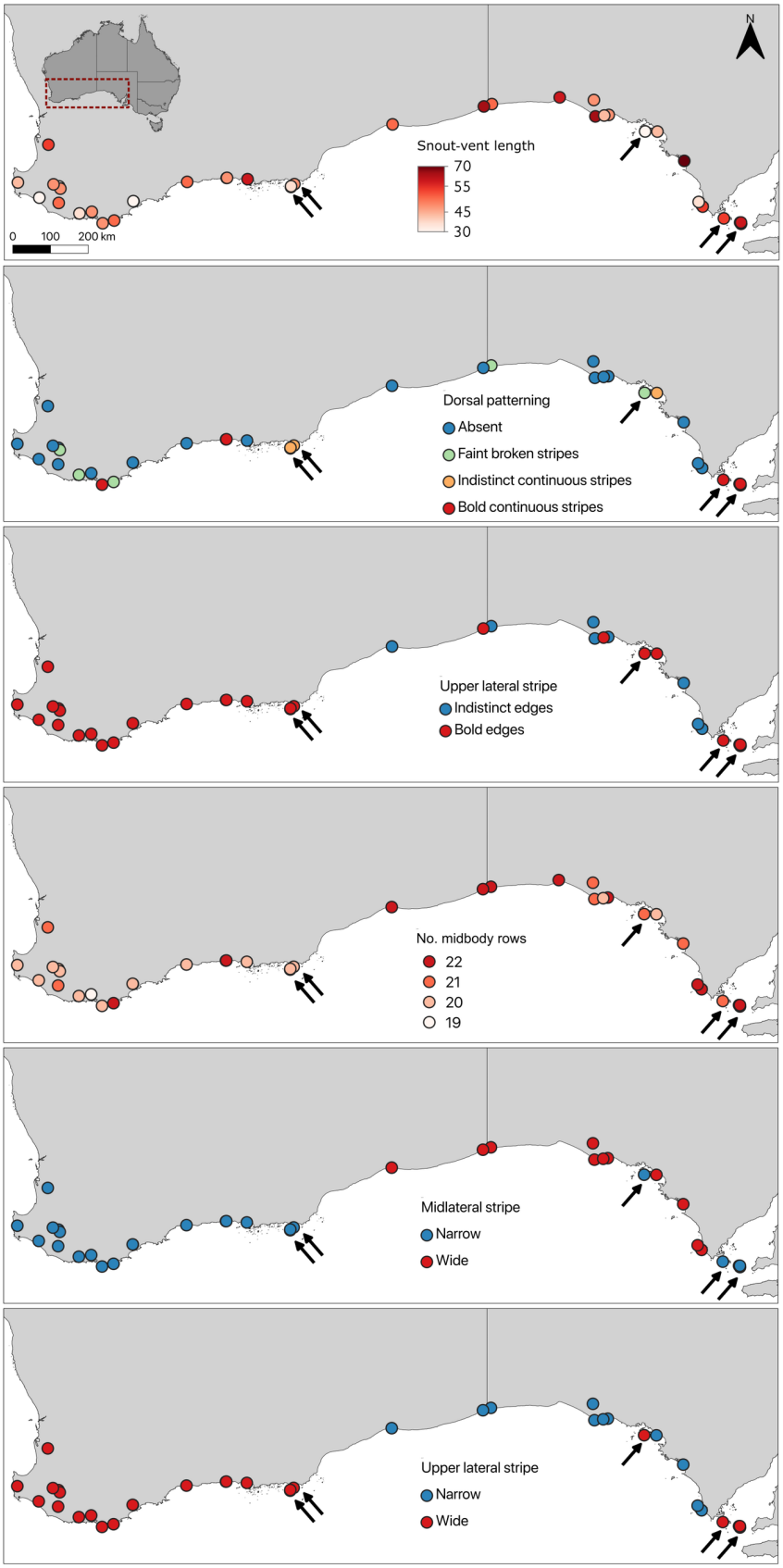

FIGURE 3. Geographical distribution of the characters states proposed by Storr (1991a) to diagnose *Lerista microtis* subspecies and *L. arenicola*. There is geographic predictability for some phenotypes (e.g., width of mid-lateral and upper lateral stripe), but less so for others (e.g., dorsal patterning). Arrows denote specimens from inlands. White points in the SVL map are juvenile specimens, which were removed from morphological analyses.

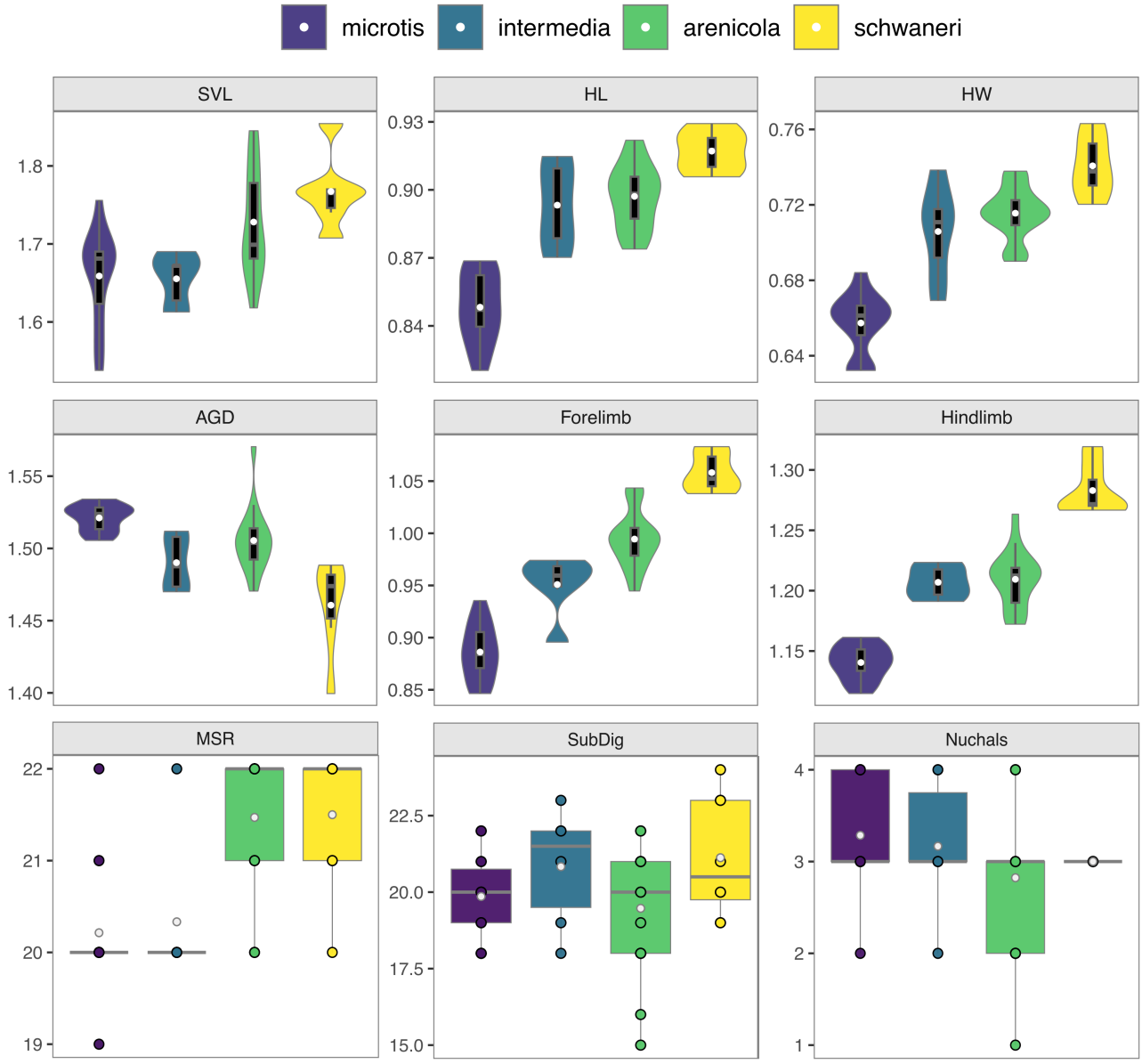

FIGURE 4. Comparative violin plots with embedded boxplots of size corrected mensural characters (top six graphs) for each taxon (*Lerista arenicola* and all *Lerista microtis* subspecies) showing the mean (white dot), range, frequency, and inter-quartile range (black rectangle). The bottom three graphs are comparative boxplots of meristic characters showing the mean (white dot), range, and inter-quartile range (coloured rectangle). Coloured dots correspond to y-axis values.

Multivariate results

Ordination of the first two principal components (PC) shows that, although there is some overlap between *L. arenicola* and *L. m. microtis*, there is generally distinct separation among groups (Figure 5). This separation in multivariate morpho-space is supported by the PERMANOVA results, which indicate that all *L. microtis* groups have significantly different centroid locations (Table 4). PC1 of the PCA is a primary axis of morpho-spatial variation, given it explained most (71.3%) of the variation in the mensural dataset, and loaded heavily for hindlimb length, forelimb length, head length and head width (Table A2, appendix). The remaining PCs were considered minimally important, and thus not analysed further, given their eigenvalues were all less than 1 (Kaiser 1960) and they explained negligible portions of variation.

Non-metric multidimensional scaling (nMDS) of qualitative characters (plus MSR) revealed phenotypic distinctiveness of *L. arenicola* from *L. microtis*, supporting Storr's (1991a) diagnoses (Figure 6). The stress value

was low (stress = 0.05), indicating a good fit of the data to the nMDS ordination. PERMANOVA results for the qualitative (plus mid-body scale rows) variables indicate that all four purported taxa have significantly different centroids from one another, except for *L. m. microtis* and *L. m. intermedia*, which are not significantly different from one another and overlap considerably (Table 5).

We detected a statistically significant positive correlation ($R^2 = 0.76$, $p = <0.0001$) between longitude and PC1 scores of individuals (Figure 7A), and a significant negative correlation between longitude and nMDS1 ($R^2 = 0.32$, $p = <0.0001$) and nMDS2 ($R^2 = 0.34$, $p = <0.0001$) scores of individuals (Figures 7B, 7C). Regarding PC scores, this indicates strong geographical structuring of characters in the *L. microtis* group; specifically, that individuals have longer limbs and longer and wider heads towards more eastern longitudes. Similarly, regarding nMDS scores, there is a geographical basis to variation in Storr's (1991a) diagnostic characters for the *L. microtis* group.

TABLE 2. Summary statistics (mean ± SE, range in parentheses) of mensural and meristic data for taxa of the *Lerista microtis* complex investigated in this study. Values for mensural characters presented here include juvenile specimens, but note that juveniles were removed before statistical analyses of mensural characters.

	***L. m. microtis* (N=14)**	***L. m. intermedia* (N=6)**	***L. m. schwaneri* (N=8)**	***L. arenicola* (N=17)**
SVL	45±7	45.3±3.4	52±13.9	54±8.6
	(32–57)	(41–49)	(31.5–71.5)	(41.5–70)
HL	6.6±0.6	7.2±0.5	8.1±1.4	8±0.5
	(5.3–7.7)	(6.5–7.8)	(5.7–9.6)	(7.2–9.4)
HW	4.2±0.4	4.6±0.4	5.3±1.0	5.3±0.4
	(3.3–4.9)	(4.3–5.3)	(3.7–6)	(4.6–6.2)
AGD	28.4±5.4	27.2±2.6	31.6±10.9	34.6±7.2
	(19.7–38.5)	(23.5–31)	(17.3–51.5)	(27.1–47.7)
Forelimb	7.3±0.7	8.3±0.7	10.3±2.0	10.0±0.8
	(5.8–8.8)	(7.4–9.1)	(7.1–11.9)	(8.8–11.4)
Hindlimb	12.9±1.4	14.8±0.9	17.3±3.7	16.4±1.1
	(8.8–14.7)	(13.3–15.7)	(11.3–20.9)	(14.4–18.0)
MSR	20.2±0.7	20.3±0.8	21.5±0.8	21.4±0.8
	(19–22)	(20–22)	(20–22)	(20–22)
SubDig	19.8±1.4	20.8±1.9	21.1±2.0	19.4±2.
	(18–22)	(18–23)	(19–24)	(15–22)
Nuchals	3.2±0.6	3.1±0.8	3±0	2.8±0.9
	(2–4)	(2–4)	(3–3)	(1–4)

TABLE 3. Results of ANOVAs (for mensural characters) or GLMs (for meristic characters) and Tukey HSD *post hoc* tests for significantly different mean character values among taxa. Green cells are characters that differed significantly among taxon comparisons. Grey cells denote non-significant differences. Significance levels of *p*-values: * < 0.05, ** < 0.01, *** < 0.001, **** < 0.0001.

	SVL	HL	HW	AGD	Forelimb	Hindlimb	MSR	SubDig	Nuchals
arenicola-intermedia					**		***		
arenicola-microtis	*	****	****		****	****	****		
arenicola-schwaneri		*	*	***	****	***			
intermedia-microtis		****	****	*	****	****			
intermedia-schwaneri	*	*	**		****	***	*		
microtis-schwaneri	**	****	****	****	****	****	****		

TABLE 4. PERMANOVA pairwise comparisons testing for significant differences among purported *Lerista* taxa (*L. arenicola* and all three subspecies of *L. microtis*) in a multivariate morpho-space described by six mensural characters (SVL, HL, HW, AGD, Forelimb, and Hindlimb).

Taxon pairs	F model	R^2	*p*-value	*p*-adjusted	Sig.
arenicola vs. *intermedia*	5.569	0.210	0.007	0.04	*
arenicola vs. *microtis*	32.619	0.538	0.0002	0.001	*
arenicola vs. *schwaneri*	9.925	0.321	0.0002	0.001	*
intermedia vs. *microtis*	11.961	0.413	0.0002	0.001	*
intermedia vs. *schwaneri*	23.896	0.705	0.0008	0.004	*
microtis vs. *schwaneri*	61.548	0.784	0.0002	0.001	*

Sig: Significance levels. *: $p < 0.05$ (5,000 permutations).

TABLE 5. PERMANOVA pairwise comparisons testing for significant differences among purported *Lerista* taxa (*L. arenicola* and all three subspecies of *L. microtis*) in a multivariate morpho-space described by five qualitative characters (DP, ULSB, ULSW, MLSW, NSS) and one meristic (MSR; i.e. an integer count) character.

Taxon pairs	F model	R^2	*p*-value	*p*-adjusted	Sig.
arenicola vs. *intermedia*	21.506	0.518	0.000	0.001	*
arenicola vs. *microtis*	32.501	0.537	0.000	0.001	*
arenicola vs. *schwaneri*	20.073	0.477	0.000	0.001	*
intermedia vs. *microtis*	3.343	0.157	0.036	0.214	NS
intermedia vs. *schwaneri*	14.721	0.551	0.001	0.005	*
microtis vs. *schwaneri*	31.449	0.611	0.000	0.001	*

Sig: Significance levels. *: $p < 0.05$ (5,000 permutations). NS: not significant.

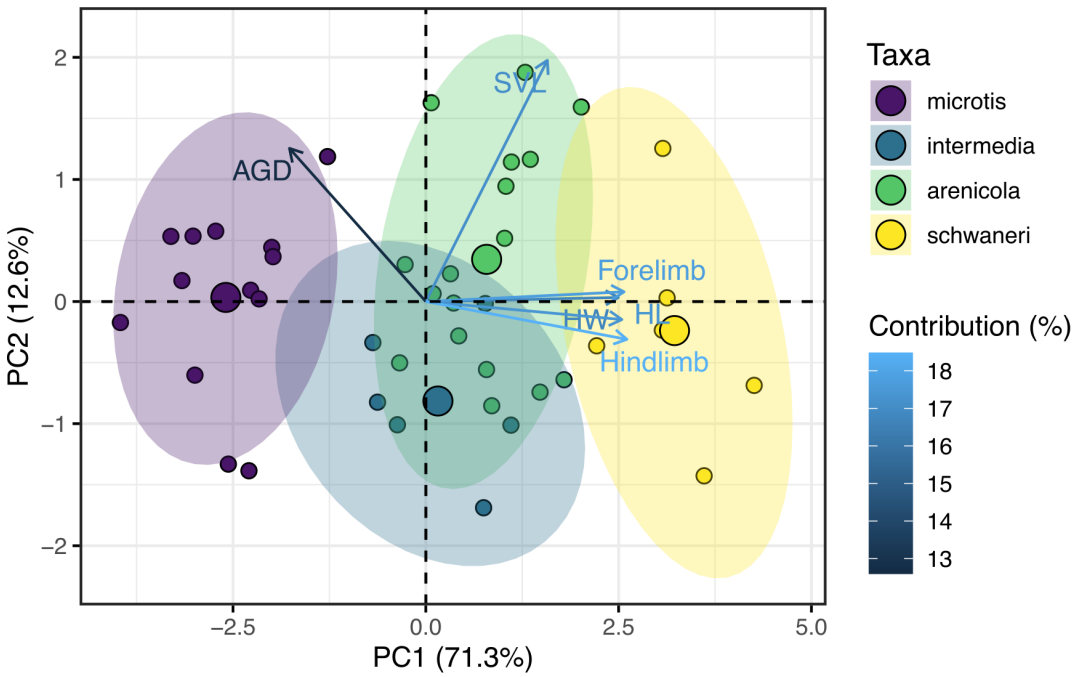

FIGURE 5. Biplot of the PCA performed on six mensural characters (SVL, HL, HW, AGD, Forelimb and Hindlimb). Axes show the first two principal components (i.e., PC1 and PC2) and their percentage of explained variation. Large, coloured ovals denote the 90% concentration ellipses for each taxonomic group proposed by Storr (1991a). Small points denote PC scores of individuals, whereas large points denote group centroids. Variables are denoted by arrows, the direction and length of which indicates their degree of contribution to each axis. Each variable is coloured according to its percentage contribution to its associated PC.

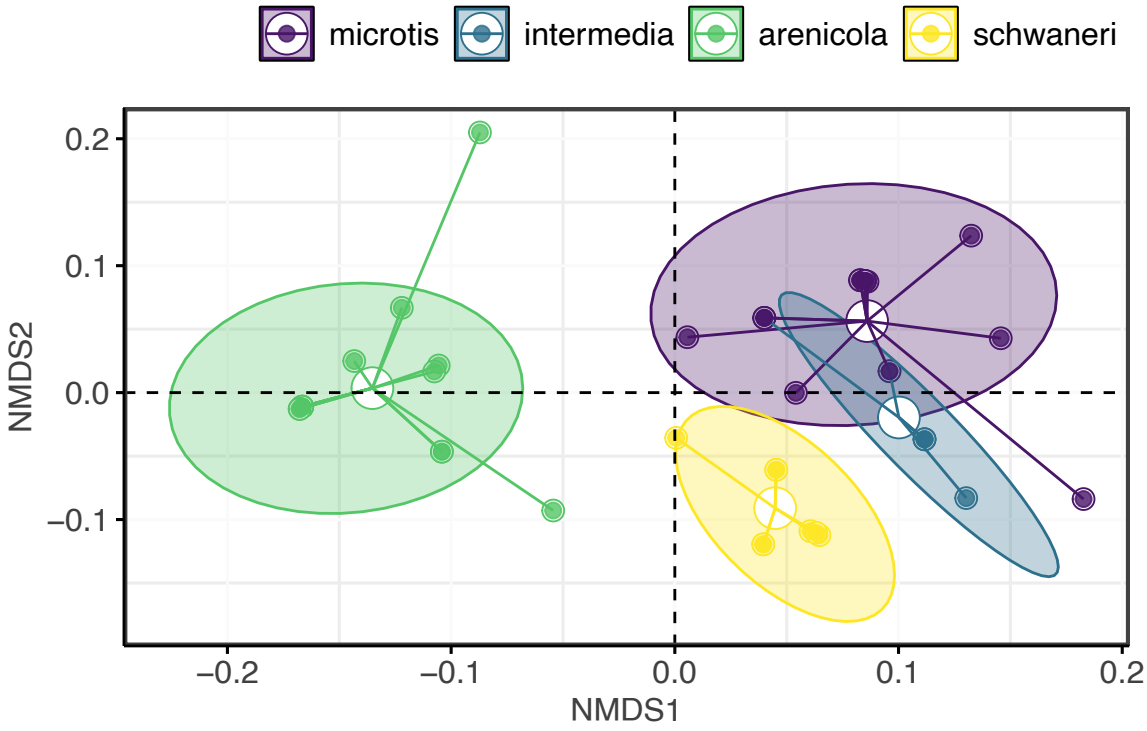

FIGURE 6. Biplot of non-metric multidimensional scaling (nMDS) performed on five qualitative characters (DP, ULSB, ULSW, MLSW, NSS) and one meristic (MSR; i.e., an integer count) character. These characters are among key traits Storr (1991a) used to diagnose these purported taxa. Specimens (coloured points) that are ordinated closer to one another are phenotypically more similar than those further apart. This graph lends support to the phenotypic distinctiveness of *Lerista arenicola* from *L. microtis*.

Phylogenetic patterns

Phylogenetic analyses based on both nuclear (Figure 8A) and mitochondrial (Figure 8B) DNA sequences support that *L. arenicola*, *L. m. intermedia*, *L. m. microtis*, and *L. m. schwaneri* compose a monophyletic group. This group is highly divergent from other major clades of *Lerista*. However, each of the four taxa in the *L. microtis* complex showed limited phylogenetic coherence and distinctiveness. For instance, both genetic datasets support that samples morphologically and geographically assigned to *L. arenicola* are phylogenetically nested among samples of *L. microtis*. Specifically, *L. arenicola* composed two (Figure 8A) to three (Figure 8B) non-sister lineages, grouping with individuals of *L. m. schwaneri* or *L. m. intermedia*. Like the case of *L. arenicola*, we found *L. m. intermedia* and *L. m. microtis* to be paraphyletic based on the mitochondrial dataset, which included more specimens, localities, and taxa than the nuclear dataset (Figure 8B). Finally, samples morphologically assigned to *L. m. microtis* largely grouped into the same clade; however, in the better sampled mitochondrial dataset, that clade also included a *L. m. intermedia* sample, while one *L. m. microtis* sample was more closely related to samples morphologically assigned to *L. arenicola* or *L. m. schwaneri*. We note that this pattern of paraphyly of the subspecies can hardly be explained by limitations of spatial sampling. Sampling gaps have been shown to exaggerate phylogenetic separation between those samples separated by such gaps (Battey *et al.* 2020). By contrast, geographically closer samples in our dataset often did not form clades, as is the case of samples morphologically assigned to *L. m. intermedia* and *L. arenicola* (Figure 8). As such, we might expect additional sampling to intensify the pattern of paraphyly currently observed in the *L. microtis* species group rather than resolving it.

Patterns of genetic structure in the *L. microtis* complex do not appear to align with levels of geographic separation, contradicting expectations from a scenario of geographically restricted populations diverging in isolation. Instead, we inferred low genetic divergence between species- or subspecies-level taxa. Often, these divergences were shallower than those inferred within other *Lerista* taxa broadly considered to correspond to single species. This is the case,

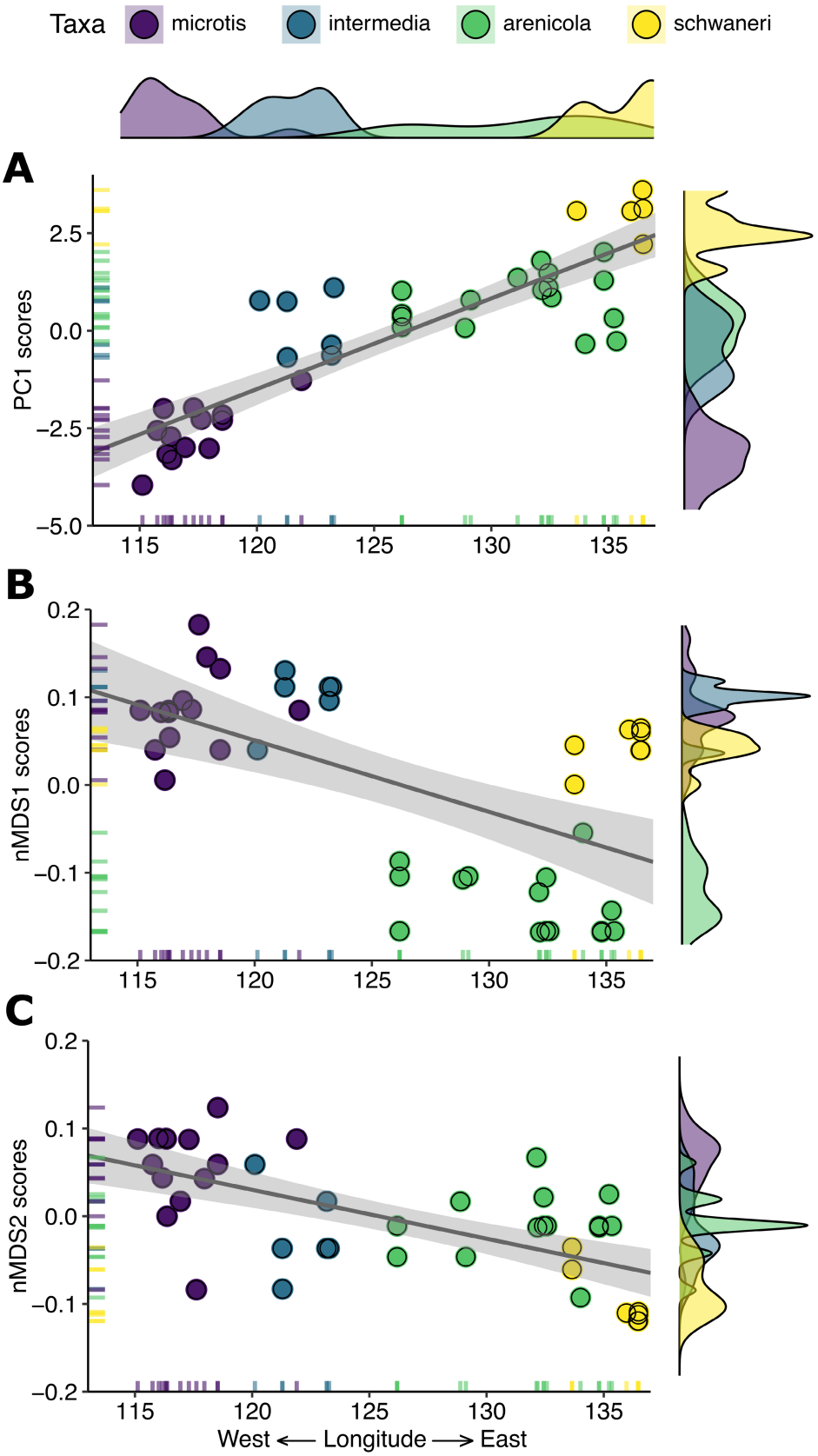

FIGURE 7. Longitudinal patterns of morphological variation in the *L. microtis* group. The x-axis represents a west–east geographical space across coastal southern Australia, and the y-axis describes important dimensions of morpho-spatial variation: (A) PC1 scores, derived from six mensural characters; (B) nMDS1 scores, and (C) nMDS2 scores, derived from five non-mensural characters. The line of best fit and 95% confidence interval are denoted by the black line and grey shaded zone, respectively. These graphs illustrate a mostly continuous and clinal structuring of phenotypic characters in the *Lerista microtis* group.

for instance, of *L. borealis*, *L. greeri*, *L. praepedita*, and *L. walkeri* (Figure 8). These taxa appear to correspond to separately evolving species lineages based on previous investigations incorporating genome-wide data (Singhal *et al*. 2017, 2018). We acknowledge, however, that levels of evolutionary divergence remain poorly characterized in several clades within *Lerista*.

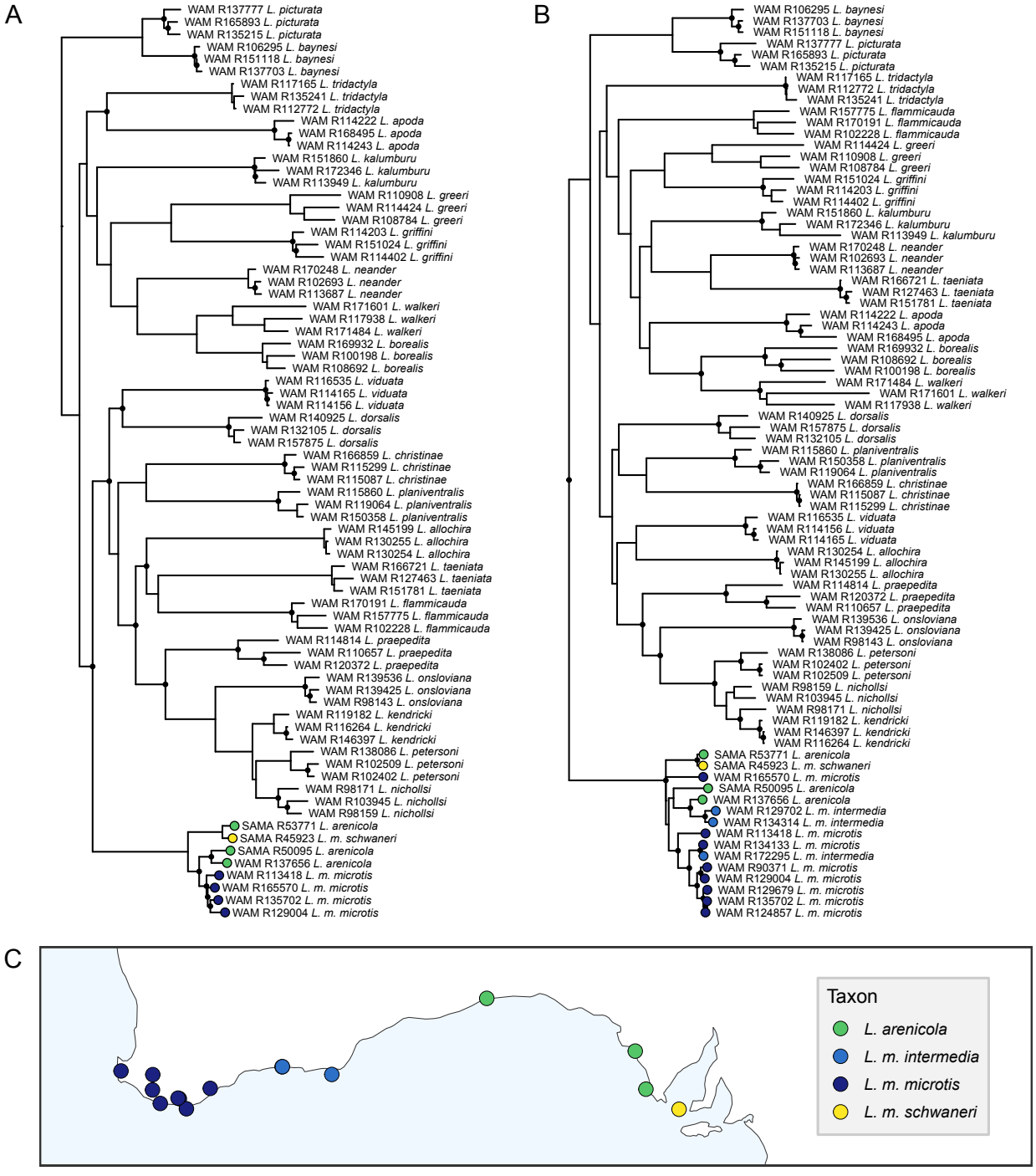

FIGURE 8. Evolutionary relationships in *Lerista* lizards with focus on taxa in the *L. microtis* complex. (A) Results from a phylogenetic analysis based on 133,163 base pairs across 940 restriction site-associated nuclear DNA (ddRAD) loci. (B) Results from an analysis based on 1,143 base pairs from the *cytochrome b* mitochondrial marker. (C) Map depicting the sampling localities of specimens included in the genetic analyses. For clarity, a maximum of three samples per taxon outside of the *L. microtis* complex is shown in each tree; to provide a reference of intra-taxon divergences across *Lerista*, these samples were selected to include the most divergent individuals within each taxon. Nodal bootstrap support values > 70 are indicated with a black dot. Information on genetic samples are provided in Table A3, appendix.

Overall, evidence of limited genetic coherence and distinctiveness support that populations assigned to *L. arenicola*, *L. m. intermedia*, *L. m. microtis*, and *L. m. schwaneri* correspond to the same evolutionary species. This species appears to show only limited spatial genetic structure. In particular, nuclear data suggest that the western populations are phylogenetically nested within eastern populations, but the relationship between mitochondrial patterns and geographic separation is less clear.

Discussion

Subspecies have a long history of being described based on somewhat subjective or poorly articulated criteria, and in consequence, they have an inertia that makes them difficult to challenge owing to an asymmetry in the degree of evidence expected of those describing them *versus* those attempting to falsify them (Prates *et al.* 2022). As such, no matter how poorly defined a subspecies is, it is difficult for future investigators to disprove their existence. The process is complicated when those original describers of subspecies do not clearly state what their criteria for subspecific recognition are, nor give details as to why their data indicates subspecies. This is certainly the case of taxa in the *L. microtis* group. In our reappraisal of this group, we have challenged traditional species and subspecies taxa using a combination of morphological and genomic data against clear criteria that would typically be expected for subspecific recognition: morphological and geographic distinctiveness of a population that is not phylogenetically distinct from other populations of the same species.

Morphological support for *Lerista arenicola* and subspecies of *L. microtis*

Our morphological analyses (with juvenile specimens removed) revealed distinctiveness among specimens assigned to each taxon in the *L. microtis* group, but this variation is continuous along a geographic axis. For mensural characters, the original descriptions claimed that *L. m. schwaneri* and *L. arenicola* are distinguishable from *L. m. microtis* and *L. m. intermedia* based on the larger size of the two former taxa (Storr 1991a). Storr's (1991a) diagnoses and descriptions also implicate *L. m. microtis* as a short-legged subspecies, and *L. m. schwaneri* as a long-legged subspecies. We found support for these patterns but emphasise that these two larger taxa (*L. arenicola* and *L. m. schwaneri*) are in the geographical east of the group's range, whereas the smaller *L. m. microtis* and *L. m. intermedia* are in the west. Not surprisingly, then, we found that the greatest differences in mensural characters exist between *L. m. microtis* and *L. m. schwaneri* (i.e., the taxa that are most widely separated in space), with longer SVL, limb length, and head dimensions in more eastern longitudes (Figure 7A).

Similar patterns were uncovered in our nMDS of colour pattern and scale characters; being closer spatially, *L. m. microtis* and *L. m. intermedia* were not significantly different in both univariate and multivariate character space. For instance, these two western taxa each have fewer MSR than those of the two eastern taxa (Table 2, 3), mirroring the size difference. Storr states that *L. m. microtis* has more complex dorsal patterning than *L. m. intermedia*, the latter of which is said to be paler and with a narrower upper lateral stripe. We found no support for this diagnosis, with the occurrence of both complex and simple dorsal patterning in specimens within the distribution of both these taxa. Moreover, *L. m. intermedia* is not markedly paler in dorsal ground colour (presumably Storr measured this subjectively), nor is its upper lateral stripe narrower than that of *L. m. microtis.* These morphological findings support *L. m. intermedia* being synonymised with *L. m. microtis*.

Storr (1991a) considered it possible that *L. m. schwaneri* could be sympatric with *L. arenicola* on the mainland, and it appears that this somewhat motivated his decision to elevate *L. arenicola*. However, as we have shown here (see text in Methods about specimen SAMA_R1599), there is no substantiated evidence suggesting such sympatry of specimens previously assigned to these taxa. Thus, specimens labelled as *L. m. schwaneri* appear to simply represent an island form, one that is morphologically more similar to *L. arenicola* on the adjacent mainland in SA than it is to the *L. microtis* of south-western WA.

In the nMDS of colour pattern and scale characters, we found that *L. arenicola* was the most distinctive taxon, being positioned further from the three *L. microtis* subspecies.

However, this distinctiveness is driven largely by the minor, but nonetheless consistent, differences in pattern that Storr used to distinguish this species from *L. microtis*. Specifically, the black upper lateral stripe of *L. arenicola*

is narrow and often with indistinct edges, whereas that of *L. microtis* is wide and sharp-edged. Storr considered this distinction important; in his introduction, he states (verbatim) that: 'In view of its substantial differences from *L. microtis* (and their possible sympatry in South Australia), *L. arenicola* is raised to full species' (p. 469, Storr 1991a).

While such superficial differences in pattern are commonly used to distinguish species and subspecies, we question whether such differences should constitute as basis for taxonomic distinction. How minute of a difference in colour pattern should warrant taxonomic splitting? Storr (1991a) considers the differences in lateral pattern between *L. microtis* and *L. arenicola* to be 'substantial', and now that such a subjective claim has been made, it is difficult to dismantle given the lack of conceptual definition of species and subspecies used by Storr. The correct decision on how best to taxonomically treat populations that differ in colour pattern is elusive, and depends on one's view of species and subspecies. We have shown that *L. arenicola* are genetically nested within *L. microtis* (Figure 8a,b), suggesting a discordance between phylogeny and the phenotypes proposed to differentiate among taxa in this group. The long branch length on which all taxa in the *L. microtis* complex occur suggests that a highly distinctive *Lerista* species has undergone selection for size and colour pattern across its narrow yet massively long distribution along the southern coast of Australia.

Phenotypic variation being poorly coupled to genetic lineages is a common phenomenon. Numerous examples from Australia's squamates are provided herein. *Ctenotus* skink species from the *C. inornatus* group were diagnosed largely on qualitative aspects of lateral and dorsal colour pattern elements, but later investigators found discordance between such morphological features and phylogeny (Rabosky *et al*. 2014). All subspecies of the widespread panther skink *Ctenotus pantherinus* were described on morphology alone, but in light of genetic data and new morphological analyses, they have recently been synonymised with the species given limited genetic and morphological coherence and distinctiveness of populations assignable to each subspecies (Prates *et al*. 2022). While revising the taxonomy of the *Ctenotus brooksi* complex, Hutchinson *et al*. (2006) found that three subspecies (*C. b. taeniatus* Storr 1970, *C. b. aranda* Storr 1970, and *C. b. iridis* Storr 1981)—which were diagnosed largely based on dorsal colour pattern differences—are weakly differentiated genetically, and hence were synonymised with *C. taeniatus*. The Corangamite water skink (*Eulamprus tympanum marnieae*) was proposed as a distinct subspecies given its differences in morphology (more mid-body scale rows and blacker throat than the nominate form; Hutchinson & Rawlinson 1995). Recent genetic evidence shows individuals assigned to the *T. t. marnieae* morphotype are nested within the nominate subspecies (Pepper *et al*. 2018). In tiger snakes, shifts in body size and colour can occur rapidly in response to local adaptation in island and mainland populations that are polyphyletic, with various subspecies synonymised by Keogh *et al*. (2005).

Given the morphological diversity found in many species, we empathise with investigators of the past, who faced difficult taxonomic decisions in the absence of knowledge of genealogical relationships. But modern taxonomists have access to such information, enabling more direct assessments of evolutionary relationships on the basis of genetic information. We suggest that species historically described based on morphology alone should be reassess in light of genomic data and a lineage-centered view of species. In the case of subspecies, where lines of evidence other than genomics are used to justify subspecific recognition, taxonomists proposing subspecies must be clear about their criteria for subspecific recognition. This further enables future investigators to test the validly of those taxonomic conclusions.

Conclusion

In the absence of genetic information, traditional taxonomists have proposed subspecies to capture purportedly diagnostic phenotypes (Zink 2004), and in doing so, they either (1) assumed that such phenotypes were markers for a cohesive evolutionary unit or (2) believed that taxonomic schemes should capture phenotypic variation irrespective of whether this variation is indicative of evolutionary separation (Mayr 1982; Patton & Conroy 2017). Traditional taxonomists did not have access to the molecular genetic techniques routinely used in taxonomic research today, and thus their investigative process was necessarily centred on morphology. Incongruencies may continue to emerge between phylogeny and phenotype in cases where subspecies have been defined based on morphology alone, as we have shown in this study of the *L. microtis* group. More broadly, the integration of morphological and genetic information has revealed the extraordinary lability of organismal phenotypic attributes. Besides challenging the

evolutionary significance of many characters traditionally used in taxonomic delimitation, integrative approaches like ours can provide insights into how processes like natural selection and isolation-by-distance shape patterns of phenotypic variation in nature.

Systematic conclusions

There was no concordance between genetic and phenotypic variation, with multiple instances of polyphyly among specimens assigned to different taxa of the *L. microtis* group. While our examinations of museum specimens confirmed a pattern of morphological variation across populations in the group, we found this variation to be continuous, forming geographic clines. These findings support our decision to here synonymise *L. arenicola*, *L. m. microtis*, *L. m. intermedia*, and *L. m. schwaneri* with *L. microtis*. This new arrangement of *L. microtis* reflects a widespread polytypic species ranging from south of Perth (WA) east to Wedge Island (SA), with geographical variation in phenotype that is poorly coupled to phylogeny. Transferring *L. arenicola* to *L. microtis* requires a redefinition of *L. microtis* to capture the morphological attributes that are typical of populations previously assigned to *L. arenicola*. Hence, a redescription of *L. microtis* is given here.

Taxonomy

Lerista microtis (Gray, 1845)

South-coast five-toed slider

Synonymy
Mocoa microtis Gray 1845
Lygosoma (Rhodona) microtis (Boulenger 1887: 223)
Rhodona microtis (Loveridge 1934: 258).
Nodohra microta (Mittleman 1952: 27)
Lygosoma (Rhodona) microtis (Glauert 1960: 94)
Lerista microtis (Greer 1967)
Lerista microtis arenicola (Storr 1971)
Lerista microtis (Cogger *et al*. 1983)
Nodorha microtis (Wells & Wellington 1985)
Lerista microtis microtis (Storr 1991)
Lerista microtis intermedia (Storr 1991)
Lerista microtis schwaneri (Storr 1991)
Lerista arenicola (Storr 1991)
Figure 9.

Holotype of *Macoa microtis*: BMNH 1946.8.18.64, Swan River, Western Australia, obtained from Mr. J. Gilbert's collection. As Storr (1971) notes, the type locality of 'Swan River' is likely incorrect, given the species does not occur near Perth; it was likely collected from Albany.

Diagnosis: A species of *Lerista* with five digits on each limb and a movable eyelid. Distinguished from the other two pentadactyl *Lerista* as follows: from *L. viduata* by its white midlateral stripe (absent in *L. viduata*) and from *L. bougainvillii* by its four supraoculars (not three) and six supraciliaries (not five).

Description: Mensural characters. Sample size is 45 unless otherwise noted. Snout-vent length = 31.5–71.5 mm (average = 49.7 mm), head length = 5.3–9.6 (average = 7.5), head width = 3.3–6.2 (average = 4.9), axilla-groin distance = 19.7–51.5 (average = 31.2), forelimb length = 5.8–11.9 (average = 9), hindlimb length = 8.8–20.9 (average = 15.3); original tail length (N = 19) = 36–79.7 (average = 57.4). There is geographic variation in body size, with size approximately increasing from west to east. For instance, the mean SVL of adults from the west (specimens previously assigned to *L. m. microtis* and *L. m. intermedia*) is 45.7, whereas mean SVL from eastern specimens (previously assigned to *L. arenicola* and *L. m. schwaneri*) is 55.3.

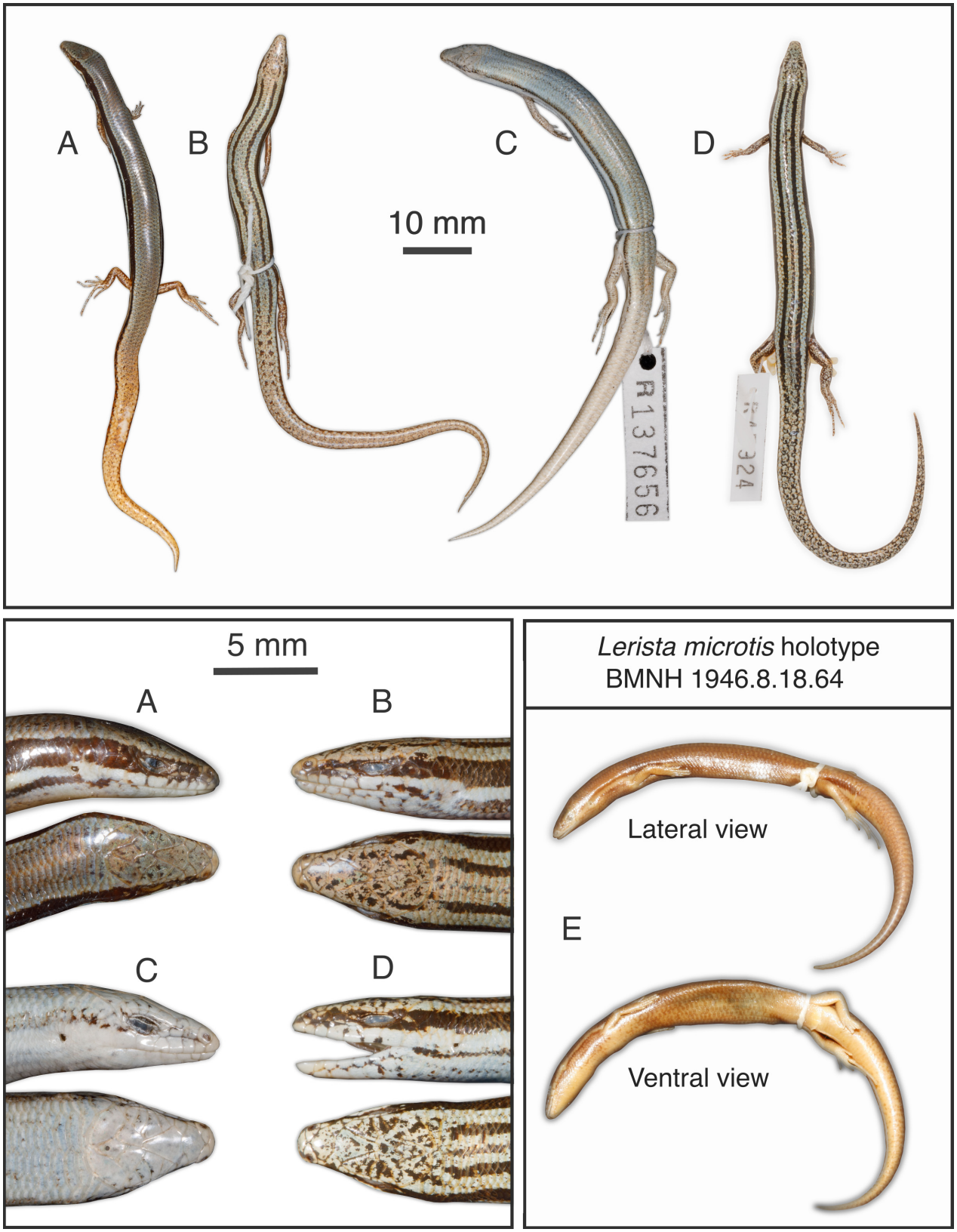

FIGURE 9. Select *Lerista microtis* specimens showing variability in size and colour pattern. (A) Specimen WAM_R113419 from Margaret River area (south-west WA) with dark grey-brown dorsal colour, orange tail and no dorsal pattering (formerly *L. m. microtis*); (B) specimen WAM_R129702 from Quagi Beach (south-west WA) with continuous paravertebral stripes and olive brown dorsal colour (formerly *L. m. intermedia*); (C) pale specimen WAM_R137656 from the Nullarbor coast in SA (formerly *L. arenicola*); (D) specimen SAMA_R45924 from Wedge Island (SA) showing continuous paravertebral stripes and vertebral stripe (formerly *L. m. schwaneri*); (E) the holotype of *Lerista microtis*.

Scalation. Nasal scales widely separated (N = 4), narrowly separated (N = 12), just touching (N = 5), in short contact (N = 9) or in broad contact (N = 15). There is geographic variation in the degree of separation/contact of the nasal scales, with western populations (previously assigned to *L. m. microtis* and *L. m. intermedia*) possessing either wide to narrowly separated nasals, or just touching nasals, whereas those from the east (populations previously assigned to *L. arenicola* and *L. m. schwaneri*) are in short to broad contact. Prefrontals widely separated. Frontoparietals divided, in broad contact and about as large as interparietal. Four supraoculars (first two in contact with frontal). Six supraciliaries (first largest). One postnasal, one loreal, two presuboculars. Nuchals 1 (N = 1), 2 (N = 7), 3 (N = 26) or 4 (N = 11) on each side. Mid-body scale rows 19 (N = 1), 20 (N = 19), 21 (N = 7) or 22 (N = 18). Subdigital lamellae under 4th toe = 15–24 (average = 20).

Colour pattern in life. Variable in colour and pattern; dorsal ground colour may be pale whitish grey to dark greyish brown. Tail colour is typically a continuation of dorsal body colour, but in some specimens the tail is dull to bright orange, sometimes only beneath tail. Dorsal patterning variable; a vertebral stripe and/or paravertebral stripes may be either absent, form faint broken stripes, or continuous stripes with either bold or indistinct edges. If present, these stripes extend from nape to the tail base, becoming broken lines and dots on tail. Pale dorsolateral stripe is usually either absent or faint and narrow (occasionally bold and broad). Black upper lateral stripe is bold and wide, bordered below by a narrower white midlateral stripe. Conversely, mainland specimens from the east of the species' range (specimens previously assigned to *L. arenicola*), have a narrow and indistinctly edged black upper lateral stripe, with wide white midlateral stripe. Black lower lateral stripe usually present and narrower than upper lateral stripe, being very narrow and diffuse in mainland specimens from the east of the species' range. SA island populations possess bolder patterning (those previously assigned to *L. m. schwaneri*). Lower flanks greyish white. Ventral surface greyish white with sparse to heavy stippling, sometimes with dark scale margins. Underside of tail and legs orange to pinkish white.

Colour pattern in preservative. Same as for live specimens, but with more faded and less vibrant colouration overall.

Distribution and habitat. Distributed over a long (2,200 km) but relatively narrow stretch of Australia's southern coastline (Figure 1), from Dwellingup State Forest (WA) east to Wedge Island (SA). Recorded from several islands, including Saint Alouarn (WA), Wickham (WA), Goat (SA), St Peter (SA) Franklin Islands (SA), Williams (SA), and Wedge (SA). Occurs in woodland, coastal heath, sandplains, and coastal dunes where it shelters within or on loose soil beneath surface cover such as leaf litter, clumps of dead vegetation, logs, and rocks. Occasionally found in abandoned stick-ant (*Iridomyrmex conifer*) nests (in south-west of range; Peterson & Metcalfe 2005) and under clumps of dry seaweed on beaches (on Eyre Peninsula).

Conservation. There are no known major threats to the species (Chapple *et al*. 2019). We calculated extent of occurrence (EOO) and area of occupancy (AOO) in GeoCat (http://geocat.kew.org; Bachman *et al*. 2011). The species occurs in multiple protected areas and has a large EOO of 651,840 km^2 (measured as the minimum convex hull around all records, including ocean areas, as per IUCN guidelines). It has a relatively small AOO (2 x 2 km grid cells) of 516 km^2, which meets the IUCN threshold of Vulnerable under Criterion B2 (AOO < 2,000 km^2; IUCN 2022). However, it is unlikely to qualify for listing given it does not meet other conditions of Criterion 2; it occurs at ≥ 10 locations, is not severely fragmented, and there is no evidence of continuing decline or extreme fluctuations in its distribution or populations. Further sampling across the species' range is required to further clarify the AOO, which is likely to be higher than current records suggest.

Acknowledgements

We thank M. Danks and N. Wilson (Molecular Systematics Unit, WAM) for generating additional sequences for this project, Domenic Capone (South Australia Museum) for loan of specimens in his care, and M. Hutchinson and S. Wilson for helping locate a photo of *L. m. schwaneri*. We thank G. Shea for a valuable critique of earlier versions of the manuscript. The project was funded by a grant from the Australian Research Council (FT200100108; to DGC) and by U.S. NSF 1754398 (DLR).

Conflict of Interest

The authors declare that they do not have any conflict of interest.

Data availability statement

Information on the specimens examined in this study are available in the appendix. Raw and size-corrected morphological data are available upon request from the corresponding author.

References

Aplin, K.P. & Adams, M. (1998) New species of gekkonid and scincid lizards (Squamata) from the Carnarvon Basin region of Western Australia: morphological and genetic studies of ''cryptic species.'' *Journal of the Royal Society of Western Australia*, 81, 201–204.

Battey, C.J., Ralph, P.L. & Kern, A.D. (2020) Space is the place: Effects of continuous spatial structure on analysis of population genetic data. *Genetics*, 215 (1), 193–214. https://doi.org/10.1534/genetics.120.303143

Braby, M.F., Eastwood, R. & Murray, N. (2012) The subspecies concept in butterflies: Has its application in taxonomy and conservation biology outlived its usefulness? *Biological Journal of the Linnean Society*, 106, 699–716. https://doi.org/10.1111/j.1095-8312.2012.01909.x

Brenneman, R.A., McLain, A.T., Taylor, J.M., Zaonarivelo, J.R., Lei, R., McGuire, S.M., Andriantompohavana, R., Rylands, A.B., Louis, E.E. Jr. (2016) Genetic analysis of the Indri reveals no evidence of distinct subspecies. *International Journal of Primatology*, 37, 460–477. https://doi.org/10.1007/s10764-016-9911-3

Burbrink, F.T., Crother, B.I., Murray, C.M., Smith, B.T., Ruane, S., Myers, E.A. & Pyron, R.A. (2022) Empirical and philosophical problems with the subspecies rank. *Ecology and Evolution*, 12 (7), e9069. https://doi.org/10.1002/ece3.9069

Chan, K.O. & Grismer, L.L. (2022) GroupStruct: an R package for allometric size correction. *Zootaxa*, 5124 (4), 471–482. https://doi.org/10.11646/zootaxa.5124.4.4

Chang, C., Wu, P., Baker, R.E., Maini, P.K., Alibardi, L. & Chuong, C.-M. (2009) Reptile scale paradigm: evodevo, pattern formation and regeneration. *The International Journal of Developmental Biology*, 53, 813–826. https://doi.org/10.1387/ijdb.072556cc

Chapple, D., Tingley, R., Mitchell, N., Macdonald, S., Keogh, J., Shea, G., Bowles, P., Cox, N. & Woinarski, J. (2019) *Action Plan for Australian Lizards and Snakes 2017*. CSIRO Publishing, Clayton South, Victoria, 680 pp. https://doi.org/10.1071/9781486309474

Darwin, C. (1859) *On the origin of species by means of natural selection*. John Murray, London. Available from: https://darwin-online.org.uk/content/frameset?itemID=F373&viewtype=text&pageseq=1 (accessed 20 March 2024)

de Queiroz, K. (1998) The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. *In*: Howard, D.J. & Berlocher, S.H. (Eds.), *Endless Forms: Species and Speciation*. Oxford University Press, Oxford, pp. 57–75.

de Queiroz, K. (2020) An updated concept of subspecies resolves a dispute about the taxonomy of incompletely separated lineages. *Herpetological Review*, 51, 459–461.

de Queiroz, K. (2021) Response to criticisms of an updated subspecies concept. *Herpetological Review*, 52 (4), 773–776.

Eaton, D.A.R. & Overcast, I. (2020) ipyrad: Interactive assembly and analysis of RADseq datasets. *Bioinformatics*, 36, 2592–2594. https://doi.org/10.1093/bioinformatics/btz966

Gray, J.E. (1845) *Catalogue of the specimens of lizards in the collection of the British Museum.* Trustees of the British Museum/ Edward Newman, London, 83 pp.

Greer, A.E. (1967) A new generic arrangement for some Australian scincid lizards. *Breviora Museum of Comparative Zoology*, 267, 1–19.

Haig, S.M., Beever, E.A., Chambers, S.M., Draheim, H.M., Dugger, B.D., Dunham, S., Elliott-Smith, E., Fontaine, J.B., Kesler, D.C., Knaus, B.J., Lopes, I.F., Loschl, P., Mullins, T.D. & Sheffield, L.M. (2006) Taxonomic considerations in listing subspecies under the U.S. Endangered Species Act. *Conservation Biology*, 20, 1584–1594. https://doi.org/10.1111/j.1523-1739.2006.00530.x

Hillis, D.M. (2019) Species delimitation in herpetology. *Journal of Herpetology*, 53, 3–12. https://doi.org/10.1670/18-123

Hillis, D.M. (2020) The detection and naming of geographic variation within species. *Herpetological Review*, 51, 52–56.

Hillis, D.M. (2021) Conceptualizations of species and subspecies: A Reply to the 'It's Species All the Way Down View'.

Herpetological Review, 52, 49–50.
Hillis, D.M. & Wüster, W. (2021) Taxonomy and nomenclature of the *Pantherophis obsoletus* complex. *Herpetological Review*, 105, 795–809.
Hillis, D.M. (2022) Distinguishing intraspecific geographic variation from distinct species boundaries. *Sonoran Herpetologist*, 35 (2), 52–57.
Hutchinson, M., Adams, M. & Fricker, S. (2006) Genetic variation and taxonomy of the *Ctenotus brooksi* species-complex (Squamata: Scincidae). *Transactions of the Royal Society of South Australia*, 130, 48–65.
https://doi.org/10.1080/3721426.2006.10887047
Hutchinson, M.N. & Rawlinson, P.A. (1995) The water skinks (Lacertilia: *Eulamprus*) of Victoria and South Australia. *Records of the South Australian Museum*, 28, 185–207.
Hutchinson, M.N., Doughty, P. & Oliver, P.M. (2009) Taxonomic revision of the stone geckos (Squamata: Diplodactylidae: *Diplodactylus*) of southern Australia, *Zootaxa*, 2167 91), 25–46.
https://doi.org/10.11646/zootaxa.2167.1.2
IUCN (2022) *The Guidelines for Using the IUCN Red List Categories and Criteria.* Version 15.1. July 2022. Available from: https://www.iucnredlist.org/resources/redlistguidelines (accessed 11 May 2023)
Jackson, N.D., Carstens, B.C., Morales, A.E. & O'Meara, B.C. (2017) Species delimitation with gene flow. *Systematic Biology*, 66, 799–812.
Jörger, K.M. & Schrödl, M. (2013) How to describe a cryptic species? Practical challenges of molecular taxonomy. *Frontiers in Zoology*, 10 (1), 1–27.
https://doi.org/10.1186/1742-9994-10-59
Kaiser, H.F. (1960) The application of electronic computers to factor analysis. *Educational and Psychological Measurement*, 20 (1), 141–151.
https://doi.org/10.1177/001316446002000116
Kassambara, A. & Mundt, F. (2020) *Factoextra: Extract and visualize the results of multivariate data analyses. R Package Version 1.0.7*. Available from: https://CRAN.R-project.org/package=factoextra (accesed 20 March 2024)
Kealley, L., Doughty, P., Edwards, D. & Brennan, I.G. (2020) Taxonomic assessment of two pygopodoid gecko subspecies from Western Australia. *Israel Journal of Ecology and Evolution*, 66 (3–4), 126–141.
https://doi.org/10.1163/22244662-20191078
Keogh, J.S., Scott, I.A. & Hayes, C. (2005) Rapid and repeated origin of insular gigantism and dwarfism in Australian tiger snakes. *Evolution*, 59 (1), 226–233.
https://doi.org/10.1111/j.0014-3820.2005.tb00909.x
Kleiber, C. & Zeileis, A. (2022) *AER: Applied Econometrics with R. R package Version 1.2–10*. Available from: https://CRAN.R-project.org/package=AER (accessed 20 March 2024)
Lê, S., Josse, J. & Husson, F. (2008) FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software*, 25, 1–18.
https://doi.org/10.18637/jss.v025.i01
Lleonart, J., Salat, J. & Torres, G.J. (2000) Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology*, 205 (1), 85–93.
https://doi.org/10.1006/jtbi.2000.2043
Maryan, B., Brennan, I.G., Hutchinson, M.N. & Geidans, L.S. (2020) What's under the hood? Phylogeny and taxonomy of the snake genera *Parasuta* Worrell and *Suta* Worrell (Squamata: Elapidae), with a description of a new species from the Pilbara, Western Australia. *Zootaxa*, 4778 (1), 1–47.
https://doi.org/10.11646/zootaxa.4778.1.1
Martinez Arbizu, P. (2017) *pairwiseAdonis: Pairwise multilevel comparison using adonis*. R Package Version 0.4. Available from: https://github.com/pmartinezarbizu/pairwiseAdonis (accessed 20 March 2024)
Mayr, E. (1963) *Animal species and evolution*. Harvard University Press, Cambridge, XVI + 797 pp.
https://doi.org/10.4159/harvard.9780674865327
Mayr, E. (1982) Of what use are subspecies? *The Auk*, 99, 593–595.
McCoy, M.W., Bolker, B.M., Osenberg, C.W., Miner, B.G. & Vonesh, J.R. (2006) Size correction: Comparing morphological traits among populations and environments. *Oecologia*, 148, 547–554.
https://doi.org/10.1007/s00442-006-0403-6
Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *2010 Gateway Computing Environments Workshop*, 2010, 1–8. [https://ieeexplore.ieee.org/document/5676129]
https://doi.org/10.1109/GCE.2010.5676129
Nankivell, J.H., Maryan, B., Bush, B.G. & Hutchinson, M.N. (2023) Whip it into shape: Revision of the *Demansia psammophis* (Schlegel, 1837) complex (Squamata: Elapidae), with a description of a new species from central Australia. *Zootaxa*, 5311 (3), 301–339.
https://doi.org/10.11646/zootaxa.5311.3.1
Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J. & Suggests, M.A.S.S. (2007) The vegan package. *Community ecology package*, 10(631–637), 719.
Owen, D.F. (1963a) Screech owl polymorphism. *Wilson Bulletin*, 75, 183–189.

Owen, D.F. (1963b) Variation in North American screech owls and the subspecies concept. *Systematic Zoology*, 12, 8–14. https://doi.org/10.2307/2411890
Padial, J.M. & De la Riva, I. (2021) A paradigm shift in our view of species drives current trends in biological classification. *Biological Reviews*, 96, 731–751. https://doi.org/10.1111/brv.12676
Patten, M.A. (2015) Subspecies and the philosophy of science. *The Auk*, 132, 481–485. https://doi.org/10.1642/AUK-15-1.1
Patton, J.L. & Conroy, C.J. (2017) The conundrum of subspecies: morphological diversity among desert populations of the California vole (*Microtus californicus*, Cricetidae). *Journal of Mammalogy*, 98 (4), 1010–1026. https://doi.org/10.1093/jmammal/gyx074
Pepper, M., Sumner, J., Brennan, I.G., Hodges, K., Lemmon, A.R., Lemmon, E.M., Peterson, G., Rabosky, D.L., Schwarzkopf, L., Scott, I.A., Shea, G. & Keogh, S. (2018) Speciation in the mountains and dispersal by rivers: Molecular phylogeny of *Eulamprus* water skinks and the biogeography of Eastern Australia. *Journal of Biogeography*, 45 (9), 2040–2052. https://doi.org/10.1111/jbi.13385
Peterson, M. & Metcalfe, C. (2005) Herpetofaunal assemblages utilising abandoned stick-nest ant (*Iridomyrmex conifer*) nests as refugia. *Herpetofauna*, 35 (1), 7–10.
Pulido-Santacruz, P., Aleixo, A. & Weir, J.T. (2020) Genomic data reveal a protracted window of introgression during the diversification of a neotropical woodcreeper radiation. *Evolution*, 74 (5), 842–858. https://doi.org/10.1111/evo.13902
Prates, I., Doughty, P. & Rabosky, D.L. (2023) Subspecies at crossroads: the evolutionary significance of genomic and phenotypic variation in a wide-ranging Australian lizard (*Ctenotus pantherinus*). *Zoological Journal of the Linnean Society*, 197 (3), 768–786. https://doi.org/10.1093/zoolinnean/zlac076
R Core Team (2022) *R: a language and environment for statistical computing. Version 4.1.2*. R Foundation for Statistical Computing, Vienna. [program]
Rabosky, D.L., Talaba, A.L., Donnellan, S.C. & Lovette, I.J. (2009) Molecular evidence for hybridization between two Australian desert skinks, *Ctenotus leonhardii* and *Ctenotus quattuordecimlineatus* (Scincidae: Squamata). *Molecular Phylogenetics and Evolution*, 53, 368–377. https://doi.org/10.1016/j.ympev.2009.06.020
Rabosky, D.L., Hutchinson, M.N., Donnellan, S.C., Talaba, A.L. & Lovette, I.J. (2014) Phylogenetic disassembly of species boundaries in a widespread group of Australian skinks (Scincidae: *Ctenotus*). *Molecular Phylogenetics and Evolution*, 77, 71–82. https://doi.org/10.1016/j.ympev.2014.03.026
Reist, J.D. (1985) An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Canadian Journal of Zoology*, 63, 1429–1439. https://doi.org/10.1139/z85-213
Remsen, J.V. (2010) Chapter 6: Subspecies as a meaningful taxonomic rank in avian classification. *Ornithological Monographs*, 67, 62–78. https://doi.org/10.1525/om.2010.67.1.62
Singhal, S., Huang, H., Grundler, M.R., Marchaìn-Rivadeneira, M.R., Holmes, I., Title, P.O., Donnellan, S.C. & Rabosky, D.L. (2018) Does population structure predict the rate of speciation? A comparative test across Australia's most diverse vertebrate radiation. *The American Naturalist*, 192, 432–447. https://doi.org/10.1086/699515
Singhal, S., Huang, H., Title, P.O., Donnellan, S.C., Holmes, I. & Rabosky, D.L. (2017) Genetic diversity is largely unpredictable but scales with museum occurrences in a species-rich clade of Australian lizards. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20162588. https://doi.org/10.1098/rspb.2016.2588
Smith, H.M. & White, F.N. (1956) A case for the trinomen. *Systematic Zoology*, 5 (4), 183–190. https://doi.org/10.2307/2411920
Smith, L.A. (1991) Obituary: Glen Milton Storr 1921–1990. *Copeia*, 1991 (2), 550–552.
Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30, 1312–1313. https://doi.org/10.1093/bioinformatics/btu033
Storr, G.M. (1970) The genus *Ctenotus* (Lacertilia: Scincidae) in the Northern Territory. *Journal of the Royal Society of Western Australia*, 52 (4), 97–108.
Storr, G.M. (1971) The genus *Lerista* (Lacertilia, Scincidae) in Western Australia. *Journal of the Royal Society of Western Australia*, 54 (3), 59–75.
Storr, G.M. (1978) Taxonomic notes on the reptiles of the Shark Bay region, Western Australia. *Records of the Western Australian Museum*, 6 (3), 303–318.
Storr, G.M. (1981) Ten new *Ctenotus* (Lacertilia: Scincidae) from Australia. *Records of the Western Australian Museum*, 9 (2), 125–146

Storr, G.M. (1991a) Revision of *Lerista microtis* (Lacertilia: Scincidae). *Records of the Western Australian Museum*, 15 (2), 469–476.
Storr, G.M. (1991b) Partial revision of the *Lerista macropisthopus* group (Lacertilia: Scincidae). *Records of the Western Australian Museum*, 15 (1) 149–161.
Storr, G.M. (1991c) A new subspecies of *Lerista planiventralis* (Lacertilia: Scincidae) from Western Australia. *Records of the Western Australian Museum*, 15 (2) 483–485.
Thorpe, R.S. (1983) A review of the numerical methods for recognising and analysing racial differentiation. *In*: Felsenstein, J. (Ed.), *Numerical Taxonomy*. *NATO ASI Series. Vol. 1*. Springer, Berlin/Heidelberg, pp. 404–423. https://doi.org/10.1007/978-3-642-69024-2_43
Thorpe, R.S. (1975) Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the ringed snake *Natrix natrix* (L.). *Biological Journal of the Linnean Society*, 7 (1), 27–43. https://doi.org/10.1111/j.1095-8312.1975.tb00732.x
Uetz, P. & Stylianou, A. (2018) The original descriptions of reptiles and their subspecies. *Zootaxa*, 4375 (2), 257–264. https://doi.org/10.11646/zootaxa.4375.2.5
Uetz, P., Freed, P. & Hošek, J. (2022) *The Reptile Database*. Available from: http://www.reptile-database.org/db-info/SpeciesStat.html (accessed 8 May 2023)
Wallis, E.J. (2006) Online Zoological Collections of Australian Museums (OZCAM): a national approach to making zoological data available on the web. *Integrative Zoology*, 1, 78–79. https://doi.org/10.1111/j.1749-4877.2006.00018.x
Wang, X., He, Z., Shi, S. & Wu, C.-I. (2019) Genes and speciation: Is it time to abandon the biological species concept? *National Science Review*, 7, 1387–1397. https://doi.org/10.1093/nsr/nwz220
Wilson, E.O. & Brown, W.L. (1953) The subspecies concept and its taxonomic application. *Systematic Zoology*, 2, 97–111. https://doi.org/10.2307/2411818
Wilson, S. & Swan, G. (2021) *A Complete Guide to Reptiles of Australia*. *6th Edition*. Reed New Holland, Wahroonga, New South Wales, 572 pp.
Zink, R.M. (2004) The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proceeding of the Royal Society B*, 271, 561–564. https://doi.org/10.1098/rspb.2003.2617

Appendix

TABLE A1. Specimens from which morphological measurements were obtained.

Voucher	Original taxon ID	Subspecies	Location	Latitude	Longitude
NMV D942	*Lerista arenicola*		SA: Fowlers Bay	-31.97	132.57
WAM R108299	*Lerista microtis*	*Lerista microtis intermedia*	WA: Wickham Island	-34.016667	123.283333
WAM R108304	*Lerista microtis*	*Lerista microtis intermedia*	WA: Middle Island, Archipelago of the Recherche	-34.1	123.183333
WAM R113419	*Lerista microtis*	*Lerista microtis microtis*	WA: 5 km SE Margaret River	-33.966667	115.116667
WAM R124857	*Lerista microtis*	*Lerista microtis microtis*	WA: Mount Lindesay	-34.8333	117.3
WAM R129004	*Lerista microtis*	*Lerista microtis microtis*	WA: Shannon Basin	-34.5722	116.3219
WAM R129702	*Lerista microtis*	*Lerista microtis intermedia*	WA: Quagi Beach	-33.8333	121.2833
WAM R132057	*Lerista microtis*	*Lerista microtis microtis*	WA: Jangardup Study Area; Dentrecasteaux National Park	-34.416667	115.75
WAM R134133	*Lerista microtis*	*Lerista microtis microtis*	WA: Kingston Forest Block	-34.0833	116.3333

.....Continued on the next page

TABLE A1. (Continued)

Voucher	Original taxon ID	Subspecies	Location	Latitude	Longitude
WAM R134314	*Lerista microtis*	*Lerista microtis intermedia*	WA: Goose Island	-34.0783	123.1853
WAM R135702	*Lerista microtis*	*Lerista microtis microtis*	WA: Kronkup Rubbish Tip; Torbay Road	-35.173	117.6206
WAM R137656	*Lerista arenicola*		SA: 12 km E WA/SA Border	-31.65	129.1167
WAM R144369	*Lerista microtis*	*Lerista microtis microtis*	WA: 8 km North Bow Bridge	-34.882222	116.935556
WAM R146223	*Lerista microtis*	*Lerista microtis microtis*	WA: Kingston Forest Block	-34.149167	116.370556
WAM R165570	*Lerista microtis*	*Lerista microtis microtis*	WA: Upper Kalgan	-34.5222	118.5317
WAM R165571	*Lerista microtis*	*Lerista microtis microtis*	WA: Upper Kalgan	-34.519444	118.525556
WAM R165593	*Lerista microtis*	*Lerista microtis microtis*	WA: Bridgetown Area	-34.022778	116.168611
WAM R172295	*Lerista microtis*	*Lerista microtis intermedia*	WA: Quagi Beach	-33.8308	121.2939
SAMA R23032	*Lerista arenicola*		WA: Old Eucla	-31.72	128.88
SAMA R25654	*Lerista arenicola*		SA: Koonalda Campsite No.1, 12.5 km NE Colona Stn	-31.53	132.13
SAMA R29496	*Lerista microtis*	*Lerista microtis microtis*	WA: Esperance	-33.87	121.9
SAMA R44277	*Lerista microtis*	*Lerista microtis schwaneri*	SA: N side of Wedge Island	-35.15	136.45
SAMA R45855	*Lerista microtis*	*Lerista microtis schwaneri*	SA: Wedge Island	-35.15	136.475
SAMA R45924	*Lerista microtis*	*Lerista microtis schwaneri*	SA: Wedge Island, N side of sandy interdune	-35.1889	136.4778
SAMA R45925	*Lerista microtis*	*Lerista microtis schwaneri*	SA: Wedge Island, N side of sandy interdune	-35.1889	136.4778
SAMA R49771	*Lerista microtis*	*Lerista microtis schwaneri*	SA: West Franklin Island, SE coast	-32.4583	133.6444
SAMA R49772	*Lerista microtis*	*Lerista microtis schwaneri*	SA: West Franklin Island, SE coast	-32.4583	133.6444
SAMA R49773	*Lerista microtis*	*Lerista microtis schwaneri*	SA: West Franklin Island, SE coast	-32.4583	133.6444
SAMA R52648	*Lerista microtis*	*Lerista microtis schwaneri*	SA: Williams Island	-35.0292	135.9697
SAMA R57756	*Lerista arenicola*		SA: 24 km WNW Coffin Bay	-34.5433	135.2258
SAMA R5860	*Lerista arenicola*		SA: Head of Bight	-31.4516	131.120795

.....Continued on the next page

TABLE A1. (Continued)

Voucher	Original taxon ID	Subspecies	Location	Latitude	Longitude
SAMA R61253	*Lerista arenicola*		SA: 5.7 km ESE Edrilpa	-32.4625	134.00717
SAMA R63259	*Lerista microtis*	*Lerista microtis microtis*	WA: Albany	-35.0925	117.9603
SAMA R64527	*Lerista arenicola*		SA: Almonta Beach approx 13 km WSW Coffin Bay	-34.6811	135.3439
SAMA R64970	*Lerista arenicola*		SA: Talia Caves, Venus Bay	-33.3294	134.8003
WAM R66915	*Lerista arenicola*		WA: 13 km W of Eyre	-32.25	126.183333
WAM R66919	*Lerista arenicola*		WA: 13 km W of Eyre	-32.25	126.183333
WAM R66920	*Lerista arenicola*		WA: 13 km W of Eyre	-32.25	126.183333
WAM R66922	*Lerista arenicola*		WA: 13 km W of Eyre	-32.25	126.183333
SAMA R71413	*Lerista arenicola*		SA: Talia Caves, Venus Bay	-33.3294	134.8003
SAMA R72097	*Lerista arenicola*		SA: Whagunyah Conservation Park, Cheetima Beach	-32.01446	132.17485
SAMA R72105	*Lerista arenicola*		SA: Fowlers Bay	-31.98777	132.4349
SAMA R72106	*Lerista arenicola*		SA: Fowlers Bay	-31.98777	132.4349
WAM R88478	*Lerista microtis*	*Lerista microtis microtis*	WA: Waroona	-32.85	116.016667
WAM R89355	*Lerista microtis*	*Lerista microtis intermedia*	WA: Hopetoun	-33.95	120.116667

TABLE A2. Summary statistics and loadings of the principal component analysis (PCA) of adjusted mensural characters. Character abbreviations are defined in materials and methods.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Proportion of Variance	0.71	0.12	0.10	0.02	0.01	0.01
Cumulative Proportion	0.71	0.83	0.94	0.97	0.98	1
Eigenvalues	4.27	0.75	0.63	0.17	0.08	0.06
Loadings						
SVL	0.57	0.72	-0.37	-0.03	-0.01	0.01
HL	0.93	-0.05	0.23	-0.13	-0.22	0.03
HW	0.91	0.01	0.26	-0.23	0.17	-0.04
AGD	-0.64	0.46	0.59	0.07	0.005	0.04
Forelimb	0.94	0.02	0.13	0.25	-0.01	-0.15
Hindlimb	0.95	-0.11	0.01	0.17	0.07	0.18

TABLE A3. Information on genetic samples used in this study for the *Lerista microtis* group.

Voucher	Original taxon ID	Subspecies	Location	Latitude	Longitude	GenBank accession	SRA accession
SAMA R45923	*Lerista microtis*	*L. m. schwaneri*	SA: Wedge Island	-35.18889	136.4778	OR026697	
SAMA R50095	*Lerista arenicola*		SA: Dunes of Talia Beach S Venus Bay	-33.33333	134.8	OR026698	SRX4232957
SAMA R53771	*Lerista arenicola*		SA: 25.4 km WNW Coffin Bay	-34.54778	135.2089	OR026699	
WAM R113418	*Lerista microtis*	*L. m. microtis*	WA: 5 km SE Margaret River	-33.9666	115.1167	OR026701	SRX4232960
WAM R124857	*Lerista microtis*	*L. m. microtis*	WA: Mount Lindesay	-34.833333	117.3	OR026702	
WAM R129004	*Lerista microtis*	*L. m. microtis*	WA: Shannon Basin	-34.5722	116.3219	OR026703	SRX4232959
WAM R129679	*Lerista microtis*	*L. m. microtis*	WA: 10 km N Denmark	-34.85	117.35	OR026704	
WAM R129702	*Lerista microtis*	*L. m. intermedia*	WA: Quagi Beach	-33.833333	121.283333	OR026705	
WAM R134133	*Lerista microtis*	*L. m. microtis*	WA: Kingston Forest Block	-34.083333	116.333333	OR026706	
WAM R134314	*Lerista microtis*	*L. m. intermedia*	WA: Goose Island	-34.078333	123.185278	OR026707	
WAM R135702	*Lerista microtis*	*L. m. microtis*	WA: Kronkup Rubbish Tip Torbay Road	-35.173	117.6206	OR026708	SRX4232954
WAM R137656	*Lerista arenicola*		SA: 12 km E WA-SA Border	-31.65	129.1167	OR026709	SRX4232953
WAM R165570	*Lerista microtis*	*L. m. microtis*	WA: Upper Kalgan	-34.5222	118.5317	OR026710	SRX4232956
WAM R172295	*Lerista microtis*	*L. m. intermedia*	WA: Quagi Beach	-33.830833	121.293889	OR026711	
WAM R90371	*Lerista microtis*	*L. m. microtis*	WA: Walpole-Nornalup National Park	-35.003889	116.620556	OR026700	