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

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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 to require synonymy or elevation to full species under current views of species as separately evolving population lineages. These modern taxonomic resolutions have resulted from a combination of new molecular genetic techniques, improved geographical sampling of specimens, and more sophisticated morphological analyses (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, Storr described an additional species (*Lerista arenicola*) and two additional subspecies (*L. m. intermedia* and *L. m. schwaneri*). We

collected data on mensural, meristic, and colour pattern characters to explore morpho-spatial relationships among Storr's proposed 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 both mitochondrial and genome-wide ddRAD DNA sequences 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 morphologically variable species – an arrangement that best reflects evolutionary history.

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 the biological species concept would predict (Jackson *et al*. 2017; Wang *et al*. 2019; de Queiroz 2020; Pulido-Santacruz *et al*. 2020). While modern biologists 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 entities of the same fundamental kind (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 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) are recognised as subspecies 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). However, 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). In the context of subspecies, we argue that such minute and inconsistent differences in morphology should not be used as a basis for taxonomic recognition, given that the primary role of the subspecific rank to denote morphologically distinctive populations of species. And unlike the boundary between species, subspecies have no clear lower limit for how much to partition populations in a geographical cline into separate taxa (Hillis 2022).

Storr used apparent spatial clustering in morphological characters as justification for partitioning populations into subspecies. However, these supposedly distinct phenotypic regions increasingly appear to overlap significantly, and reflect incompleteness of spatial sampling rather than evolutionarily relevant distinctions (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 Storr's (1991a) proposed species- and subspecies-level taxa in the *Lerista microtis* group (Fig. 1). Here we outline our definitions of species and subspecies, so it is clear how our data is being used to evaluate support for Storr's taxa:

Species: populations that are genetically distinct, independently evolving entities, 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 independence. 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 delimitating species.

Subspecies: populations that are not phylogenetically independent, but warrant nomenclatural and taxonomic recognition as morphologically and geographically distinct entities below the species level. We emphasise the dual condition of morphological and geographic distinct because this is the classical criteria used to describe subspecies. For instance, a morphologically distinct population that is the product of clinal variation and overlaps significantly with neighbouring morphs should not be, in our view, considered a subspecies—this is simply clinal phenotypic variation over the range of a continuously distributed species. We believe that such patterns of variation should not be incorporated into the classification system and receive a trinomial name.

2 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). 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 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.

198 Meristic characters were: number of mid-body scale rows (***MSR***); number of subdigital
199 lamellae under the fourth toe of left foot (***SubDig***); number of nuchal scales on the left side
200 (***Nuchals***).
201 Qualitative characters (e.g., Figure 2) were: dorsal patterning (***DP***), upper lateral stripe
202 boldness (***ULSB***), upper lateral stripe width (***ULSW***), mid-lateral stripe width (***MLSW***), and
203 nasal scale separation (***NSS***) (Table 1).
204
205 **Statistical analysis of morphology**
206 Univariate and multivariate analyses were used to determine whether morpho-spatial
207 variation could form the basis of detectable group structure among the *Lerista* taxa posited by
208 Storr (1991a), namely *L. arenicola* and the subspecies of *L. microtis*.
209
210 *Size correction of mensural data*
211 To remove potential bias caused by ontogenetic variation, juvenile specimens (n = 3,
212 assessed based on their very small size compared to adult specimens) were excluded from
213 mensural analyses, and adult size variation in mensural characters was normalised using a
214 modification of the Thorpe (1975) allometric growth equation: $X_{adj} = \log(X) - \beta[\log(SVL) -$
215 $\log(SVL_{mean})]$, where X_{adj} = size corrected value; X = measured trait value; β =
216 unstandardized regression coefficient for each taxon; and SVL_{mean} = the mean SVL of each
217 taxon (different SVL_{mean} calculated for each taxon) (Thorpe 1975, 1983; Turan 1999;
218 Lleonart *et al*. 2000; Chan & Grismer 2022). There is no inter-lineage conflation of variation,
219 given that mensural character adjustments were conducted separately on each taxon (Reist
220 1985; McCoy *et al*. 2006). Logarithmic transformations were performed at base 10. This
221 allometric correction was implemented with the '*allom()*' function in the *GroupStruct*
222 package (v0.1.0; Chan & Grismer 2022). All downstream mensural character analyses were

223 performed on these adjusted values. No size adjustments were made to meristic data because
224 scale characters do not change during ontogeny (Chang *et al*. 2009).
225
226 *Univariate analysis*
227 Given that many specimens (35%) had incomplete tails (i.e., regenerated, broken, or
228 missing), tail length was excluded from analyses. One-way analyses of variance (ANOVA)
229 were performed on the mensural characters to test for the presence of statistically significant
230 (p<0.05) mean inter-taxon differences. Tukey HSD *post hoc* tests were used to determine
231 which taxon pairs had significantly different mean values for each character, after adjusting
232 for multiple comparisons. For characters that did not meet the parametric assumption of
233 normality (Shapiro-Wilk test p<0.05) or equal variance across groups (i.e., Levene's test
234 p<0.05), we used Welch's F-test and Games-Howell *post hoc* test. Meristic characters (i.e.,
235 positive integer count data) were analysed using generalised linear models (GLMs) to explore
236 significant differences among linages. Tests for over-dispersion of meristic variables, using
237 the '*dispersiontest*' function in the *AER* package (v1.2-10; Kleiber & Zeileis 2008), revealed
238 that all meristic traits were under-dispersed, hence we used Quasi-Poisson errors for all
239 GLMs. To visualise the distribution of trait variation across taxa, we produced violin plots
240 with embedded boxplots for the mensural (continuous) characters, and boxplots for the
241 meristic (discrete) characters.
242
243 *Multivariate analysis*
244 For mensural characters, we first created low-dimensional representations of variation
245 in the data, achieved by performing principal component analyses (PCA) implemented with
246 the packages *FactorMineR* (v2.4; Lê *et al*. 2008) and *factoextra* (v1.0.7; Kassambara &
247 Mundt 2017). Eigenvalues >1 were retained according to Kaiser's criterion (Kaiser 1960),

248 resulting in the first PC retained. To visualise multivariate group structure among taxa in
249 qualitative characters (plus MSR), we employed non-metric multidimensional scaling (MDS)
250 using the *'metaMDS()'* function of the *vegan* package (v2.6–5; Oksanen *et al*. 2020). We then
251 tested whether longitude predicts morphological variation by performing linear regression of
252 longitude against major axes of morphological variation (i.e. PC1, nMDS1, nMDS2).
253 Separately for the mensural character dataset and the qualitative character (plus MSR)
254 dataset, we used the *'adonis2()'* function of the *vegan* package (v2.6–5; Oksanen *et al*. 2020)
255 to perform non-metric permutation multivariate analysis of variance (PERMANOVA) to
256 determine if the centroid locations of each taxon are statistically different from one another.
257 PERMANOVAs were based on the calculation of a Euclidean (dis)similarity matrix using
258 5,000 permutations for each dataset. The *'pairwise.adonis()'* function of the *pairwiseAdonis*
259 package (v0.4; Martinez 2017) was used to generate summary statistics of *post hoc* pairwise
260 comparison tests between lineages, providing a pseudo-F statistic, R^2 value, *p*-value, and
261 adjusted *p*-value for each comparison. Significant *p*-values ($p<0.05$) indicate segregation of
262 taxon pairs, the strength of which is denoted by larger pseudo-F statistics. All morphological
263 analyses were performed and visualized in R (v4.1.2, R Core Team 2022).
264
265 *Sampling of genetic data*
266 To assess the genetic coherence and distinctiveness of currently recognized taxa in the
267 *L. microtis* complex, we inferred evolutionary relationships based on both mitochondrial and
268 genome-wide nuclear loci. Our genetic analyses incorporated data from 15 ingroup
269 individuals, namely *L. arenicola* (N = 3), *L. m. intermedia* (3), *L. m. microtis* (8), and *L. m.*
270 *schwaneri* (1). To provide a reference of levels of intra-taxon divergence across *Lerista*, we
271 also incorporated data from 94 individuals representing 22 taxa from other major *Lerista*
272 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 preliminary analyses and previous investigations incorporating genome-wide data (Singhal *et al*. 2017, 2018). As outgroups, we included two representatives of each of *Ctenotus atlas*, *C. pantherinus*, *C. schomburgkii*, *Eremiascincus fasciolatus*, and *E. musivus* for a total of 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.

297 To infer evolutionary relationships based on the mitochondrial genome, we PCR-
298 amplified, sequenced, edited, and aligned a 1,143 base pair fragment of the *cytochrome B*
299 gene following standard protocols described in Rabosky *et al*. (2009). Newly generated
300 mitochondrial sequences were uploaded to GenBank (OR026697-OR026711).
301
302 *Inferring evolutionary coherence and distinctiveness*
303 To infer evolutionary relationships, we analysed the nuclear and mitochondrial
304 datasets separately. In each case, we used an individual-based approach for phylogenetic
305 inference under Maximum Likelihood, allowing us to assess whether individuals assigned to
306 the same taxon (at the level of species or subspecies) are phylogenetically clustered. To this
307 goal, we used RaxML-HPC v. 8.2.12 (Stamatakis 2014) through the CIPRES Science
308 Gateway (Miller *et al.* 2010) using the GTRCAT model of nucleotide evolution and
309 estimating node support based on 1,000 bootstrap replicates. All phylogenetic analyses
310 included both variant and invariant sites.
311
312 **3 RESULTS**
313 **Mapping morphological characters in geographic space**
314 There is evidence of geographical partitioning in some morphological characters, but not
315 others (Figure 3). The main geographical distinction is in the colour pattern characters that
316 Storr (1991a) used to distinguish *L. arenicola* from *L. microtis*. Specifically, we found that
317 mainland specimens from the Eyre Peninsula and the Nullarbor tend to have wide white
318 midlateral stripes and narrow black upper lateral stripes with indistinct edges; these typically
319 were specimens that had been assigned to *L. arenicola* (Figure 3). Dorsal patterning was
320 largely inconsistent across southern Australia; for example, within the supposed region of *L.*
321 *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

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 2). 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.

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 3). 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 4).

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,

371 regarding nMDS scores, there is a geographical basis to variation in Storr's (1991a)
372 diagnostic characters for the *L. microtis* group.
373
374 *Phylogenetic patterns*
375 Phylogenetic analyses based on both nuclear (Figure 8A) and mitochondrial (Figure
376 8B) DNA sequences support that *L. arenicola*, *L. m. intermedia*, *L. m. microtis*, and *L. m.*
377 *schwaneri* compose a monophyletic group. This group is highly divergent from other major
378 clades of *Lerista*. However, each of the four taxa in the *L. microtis* complex showed limited
379 phylogenetic coherence and distinctiveness. For instance, both genetic datasets support that
380 samples morphologically and geographically assigned to *L. arenicola* are phylogenetically
381 nested among samples of *L. microtis*. Specifically, *L. arenicola* composed two (Figure 8A) to
382 three (Figure 8B) non-sister lineages, grouping with individuals of *L. m. schwaneri* or *L. m.*
383 *intermedia*. Like the case of *L. arenicola*, we found *L. m. intermedia* and *L. m. microtis* to be
384 paraphyletic based on the mitochondrial dataset, which included more specimens, localities,
385 and taxa than the nuclear dataset (Figure 8B).
386 Patterns of genetic structure in the *L. microtis* complex do not appear to align with
387 levels of geographic separation, contradicting expectations from a scenario of geographically
388 restricted populations diverging in isolation. Instead, we inferred low genetic divergence
389 between species- or subspecies-level taxa. Often, these divergences were shallower than
390 those inferred within other *Lerista* taxa broadly considered to correspond to single species.
391 This is the case, for instance, of *L. borealis*, *L. greeri*, *L. praepedita*, and *L. walkeri* (Figure
392 8).
393 Overall, evidence of limited genetic coherence and distinctiveness support that
394 populations assigned to *L. arenicola*, *L. m. intermedia*, *L. m. microtis*, and *L. m. schwaneri*
395 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 mitochondrial patterns appear largely decoupled from geographic separation.

4 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 proof expected of those describing them *versus* those attempting to falsify them. 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 with many of Storr's descriptions, including for his descriptions of taxa in the *L. microtus* group. In our reappraisal of this group, we have challenged Storr's 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 the 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 largely has a geographical basis. For mensural characters, Storr 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

421 descriptions also implicate *L. m. microtis* as a short-legged subspecies, and *L. m. schwaneri*
422 as a long-legged subspecies. We found support for these patterns but emphasise that these
423 two larger taxa (*L. arenicola* and *L. m. schwaneri*) are in the geographical east of the group's
424 range, whereas the smaller *L. m. microtis* and *L. m. intermedia* are in the west. Not
425 surprisingly, then, we found that the greatest differences in mensural characters exist between
426 *L. m. microtis* and *L. m. schwaneri* (i.e., the taxa that are most widely separated in space),
427 with longer SVL, limb length, and head dimensions in more eastern longitudes (Figure 7A).
428 Similar patterns were uncovered in our nMDS of colour pattern and scale characters;
429 being closer spatially, *L. m. microtis* and *L. m. intermedia* were not significantly different in
430 both univariate and multivariate character space. For instance, these two western taxa each
431 have fewer MSR than those of the two eastern taxa (Table 2), mirroring the size difference.
432 Storr states that *L. m. microtis* has more complex dorsal patterning than *L. m. intermedia,* the
433 latter of which is said to be paler and with a narrower upper lateral stripe. We found no
434 support for this diagnosis, with the occurrence of both complex and simple dorsal patterning
435 in specimens within the distribution of both these taxa. Moreover, *L. m. intermedia* is not
436 markedly paler in dorsal ground colour (presumably Storr measured this subjectively), nor is
437 its upper lateral stripe narrower than that of *L. m. microtis.* These morphological findings
438 support *L. m. intermedia* being synonymised with *L. m. microtis*.
439 Storr (1991a) considered it possible that *L. m. schwaneri* could be sympatric with *L.*
440 *arenicola* on the mainland, and it appears that this somewhat motivated his decision to
441 elevate *L. arenicola*. However, as we have shown here (see text in Methods about specimen
442 SAMA_R1599), there is no substantiated evidence suggesting such sympatry of specimens
443 previously assigned to these taxa. Thus, specimens labelled as *L. m. schwaneri* appear to
444 simply represent an island form, one that is morphologically more similar to *L. arenicola* on
445 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 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 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 by Storr, 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 by Storr, 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 of Storr's 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*. (Amey & Worthington Wilmer 2014). 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 phylogenetic relationships. But modern taxonomists have access to such information, enabling a detailed assessment of evolutionary relationships under the phylogenetic species concept. We suggest that species historically described based on morphology alone should be reassess in light of genomic data and the phylogenetic species concept. In the case of subspecies, where lines of evidence other than genomics are used to

496 justify subspecific recognition, taxonomists proposing subspecies must be clear about their
497 criteria for subspecific recognition. This further enables future investigators to test the validly
498 of those taxonomic conclusions.
499
500 **Conclusion**
501 In the absence of genetic information, traditional taxonomists have proposed
502 subspecies to capture purportedly diagnostic phenotypes (Zink 2004), and in doing so, they
503 (1) assumed that such phenotypes were markers for a cohesive evolutionary unit, or (2)
504 believed that taxonomic schemes should capture phenotypic variation irrespective of whether
505 this variation is indicative of evolutionary separation (Mayr 1982; Patton & Conroy 2017).
506 Traditional taxonomists did not have access to the molecular genetic techniques routinely
507 used in taxonomic research today, and thus their investigative process was necessarily
508 centred on morphology. Incongruencies may continue to emerge between phylogeny and
509 phenotype in cases where subspecies have been defined based on morphology alone, as we
510 have shown in this study of the *L. microtis* group. More broadly, the integration of
511 morphological and genetic information has revealed the extraordinary lability of organismal
512 phenotypic attributes. Besides challenging the evolutionary significance of many characters
513 traditionally used in taxonomic delimitation, integrative approaches like ours can provide
514 insights into how processes like natural selection and isolation-by-distance shape patterns of
515 phenotypic variation in nature.

516 **Systematic conclusions**
517 There was no concordance between genetic and phenotypic variation, with multiple
518 instances of polyphyly among specimens assigned to different taxa of the *L. microtis* group.
519 While our examinations of museum specimens confirmed a pattern of morphological
520 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.

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

596 to Wedge Island (SA). Recorded from several islands, including Saint Alouarn (WA),
597 Wickham (WA), Goat (SA), St Peter (SA) Franklin Islands (SA), Williams (SA), and Wedge
598 (SA). Occurs in woodland, coastal heath, sandplains, and coastal dunes where it shelters
599 within or on loose soil beneath surface cover such as leaf litter, clumps of dead vegetation,
600 logs, and rocks. Occasionally found in abandoned stick-ant (*Iridomyrmex conifer*) nests (in
601 south-west of range; Peterson & Metcalfe 2005) and under clumps of dry seaweed on
602 beaches (on Eyre Peninsula).

603 **Conservation.** There are no known major threats to the species (Chapple *et al*. 2019).
604 We calculated extent of occurrence (EOO) and area of occupancy (AOO) in GeoCat
605 (http://geocat.kew.org; Bachman *et al*. 2011). The species occurs in multiple protected areas
606 and has a large EOO of 651,840 km^2 (measured as the minimum convex hull around all
607 records, including ocean areas, as per IUCN guidelines). It has a relatively small AOO (2 x 2
608 km grid cells) of 516 km^2, which meets the IUCN threshold of Vulnerable under Criterion B2
609 (AOO < 2,000 km^2; IUCN 2022). However, it is unlikely to qualify for listing given it does
610 not meet other condition of Criterion 2; it occurs at ≥ 10 locations, is not severely
611 fragmented, and there is no evidence of continuing decline or extreme fluctuations in its
612 distribution or populations. Further sampling across the species' range is required to further
613 clarify the AOO, which is likely to be higher than current records suggest.
614

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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.

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FIGURE CAN BE FOUND IN THE SECOND DOCUMENT PART OF THIS SUBMISSION

Appendix begins on next page,

829 **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
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
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

861 **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

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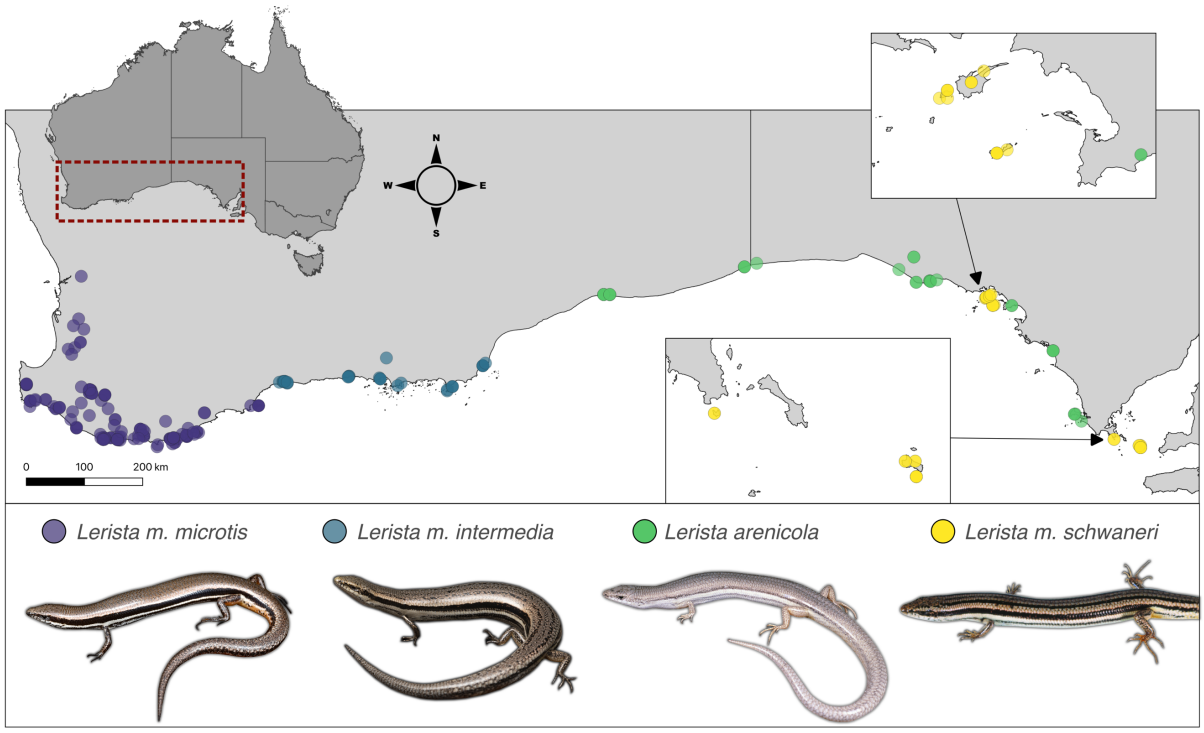


Figure 1. Distribution of currently recognized *Lerista microtis* subspecies and *Lerista arenicola.* Taxon assignment reflects that of the original museum records and the purported distribution as described in the literature (e.g., Storr 1991a; Wilson & Swan 2021). Note that all confirmed records of *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.

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	-
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	**L. m. microtis* have few dorsal markings, whereas *L. m. intermedia* tend to have indistinct dorsal stripes	Weak
	1: Faint traces of broken stripes		
	2: Indistinct continuous stripes	**L. m. schwaneri* has more complex dorsal pattern than that of *L. m. microtis*	Weak
	3: Bold continuous stripes		
ULSB	1: Indistinct edges	*Indistinct in *L. arenicola*, bold in *L. microtis*	Consistent
	2: Bold edges		
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	Considered relevant given our prior observation that *L. arenicola* tend to have wider mid-lateral stripes than that of *L. microtis*	-
	2: Wider than upper lateral		
NSS	0: Wide separation	Typically used in lizard taxonomy	-
	1: Narrowly separated		
	2: Just touching		
	3: Short contact		
	4: Broad contact		
* Denotes important diagnostic claims made by Storr (1991a).			

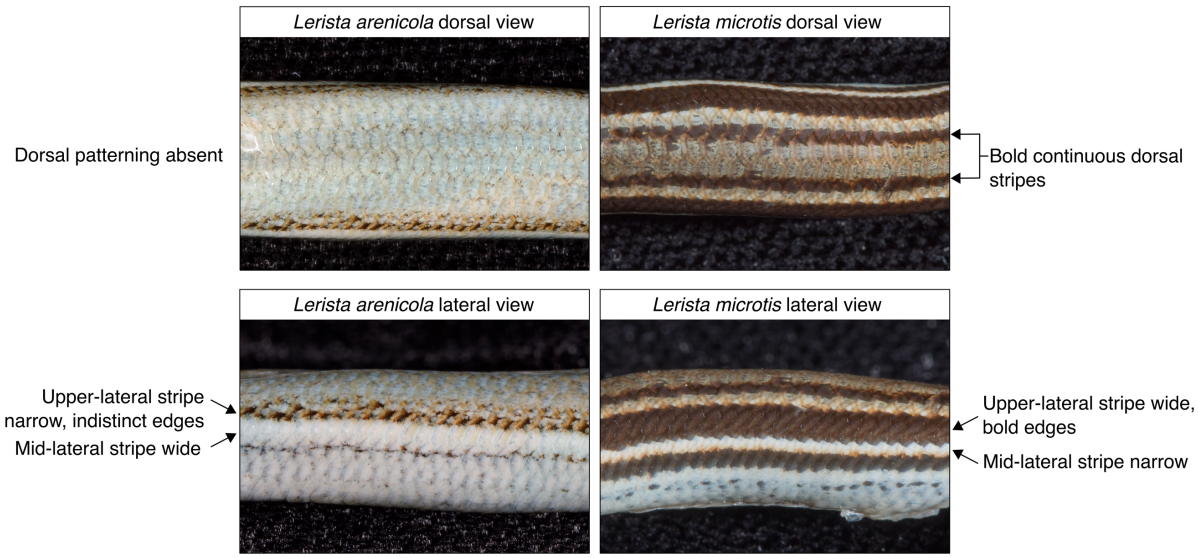


Figure 2. Examples of variation in colour pattern characters in the *Lerista microtis* group: upper row – dorsal view; lower row – lateral view. Storr (1991a) proposed that the black upper lateral stripe of *L. arenicola* (left) is narrow with indistinct edges, whereas that of *microtis* (right) is wide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

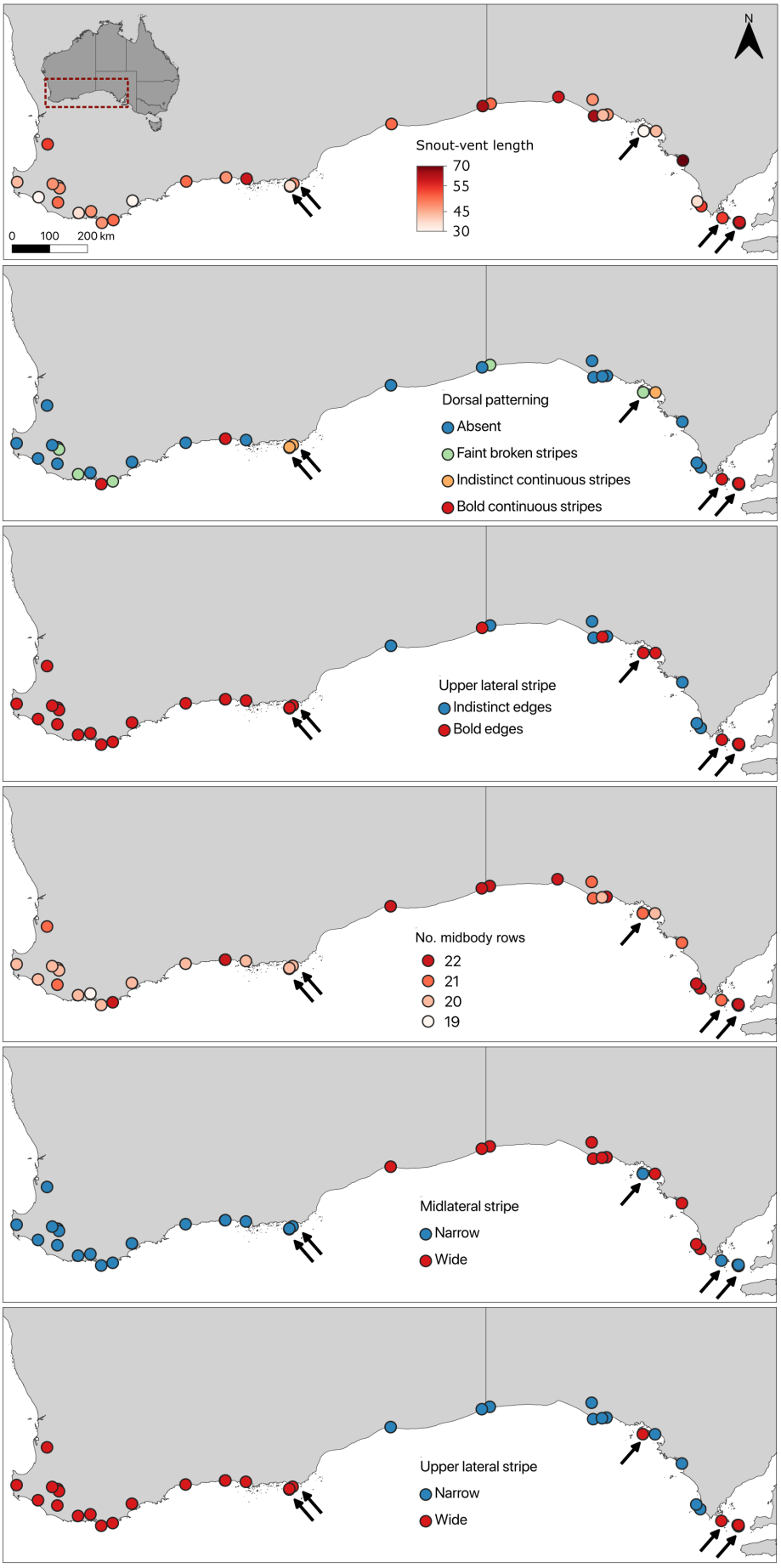

N
Snout-vent length
70
55
45
30
0 100 200 km
Dorsal patterning
Absent
Faint broken stripes
Indistinct continuous stripes
Bold continuous stripes
Upper lateral stripe
Indistinct edges
Bold edges
No. midbody rows
22
21
20
19
Midlateral stripe
Narrow
Wide
Upper lateral stripe
Narrow
Wide

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.

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

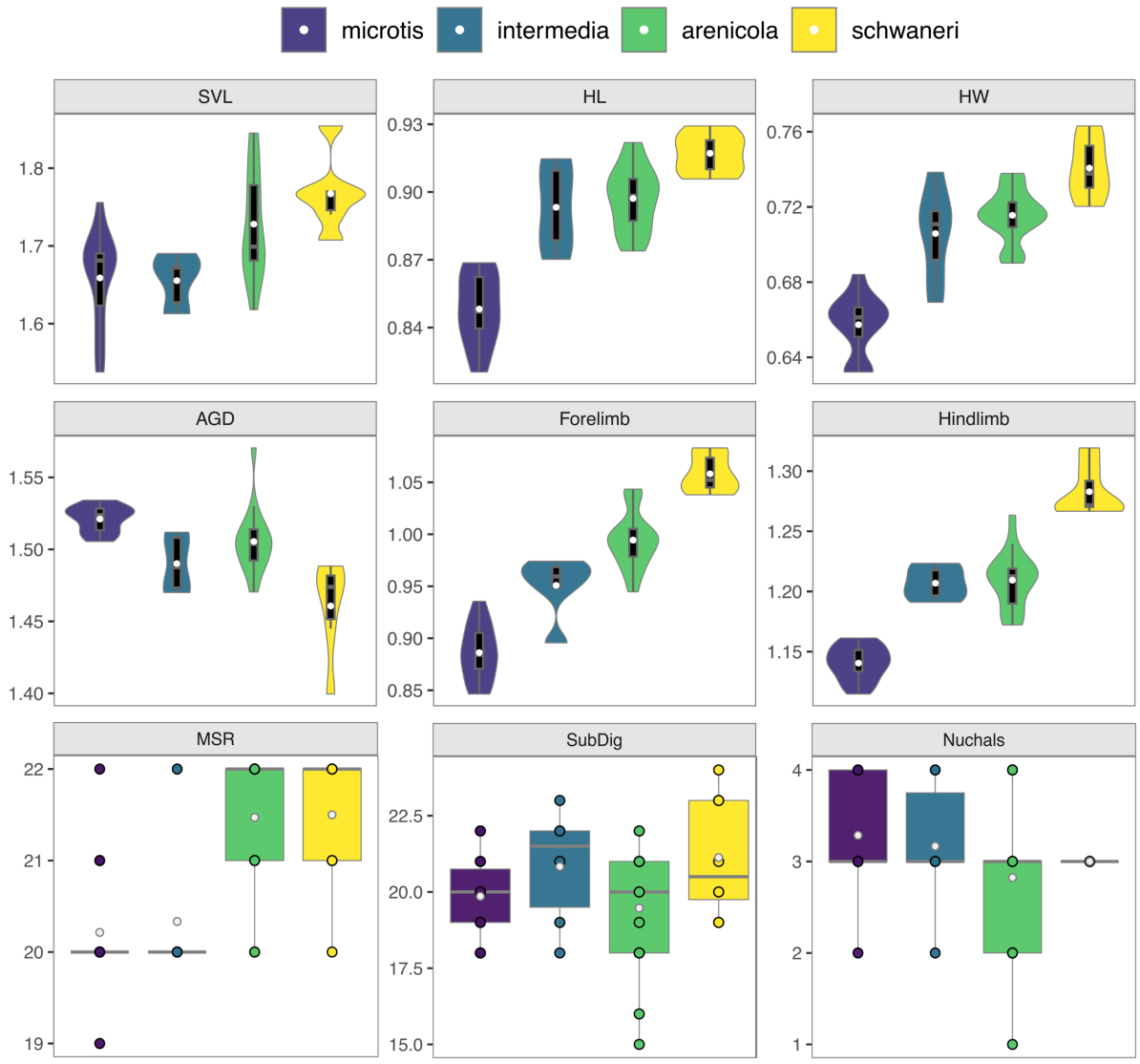


Figure 4. Comparative violin plots with embedded boxplots of size corrected mensural characters (top six graphs) for each taxon (*Lerista arenicola* and all *Lerista microtis* subspecies) showing the mean (white dot), range, frequency, and inter-quartile range (black rectangle). The bottom three graphs 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.

Table 2. 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	**	****	****	****	****	****	****		

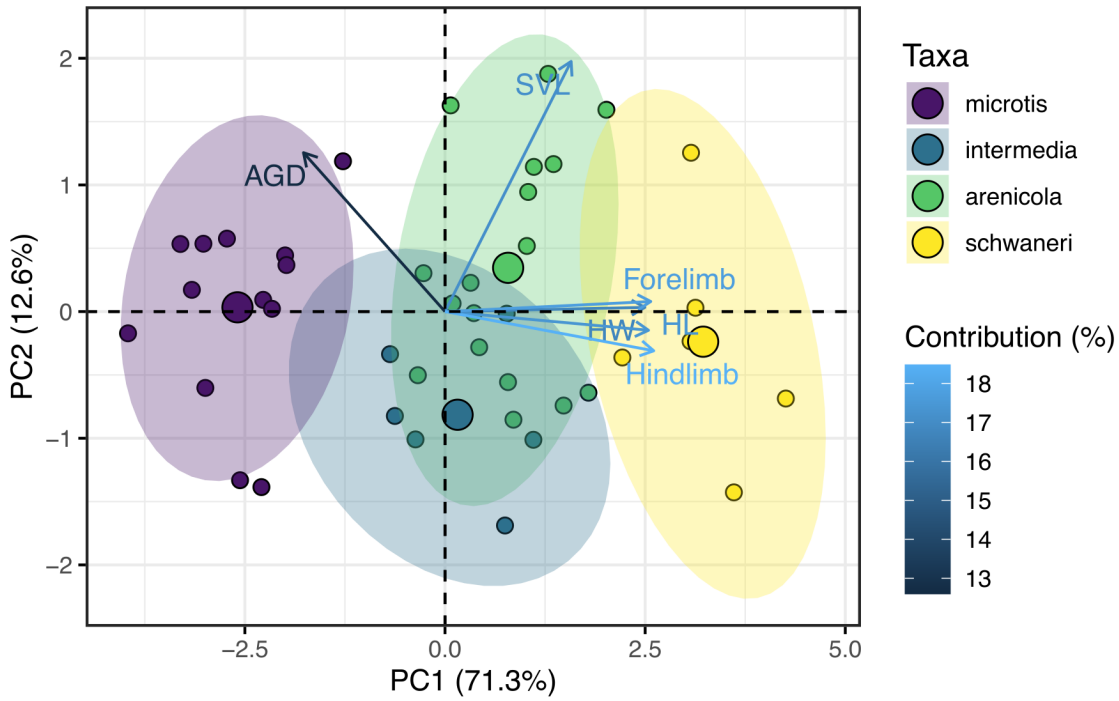


Figure 5. Biplot of the PCA performed on six mensural characters (SVL, HL, HW, AGD, Forelimb and Hindlimb). Axes show the first two principal components (i.e., PC1 and PC2) and their percentage of explained variation. Large, coloured ovals denote the 90% concentration ellipses for each taxonomic group 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.

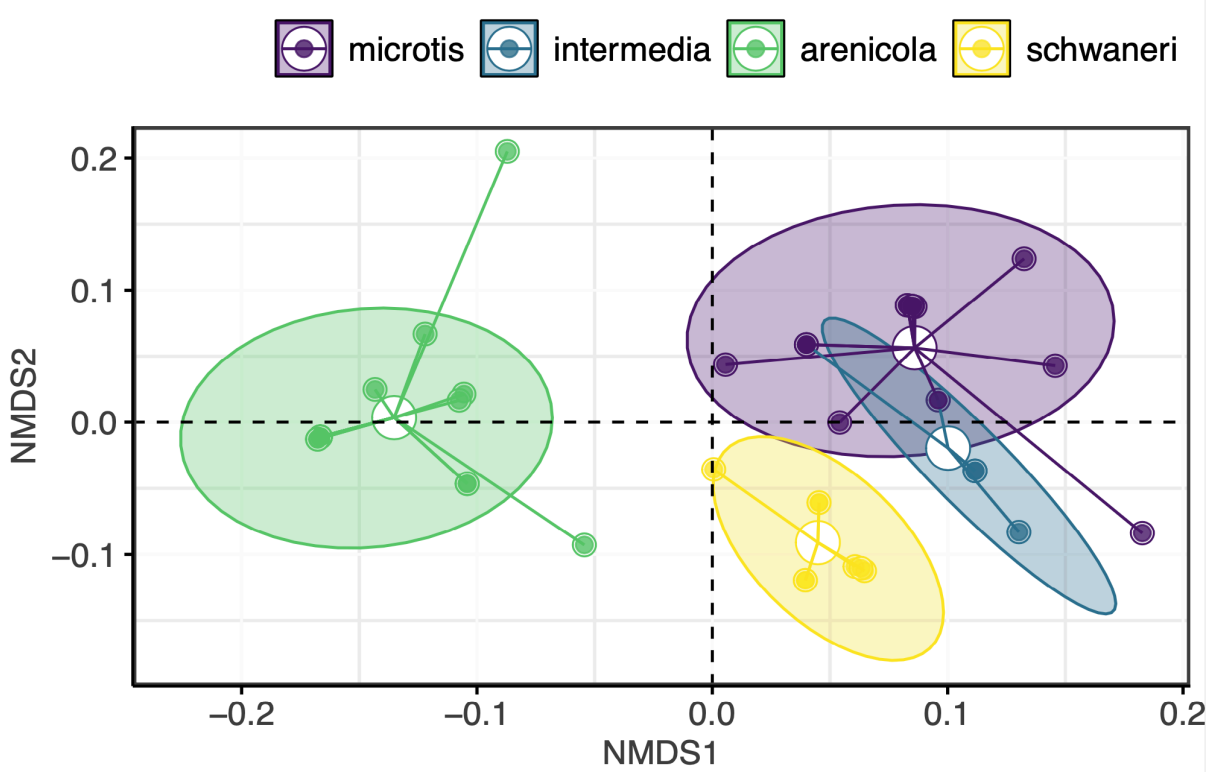


Figure 6. Biplot of non-metric multidimensional scaling (nMDS) performed on five qualitative characters (DP, ULSB, ULSW, MLSW, NSS) and one meristic (MSR; i.e., an integer count) character. These characters are among key traits Storr (1991a) used to diagnose these purported taxa. Specimens (coloured 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*.

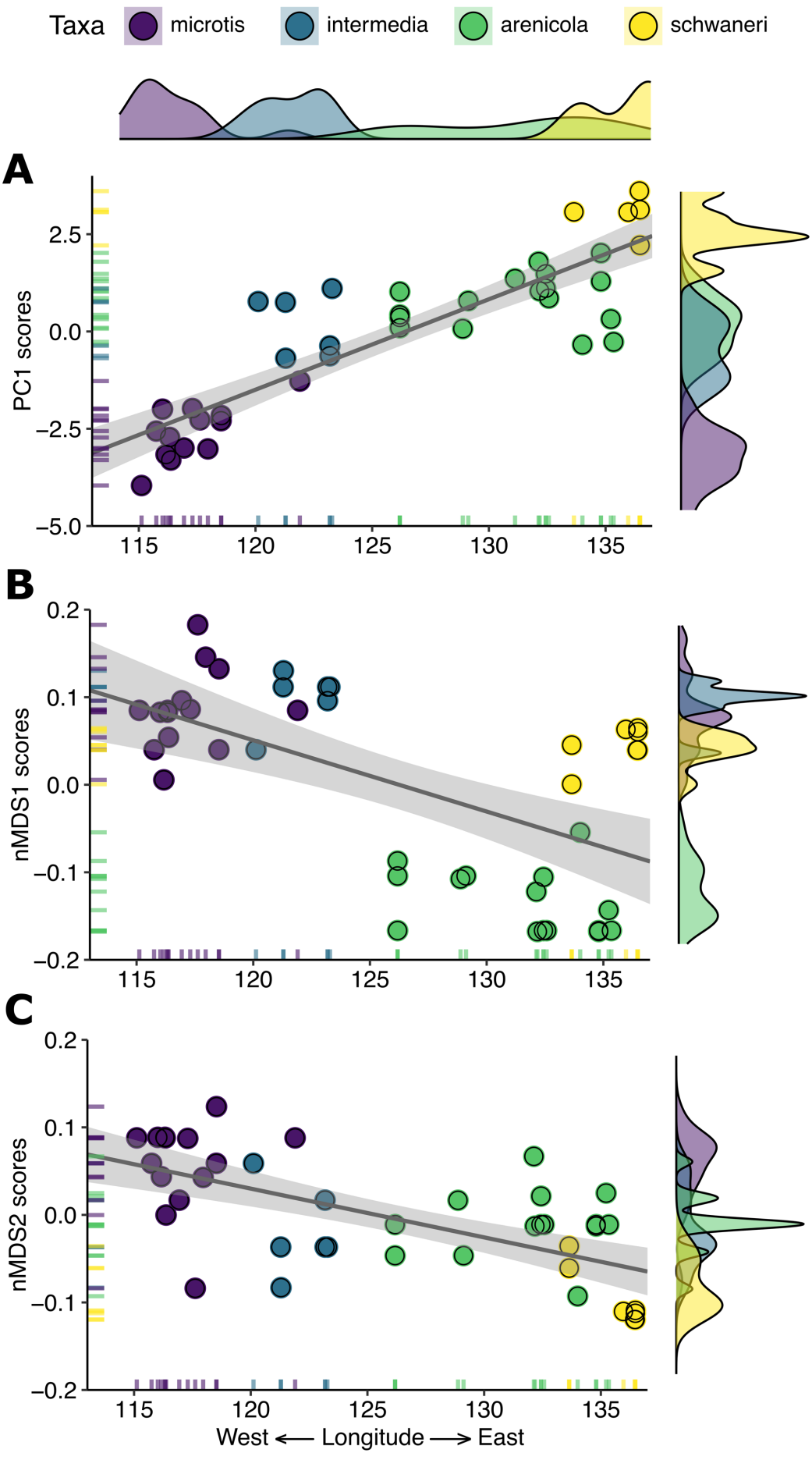

Taxa
microtis
intermedia
arenicola
schwaneri
A
PC1 scores
2.5
0.0
−2.5
−5.0
115
120
125
130
135
B
nMDS1 scores
0.2
0.1
0.0
−0.1
−0.2
C
nMDS2 scores
West ⟵ Longitude ⟶ East

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 clear geographical structuring of phenotypic characters in the *Lerista microtis* group.

Table 3. 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 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 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.

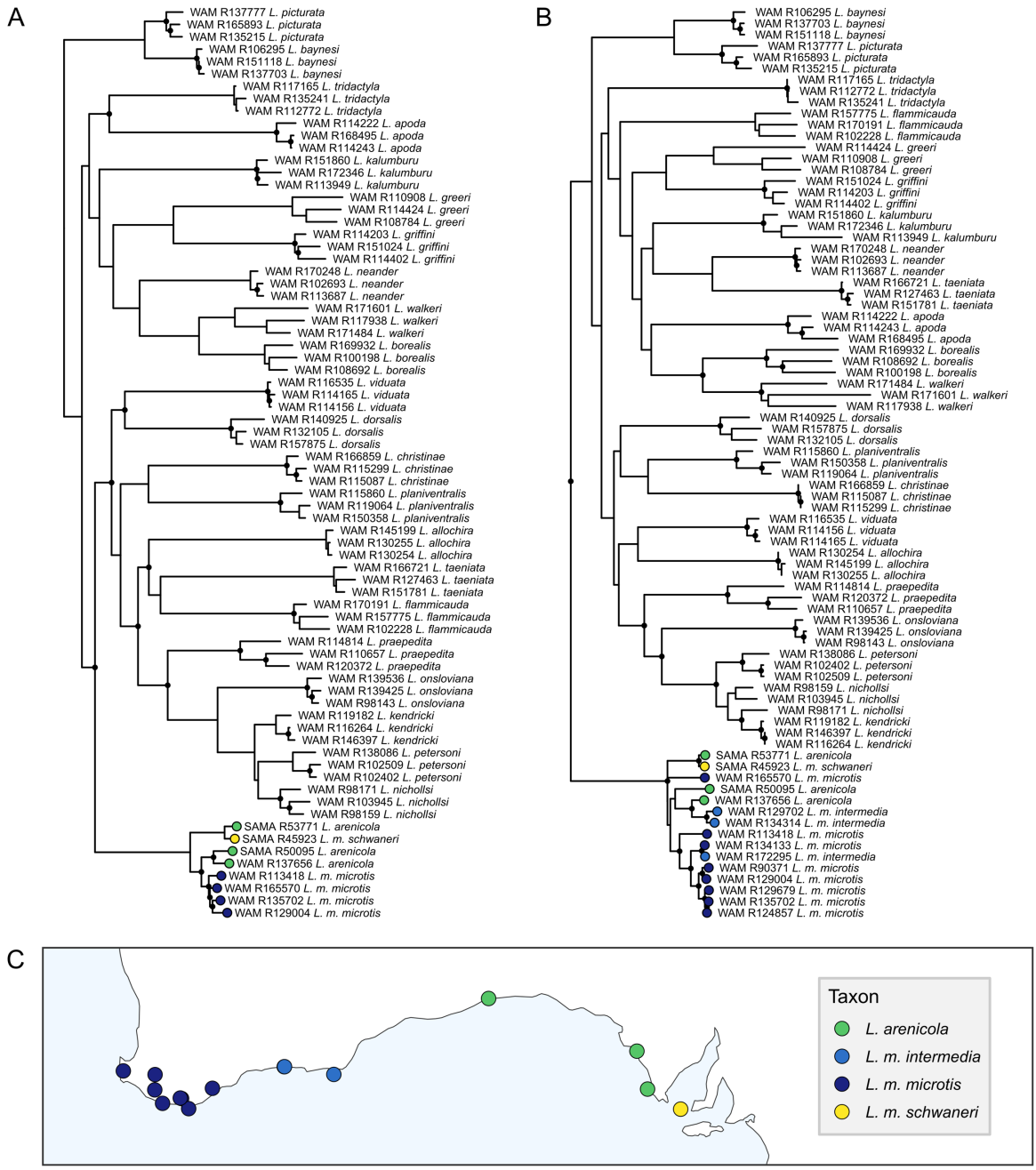
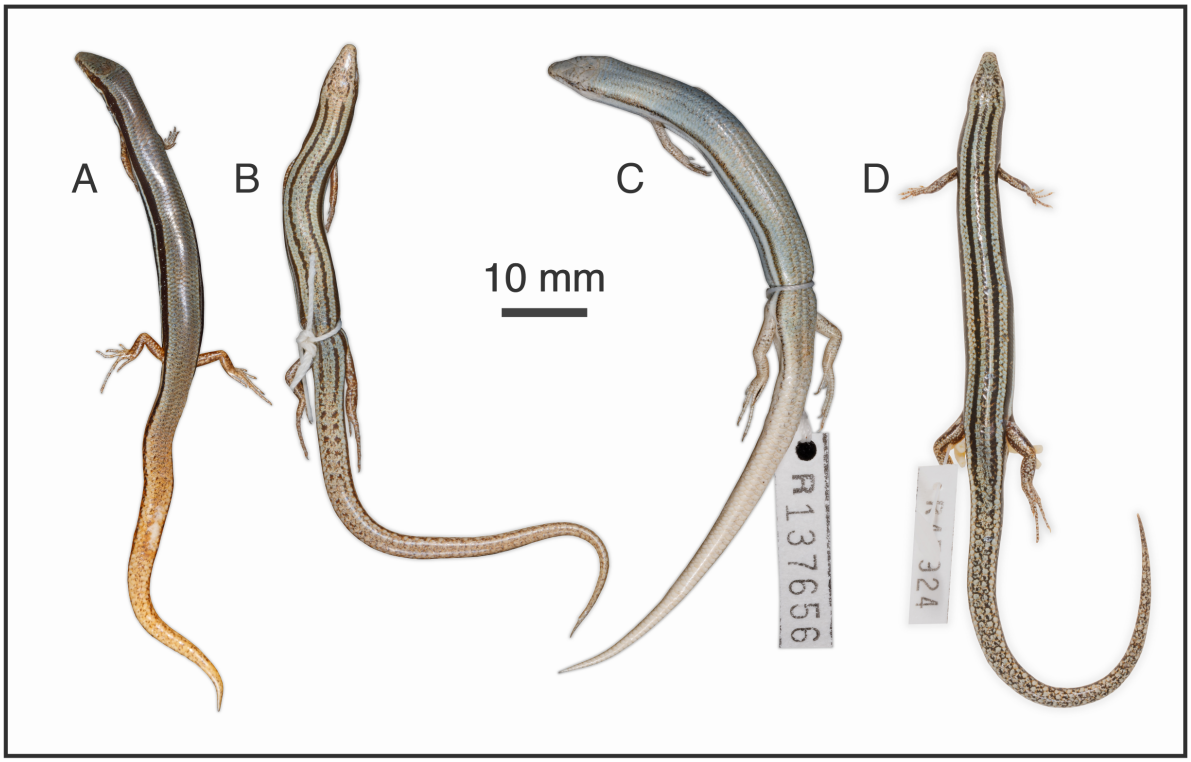
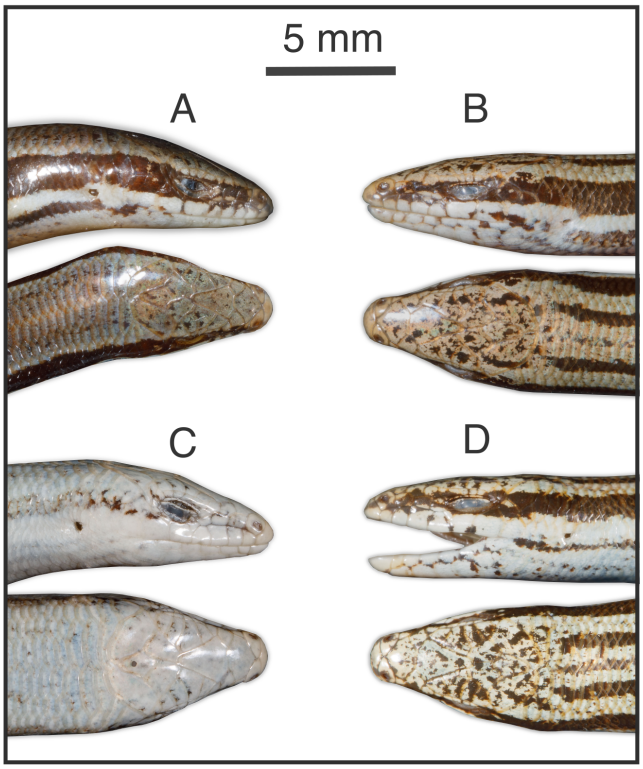


Figure 8. Evolutionary relationships in *Lerista* lizards with focus on taxa in the *L. microtis* complex. (A) Results from a phylogenetic analysis based on 133,163 base pairs across 940 restriction site-associated nuclear DNA (ddRAD) loci. (B) Results from an analysis based on 1,143 base pairs from 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.





Lerista microtis holotype
BMNH 1946.8.18.64

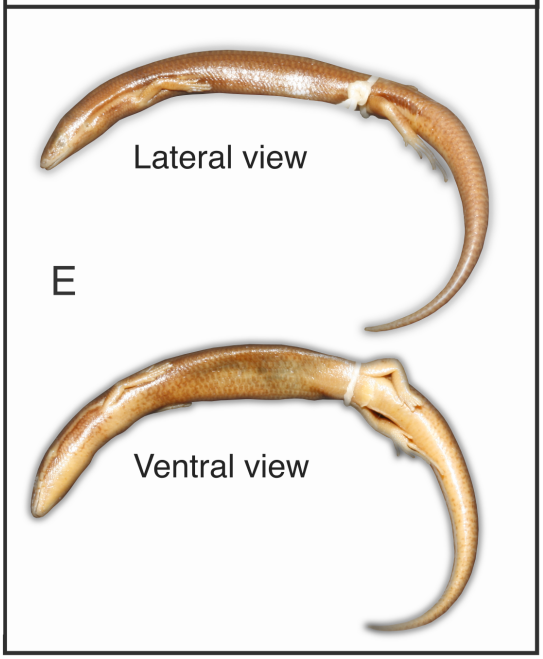


Figure 9. Select *Lerista microtis* specimens showing variability in size and colour pattern. (A) Specimen WAM_R113419 from Margaret River area (south-west WA) with dark grey-brown dorsal colour, orange tail and no dorsal pattering (formerly *L. m. microtis*); (B) specimen WAM_R129702 from Quagi Beach (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.*