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First genetic data from *Eutropis englei* (Squamata: Scincidae) provide phylogenetic insights after a century since its discovery

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Abstract. The *Eutropis multicarinata* species complex comprises lineages that have diversified genetically across the Philippine archipelago and nearby islands, largely without corresponding phenotypic differentiation in external morphology. Although recent work has clarified the systematics and evolutionary history of most members of the complex, their relationship to *E. englei,* a poorly known and enigmatic species from south-central Mindanao, has remained phylogenetically unresolved since the original description of the species. For the first time in 100 years since its first (and only) known collection, we collected new specimens and fresh tissue samples of *E. englei* and assembled a DNA sequence dataset to determine its phylogenetic placement. Unexpectedly, our multilocus phylogeny recovers *E. englei* as the sister taxon to *E. palauensis*, a species endemic to the Palau archipelago (~1,500 km to the east), with shallow genetic divergence (3–4% based on concatenated sequences) – the lowest interspecific genetic distance documented within the *E. multicarinata* complex. The new specimens also reveal sexual dimorphism in size and coloration not previously reported in earlier work on this species. We briefly discuss biogeographic implications of these findings and identify priorities for future research. This work helps fill a long-standing phylogenetic gap in Philippine reptile systematics and underscores the urgent need for targeted wildlife genetic sampling, especially in species' type locality or other hard-to-access specific sites, enabled by collaborative, collections-based fieldwork.

Key words. Skinks, lizards, molecular phylogeny, Philippines, Southeast Asia.

Introduction

The *Eutropis multicarinata* species complex is a diverse evolutionary radiation in which genetic divergence is weakly correlated with phenotypic differentiation (Barley et al. 2013). Comprising nine recognized species widely distributed across the Philippine archipelago, including a few species in Palau Island, Lanyu Island, and Borneo, this group has long challenged systematists attempting to resolve its evolutionary relationships (Taylor 1922, Brown & Alcala 1980, Ota 1991, Crombie & Pregill 1999, Mausfeld & Schmitz 2003). Only in recent decades have genetic studies begun to clarify its taxonomy, evolutionary history, and biogeography (Barley et al. 2013, 2015, 2020). Despite these advances, relationships within the complex remain not fully resolved, largely due to the lack of genetic data for *E. englei*, uncertainty surrounding non-Philippine populations (e.g., Lanyu Island), and incomplete taxonomic studies for certain populations that may represent putatively divergent lineages (Ota 1991, Barley et al. 2020, Pitogo et al. 2020). These data shortfalls have important implications for biodiversity studies that rely on accurate phylogenetic frameworks and for conservation planning (Diniz-Filho et al. 2013, Guedes et al. 2024). These phylogenetic blind spots disproportionally affect narrowly distributed species occupying remote or difficult-to-access geographic regions, where obtaining fresh genetic material is often challenging (Pitogo 2025).

Among all recognized species of the *E. multicarinata* species complex, only *E. englei* has remained phylogenetically unplaced due to the absence of fresh tissue samples. Known historically only from its type specimens, *E. englei* can nonetheless be readily distinguished by their five prominent longitudinal stripes on the dorsum; these longitudinal stripes are shared only with *E. bontocensis* from Luzon Island within the complex (Taylor 1923, 1925, Brown & Alcala 1980, Pitogo et al. 2020). For nearly a century, *E. englei* was "lost" to systematists: known only from its original description, and virtually nothing was recorded about its biology or distribution. Recent surveys, howev-

er, suggest that *E. englei* is locally common around its type locality in Maitum, Sarangani Province (Mindanao Island, Philippines), occurring up to roughly 500 meters above sea level and showing tolerance (or preference) for disturbed habitats (Pitogo et al. 2020). An individual was also recently documented approximately 115 kilometers from the type locality and farther inland, hinting at a broader distribution than previously recognized (Tirona et al. 2023). Nevertheless, no new specimens had been collected since the species' original description in 1925, until now.

In June 2024, after a gap of 100 years since its original discovery, we obtained new collections of specimens of *E. englei* through targeted surveys approximately 23 km from the type locality (Saub, Cotabato Province [now Sarangani], Mindanao; Taylor 1925). This enabled us to determine the phylogenetic placement of this species and identify its closest relatives for the first time, resolving a long-standing evolutionary mystery in Philippine herpetology. Our observations and morphometric measurements also revealed sexual dimorphism in color and size, previously undocumented characteristics for the species. By generating the first genetic data for *E. englei*, this study helps address long-standing phylogenetic gaps in Philippine reptiles – the least genetically sampled group among endemic vertebrates – and contributes to reducing the broader Darwinian shortfall, as 22.4% of Philippine endemic vertebrate species remain unplaced in phylogenetic frameworks (Pitogo 2025). Our findings highlight the critical role of sustained collections-based fieldwork and wildlife genetic sampling in advancing knowledge and appreciation of one of the world's most biodiverse regions.

Materials and methods

Specimen collection

Fieldwork was carried out by KMEP and AJLS in June 2024 at Sitio Angko, Municipality of Maitum, Sarangani Province, Philippines (6.1555° N, 124.4915° E), the site where the species was confirmed to occur (Pitogo et al. 2020). A total of 17 *E. englei* specimens were collected and euthanized following the protocol approved by the University of Kansas Institutional Animal Care and Use Committee (Animal Use Statement No. 279-01). Specimens were initially fixed in 10% buffered formalin then transferred to 70% ethanol for long-term preservation, and these were subsequently deposited in the University of Kansas Natural History Museum (KU). Fieldwork was conducted with prior informed consent from the Municipal Local Government Unit of Maitum and under the Wildlife Gratuitous Permit No. 337 issued by the Philippine Department of Environment and Natural Resources Biodiversity Management Bureau.

Genetic sampling

DNA was extracted and purified by lysing tissue samples with 20 μL of Proteinase K, followed by a modified Solid Phase Reversible Immobilization (SPRI) bead extraction protocol adapted from the Phyletica Lab (Auburn University) (Cobb 2019). Polymerase chain reaction (PCR) was performed on a C1000™ thermal cycler (Bio-Rad Laboratories, Inc.) to amplify 500–800 base pairs (bp) of the nicotinamide adenine dinucleotide dehydrogenase subunit 2 (ND2), selenoprotein-T intron (SELT), and nitric oxide synthase 1 intron (NOS1) genes, using primers and conditions reported in Barley et al. (2013). Amplification success was confirmed by electrophoresis on a 1.5% agarose gel, and PCR products were purified for cycle sequencing at Functional Biosciences® following standard protocols. The resulting DNA sequences were submitted to GenBank for deposition (accession numbers shown in Supplementary Table 1).

Phylogeny and genetic distances

Sequence assembly and editing were performed de novo for each gene and then concatenated in Geneious Prime® 2025.1.3 (Kearse et al. 2012). In addition to our newly generated sequences, we obtained ND2, SELT, and NOS1 sequences from GenBank for 39 individuals representing 10 species in two genera, comprising all recognized members of the *E. multicarinata* complex (Barley et al. 2020), along with *Dasia grisea* and *E. multifasciata* as outgroups (Supplementary Table 1). All sequences were concatenated by specimen in Geneious Prime® 2025.1.3 and aligned with *E. englei* data using Clustal Omega 1.2.3 (Sievers et al. 2017, 2020). Maximum Likelihood (ML) analyses were conducted in IQ-TREE v2.3.6 (Nguyen et al. 2015), with TIM3+F+I+G4 selected as the best-fit substitution model under the Bayesian Information Criterion using ModelFinder (Chernomor et al. 2016). Branch support was assessed with 10,000 ultrafast bootstrap (UFBS) replicates, with UFBS ≥95 considered strong support (Minh et al. 2013). The resulting phylogenetic tree was visualized using ggtree (Yu et al. 2017) in R Statistical Software Version 4.2.2 (R Core Team 2022). Pairwise Maximum-Likelihood (ML) genetic distances for concatenated sequences were calculated in IQ-TREE using the best-fit substitution model, with full tree searches disabled. The same procedure was applied separately to the ND2 and SELT genes, as sequence lengths for NOS1 were inconsistent across samples and could influence results; the substitution model for each gene was selected independently using ModelFinder. The resulting PHYLIP-formatted distance matrices were imported into R, converted into symmetrical matrices, and visualized as heatmaps using the 'pheatmap' package (Kolde 2025).

Morphology

Standard morphometric characters used in *Eutropis* taxonomy were recorded from all adult individuals for which sex could be determined (12 out of 17 specimens collected). All measurements were taken by KMEP on the right

Table 1. Summary of mensural and meristic data for newly collected *Eutropis englei* specimens. Values are presented as mean ± standard deviation, with ranges in parentheses.

Character	Males (n = 7)	Females (n = 5)	Combined (n = 12)
Snout–vent length (SVL) (mm)	72.5±4.2 (64.9–77.4)	66.6±2.51 (63.4–69.5)	70.0±4.6 (63.4–77.4)
Axilla–groin distance / SVL	0.48±0.01 (0.47–0.49)	0.51±0.03 (0.47–0.54)	0.49±0.03 (0.47–0.54)
Head length / SVL	0.20±0.01 (0.19–0.21)	0.19±0.01 (0.18–0.20)	0.20±0.01 (0.18–0.21)
Forelimb length / SVL	0.21±0.01 (0.21–0.22)	0.20±0.01 (0.19–0.22)	0.21±0.01 (0.19–0.22)
Hindlimb length / SVL	0.32±0.01 (0.30–0.34)	0.29±0.01 (0.28–0.31)	0.31±0.02 (0.28–0.34)
Total toe lamellae	79±2 (76–82)	80±2 (77–82)	80±2.1 (76–82)
Vertebral scale rows	41±1 (41–43)	42±2 (41–44)	42±1 (41–44)
Ventral scale rows	29±1.5 (26–30)	29±1 (28–30)	29±1 (26–30)
Midbody scale rows	32±1 (31–33)	31±1 (31–33)	32±1 (31–33)
Upper, lower labials	7–8, 7–8	7–8, 7–8	7–8, 7–8
Dorsal scale keels	7–8	7–8	7–8
Primary temporals	2–3	2–3	2–3
Enlarged pretemporals	4–6	4–5	4–5
Supraciliaries	4–5	4–5	4–5

side of the body to the nearest 0.01 mm using a digital caliper (Mitutoyo 500-196-30, Japan). Mensural and meristic characters followed Barley et al. (2020) and included snout–vent length (SVL), axilla–groin distance (AGD), head length, head width, forelimb length (humerus and forearm), hindlimb length (femur and tibia), subdigital lamellae on each toe of the right foot, upper and lower labial counts, ventral scale rows between limbs, vertebral and midbody scale rows, number of supraciliaries, number of dorsal keels (scored from 10 randomly selected scales), primary temporals, and enlarged pretemporals. The ratio of AGD to SVL (AGD/SVL) was additionally calculated to assess proportional differences in body shape.

We examined sexual dimorphism in *E. englei* using only mensural traits, as scale counts are largely similar between sexes (Table 1). To remove the effect of overall body size, each trait was regressed against SVL, and the resulting residuals were used as size-corrected variables representing shape independent of size. Patterns of shape variation were explored using principal components analysis (PCA) on size-corrected traits, implemented with prcomp function in the stats package in R Statistical Software Version 4.2.2 (R Core Team 2022). Biplots of the first two principal components included 95% confidence ellipses and variable loadings.

For univariate comparisons between sexes, normality was assessed using the Shapiro–Wilk test (shapiro.test, stats package), and equality of variances was assessed using an F-test (var.test, stats package). Because normality assumptions were not consistently met across traits and variance heterogeneity was detected in at least one variable (AGD/SVL), sexual differences in both raw (including AGD/SVL) and size-corrected measurements were assessed using Welch's t-tests (t.test, stats package). Statistical significance was determined at $\alpha = 0.05$. Effect sizes were quantified using Cohen's d in the R package effsize (Torchiano 2020).

Results and discussion

The concatenated ND2, SELT, and NOS1 sequences produced an alignment of 1570 bp. In the resulting multilocus ML phylogeny, *E. englei* was surprisingly recovered as the sister to the only non-Philippine species in the complex, *E. palauensis*, with high support (UFBS 100; Fig. 1, Supplementary Fig. 1). This pair was, in turn, sister to the Mindanao endemic species *E. caraga*, also with high support (UFBS 100). Together, these three species form a well-supported clade (UFBS 100) that is sister to the remaining members of the *E. multicarinata* complex. However, relationships within the clade sister to *E. caraga*, *E. palauensis*, and *E. englei* differ from previously published phylogenies of the group (Barley et al. 2013, 2020). Overall bootstrap support for many nodes in this clade was low (UFBS < 75), except for the strongly supported sister relationship between *E. bontocensis* and *E. gubataas* (UFBS 95). This incongruent topology likely reflects high gene tree variation, even among the seven loci sequenced by Barley et al. (2013).

The inferred sister relationship between *E. englei* and *E. palauensis* suggests a long-distance overwater dispersal event from the Philippines to the Palau archipelago. This dispersal was first suggested by Mausfeld & Schmitz (2003), who only included genetic data for *E. borealis* specimens in their mitochondrial phylogeny, a species distributed in Luzon and West Visayan islands. However, an expanded geographic sampling clarified that *E. palauensis* is sister to a lineage from Mindanao, later described as *E. caraga* (Barley et al. 2015, 2020). This direct dispersal from Mindanao to Palau represents the only known instance of a direct overwater dispersal event between these archipelagos, separated by ~1500 km of deep water (Jones & Kennedy 2008, but see Linkem et al. 2013). Such dispersal is nonetheless not surprising, given that Philippine and

Palau *Eutropis* colonized the Philippines from mainland Asia, crossing the South China Sea, demonstrating their capacity for long-distance overwater dispersal (Mausfeld & Schmitz 2003, Barley et al. 2015, Karin et al. 2024). Consistent with this point, some species have distributions that span deep-water barriers. For example, *E. islamaliit* occurs across small islands throughout the archipelago, including the Turtle Islands just north of Sabah, Malaysia; while *E. borealis*, known from Luzon and West Visayan islands, has also been recorded on Lanyu Island off Taiwan (Ota 1991, Barley et al. 2020).

Interestingly, our multilocus ML tree indicates that the genetic divergence between *E. palauensis* and *E. englei* is only 3.5–4.0%, representing the smallest pairwise ML distance among all *E. multicarinata* complex species (> 10%; Supplementary Fig. 2). This pattern is consistent across both ND2 and SELT, although divergence is slightly higher for ND2 (6.2%; Supplementary Fig. 3) than for SELT (0.92%; Supplementary Fig. 4). This shallow divergence is comparable to within-species distances based on concatenated sequences among *E. caraga* individuals and is substantially lower than divergences within *E. multicarinata* (~14–20%) or between Luzon and West Visayan populations of *E. borealis* (~18–21%). Such shallow divergence may suggest a recent split between *E. englei* and *E. palauensis*, with *E. englei* subsequently evolving the distinctive five longitudinal stripes (absent in *E. palauensis*). Because some stripeless *Eutropis* occurred at the same site as *E. englei*, we sequenced a stripeless specimen (KU 353192) to see if it might simply represent a color variant of *E. englei*. It instead formed clade with *E. caraga* (Fig. 1), confirming that the five-stripe pattern is indeed diagnostic for *E. englei* (Taylor, 1925).

Our measurements of newly collected *E. englei* specimens (Table 1) generally agree with those reported by Brown & Alcala (1980). However, our data make sexual size differences more explicit: males are significantly larger overall (SVL mean ± SD, range; 72.5 ± 4.2, 64.9–77.4 mm in males vs. 66.6 ± 2.51; 63.4–69.5 mm in females; Welch's t-test, t = 3.02, p = 0.013), and this pattern extends across

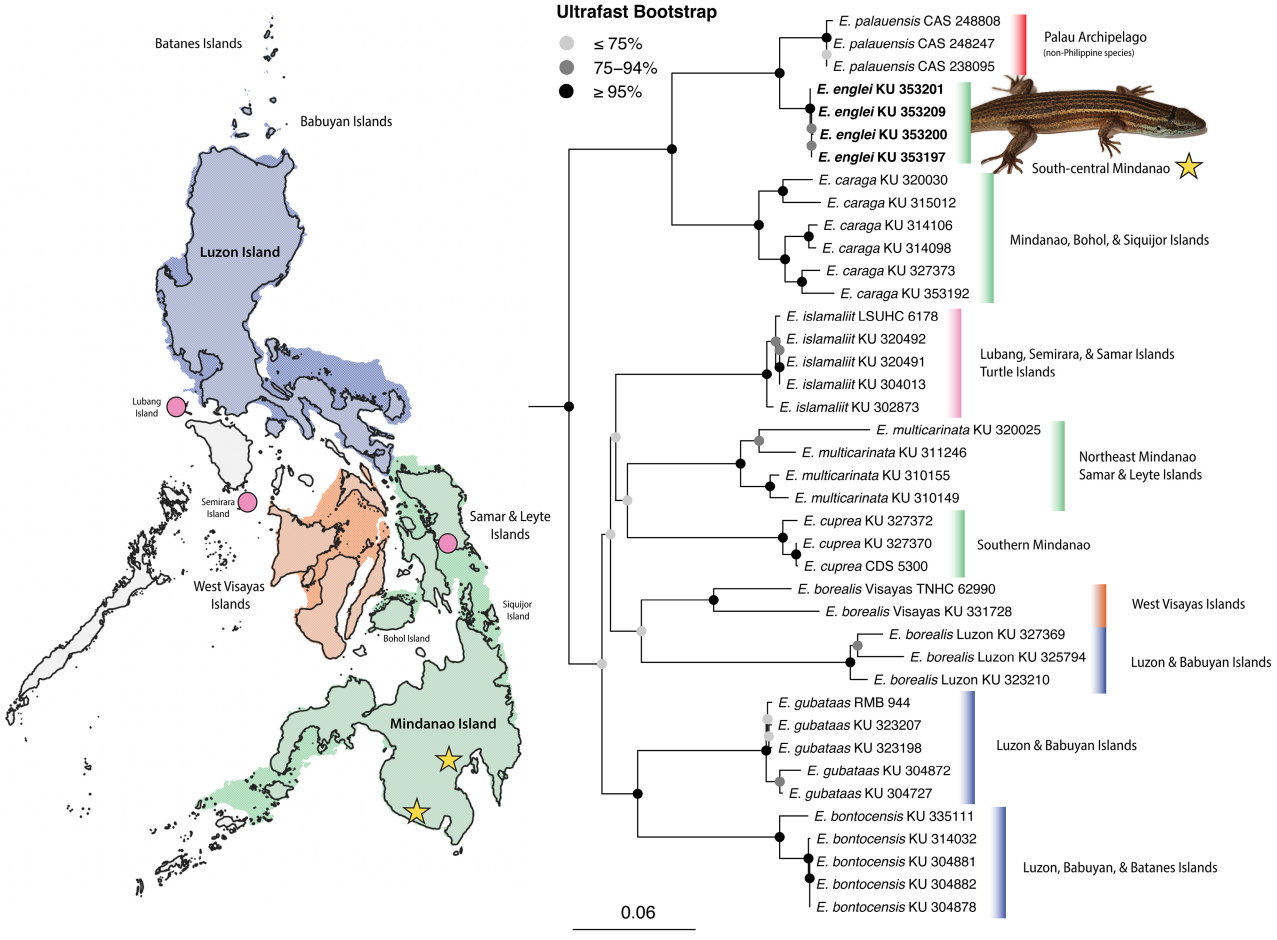

Figure 1. Maximum-likelihood phylogeny of the *Eutropis multicarinata* species complex inferred from ND2, SELT, and NOS1 sequences. Outgroups (*Dasia grisea* and *E. multifasciata*) were omitted in visualization but are shown in Figure S1. Node circles denote ultrafast bootstrap support. Colored bars mark each clade's Philippine island distribution as reported in Barley et al. (2020). The yellow star indicates the confirmed localities of *E. englei*.

most mensural traits (all $p < 0.01$, Supplementary Table 2). In contrast, size-corrected analyses indicate limited shape dimorphism, with only forearm length remaining significantly male-biased ($t = 2.62$, $p = 0.029$). Females tend to have proportionally longer trunks, although this could be due to the inclusion of gravid individuals (AGD/SVL 0.51 ± 0.03, 0.47–0.54 in females vs. 0.48 ± 0.01, 0.47–0.49 in males). However, this difference was not statistically significant (AGD/SVL $t = -2.28$, $p = 0.08$), possibly reflecting a small sample size. This weak trend is broadly consistent with multivariate results, where females show slight separation in morphospace along PC1 and PC2 (explaining 60.9% and 16.8% of the variance, respectively; Fig. 2), although overall shape differentiation between sexes remains limited. Negative loadings in PC1 is primarily associated with overall limb proportions, whereas PC2 contrasts AGD, head length, humerus length, and forelimb length (negative loadings) against the remaining traits (positive loadings) (Supplementary Table 3).

We also observed that live males consistently exhibit a cream to light orange belly and a bluish throat (Taylor 1925, Brown & Alcala 1980, Pitogo et al. 2020), whereas all females possess uniformly cream-colored venters (Fig. 3). Although Brown & Alcala (1980) described this range in ventral and throat coloration, they did not report whether it was sexually associated. Of the four gravid females, two specimens contained three fully developed eggs, and another two specimens contained two eggs, consistent with reproductive observations in the closely related *E. caraga* (Taylor 1922, Brown & Alcala 1980, Barley et al. 2020). As in previous ecological reports (Taylor 1925, Brown & Alcala 1980, Pitogo et al. 2020, Tirona et al. 2023), all individuals were found in open-canopy habitats, and none were encountered inside forested areas.

Although this study provides the phylogenetic placement of *E. englei* and completes genetic sampling for all recognized species in the *E. multicarinata* complex, much remains to be resolved regarding the group's evolutionary history. Fully clarifying species boundaries and deeper relationships will likely require genome-wide data, which will in turn reshape interpretations of biogeography and diversification across the archipelago. Expanded geographic sampling, particularly of populations spanning the full environmental and elevational range of each taxon, will be essential for refining distributional limits and detecting cryptic diversity. For example, in southern Mindanao, three species (*E. englei*, *E. caraga*, and *E. cuprea*) are genetically confirmed to occur within the same mountain range and adjacent forests (this study; Barley et al. 2020), highlighting the need for finer-scale sampling to understand space or niche partitioning. Similarly, *E. borealis* populations from Luzon and the West Visayan Islands exhibit deep divergence, which may require detailed analysis of phenotypic data to address the taxonomic implications of the extensive genetic divergence reported here. The presence of three-striped *Eutropis* populations in other parts of Mindanao further indicates the possibility of another undescribed, evolutionarily distinct lineage (Brown & Alca-

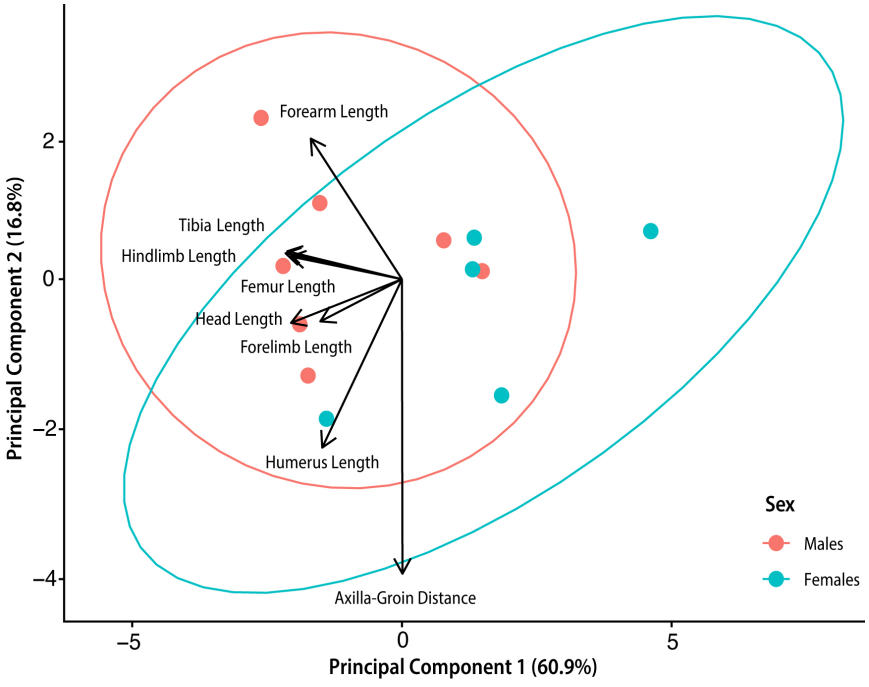

Figure 2. Principal components analysis (PCA) of size-corrected mensural traits in *Eutropis englei*, showing minimal separation between males and females. PC1 is primarily associated with overall limb proportions (all traits loading negatively, except axilla–groin distance [AGD] with a slight positive loading), whereas PC2 contrasts AGD, head length, humerus length, and forelimb length (negative loadings) against the remaining traits (positive loadings).

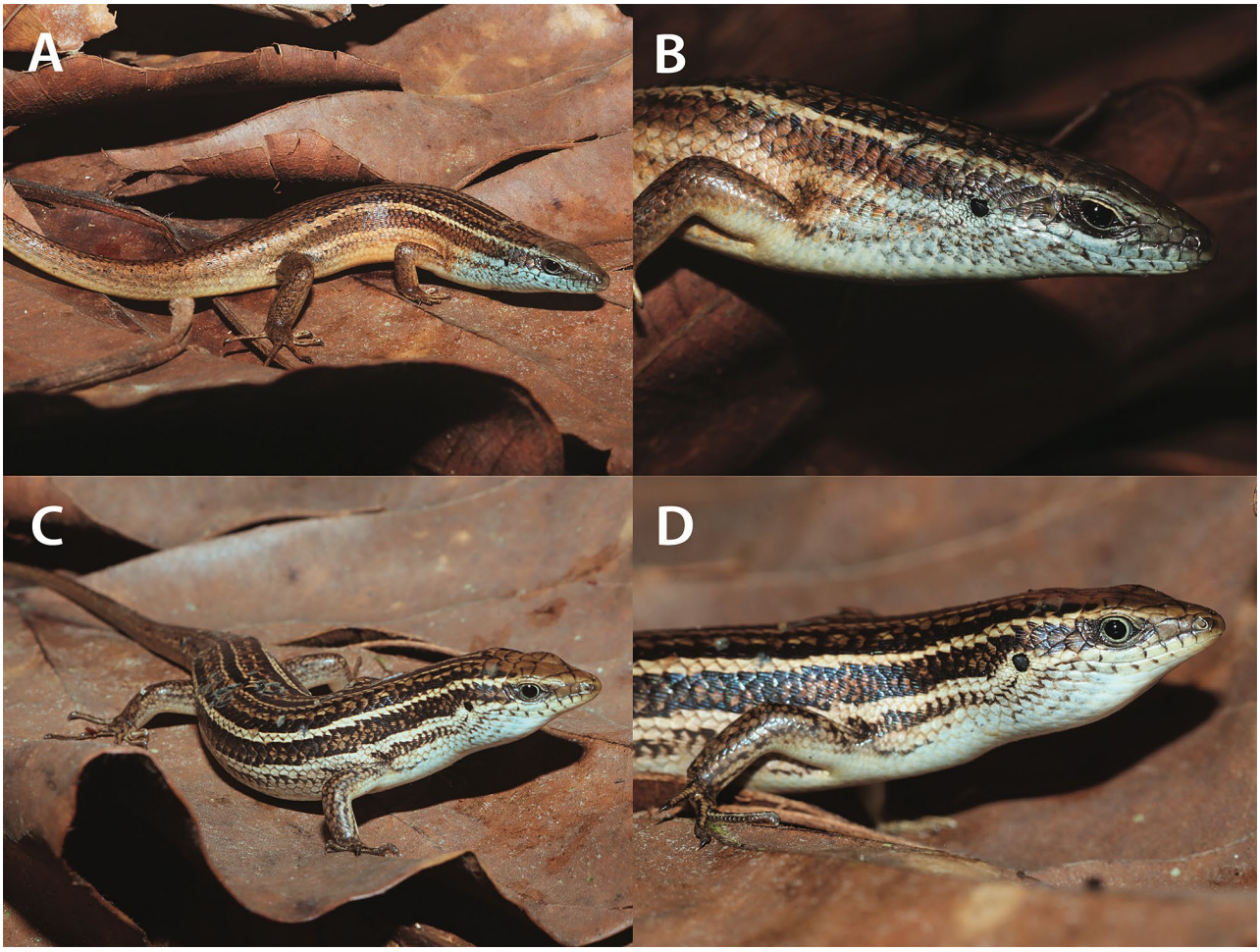

Figure 3. Photographs *Eutropis englei* from Sarangani Province, Mindanao, Philippines, in life. Males (A, B) exhibit cream to light orange ventrum and bluish throat coloration, whereas females (C, D) show a uniform cream color. Photos by A. J. L. Saavedra.

la 1980, Barley et al. 2020, Pitogo et al. 2020). Addressing these outstanding questions will require continued fieldwork in poorly sampled habitats and difficult-to-access regions, as well as sustained, collaborative efforts with local institutions and communities (Meneses et al. 2024; Pitogo 2025). Nevertheless, this work establishes a critical foundation upon which future work can build.

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Supplementary data

The following data are available online:

Supplementary Table 1. List of genetic samples used in this paper and associated Genbank numbers for each gene.

Supplementary Table 2. Results of Welch's t-tests for raw and size-corrected mensural traits, including associated effect sizes and the direction of sexual dimorphism.

Supplementary Table 3. Loadings of size-corrected mensural traits on the first two principal components and corresponding standardized coefficients from multivariate analyses.

Supplementary Figure 1. Maximum-likelihood phylogeny of the *Eutropis multicarinata* species complex inferred from ND2, SELT, and NOS1 sequences with *Dasia grisea* and *E. multifasciata* as outgroups.

Supplementary Figure 2. Heatmap of pairwise Maximum-Likelihood (ML) genetic distances among all sampled *Eutropis* individuals based on concatenated ND2, SELT, and NOS1 sequences.

Supplementary Figure 3. Heatmap of pairwise Maximum-Likelihood genetic distances among all sampled *Eutropis* individuals based on mitochondrial ND2 gene.

Supplementary Figure 4. Heatmap of pairwise Maximum-Likelihood genetic distances among all sampled *Eutropis* individuals based on SELT.