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Sphenomorphini unravelled: a phylogenomic framework and generic reassessments for Australia's most species-rich vertebrate radiation

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ABSTRACT

Australia has the world's most species-rich scincid lizard fauna (family Scincidae) with over 500 recognised species across three highly diverse radiations. One of these radiations is Tribe Sphenomorphini which comprises Australia's most species-rich endemic vertebrate radiation, with ~280 recognised species plus considerable undescribed diversity. The varied ecomorphology and high species richness of Australian Sphenomorphini has been a focus of biogeographic and macroevolutionary analyses, however some relationships remain unresolved. Here, we combine a new phylogenomic dataset with weighted summary-coalescent tree inference and data filtering methods to produce a robust phylogeny spanning all Australian sphenomorphine genera and most recognised species-level taxa. Our results align with prior studies showing an early-burst signature of rapid speciation in the Miocene. Our phylogeny exhibits a deep split between lineages concentrated in arid (~220 species, 3 genera) versus more mesic and temperate lineages (~76 species, 18 genera) some 27.8–25.4 Ma, implying early divergence and widespread niche conservatism within these relatively arid- versus mesic-biome associated lineages. Analyses also support most established genera and supra-generic clades but find some conflicting relationships that challenge monophyly and current systematics within the genera *Concinnia* and *Saiphos* and allied taxa. We provide generic reassignments to address these issues. Species delimitation analyses support previous work indicating Australian species diversity remains moderately underestimated by current taxonomy.

1. Introduction

Scincid lizards (family Scincidae) are a diverse family including over 1700 species occurring across temperate, arid and tropical biomes globally (Chapple et al. 2023). Australia is a world hotspot of skink diversity, with over 500 species that together represent approximately two-thirds of the continental lizard fauna (Uetz et al., 2025). Species richness is considerably higher within the Tribe Sphenomorphini (~274 species, Australian Society of Herpetologists, 2025) than in the two other major Australian scincid radiations (Eugongylini: 140 species; Tiliquini: 53 species, (Australian Society of Herpetologists, 2025). Sphenomorphines occur across most of Australia, but alpha diversity is highest in the arid zone, where sphenomorphines are often the most species-rich vertebrate clade present – with over twenty species occurring in sympatry in some areas (Pianka, 1981; Atlas of Living Australia, 2025). Several lineages (*Ctenotus, Eremiascincus* and *Lerista*) appear to have radiated in the arid zone independently (Skinner et al. 2013). Morphological diversity among them often varies along strongly contrasting axes – e.g. body size variation versus limb reduction (Camaiti et al. 2023). Diversity attenuates in the temperate south, and sphenomorphines are absent from most of the island of Tasmania. However, mesic areas of eastern Australia contain numerous ecomorphologically diverse lineages (Wilson & Swan, 2025). This includes many deeply divergent, species-poor, and putatively relictual genera associated with isolated patches of rainforest or deciduous tropical forest, indicative of a contracting mesic biome (e.g. *Tumbunascincus*, *Calorodius*,

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Gnypetoscincus, *Coggeria, Nangura*; Stuart-Fox et al. 2001; O'Connor & Moritz, 2003; Byrne et al. 2011; Skinner et al. 2013). Together, the Sphenomorphini comprise Australia's most species-rich vertebrate radiation (Rabosky et al. 2007; Singhal et al. 2018; Shea, 2021) spanning considerable ecomorphological diversity (Skinner et al. 2013; Rabosky et al. 2014; Singhal et al. 2025).

The Australian Sphenomorphini have been the subject of numerous macroevolutionary studies that have broadly sought to test ideas concerning the evolution of exceptional species-level and morphological diversity. Past work has examined species diversification (Rabosky et al. 2007; Singhal et al. 2018; Singhal et al. 2025), morphological evolution (Rabosky et al. 2014; Brennan & Keogh, 2018; Camaiti et al. 2024), community assembly (Pianka, 1969; James & Shine, 2000), and environmental niche evolution (Prates et al. 2022; Camaiti et al. 2023). Published phylogenies show the Australian clade diverged from a southeast Asian ancestor and subsequently radiated rapidly into major lineages and genera, with substantial ecomorphological diversity arising by the early to mid-Miocene (Skinner et al. 2013; Rabosky et al 2014). It has been hypothesised that adaptation to arid conditions may have played a critical role in the relatively high rate of lineage accumulation in the two most diverse genera, *Ctenotus* and *Lerista,* which comprise ~75% of Australian sphenomorphine species (Rabosky et al. 2014). Across studies, diversification rates show a signal of "early burst" speciation, likely during early Miocene aridification of Australia (Brennan & Keogh, 2018; Singhal et al. 2025).

Generic and intergeneric relationships within the Sphenomorphini have also been investigated in some detail, however, most systematic treatments have been based on Sanger-sequencing datasets (Reeder, 2003; Skinner et al. 2013; Rabosky et al. 2014). Prior phylogenetic studies, ranging from Sanger sequencing data (Skinner et al. 2013; Pyron et al. 2013; Title & Rabosky, 2017) to genomic scale datasets (Singhal et al. 2018; Singhal et al. 2025), recover most currently recognised genera as well supported monophyletic groups. Genetic data has been crucial in resolving previous uncertainties, and taxonomic changes arising from these phylogenetic hypotheses have resulted in a suite of genera that have been recently described or redescribed, including *Silvascincus, Suppressascincus, Tumbunascincus, Praeteropus,* and *Calorodius* (Skinner et al. 2013; Hutchinson et al. 2021; Torkkola et al. 2022).

Rapid early speciation producing short basal branches, and variable branch lengths between some clades, suggest both rapid radiation and rate heterogeneity potentially underpin the challenges in resolving intergeneric relationships seen in molecular phylogenetic analyses of the Sphenomorphini. The rapid splitting of species can result in high levels of incomplete lineage sorting, obscuring phylogenetic signal (Linkem et al. 2016; Yu et al. 2024). In addition, the variable pace of molecular evolution (rate heterogeneity) between lineages can further mislead tree inference (Edwards, 2009; Ritchie et al. 2022). For example, Australia's two largest lizard genera, *Lerista* and *Ctenotus,* are recovered as sister taxa in some studies (Reeder, 2003; Pyron et al. 2013; Rabosky et al. 2014; Singhal et al. 2018), but not in others (Skinner et al. 2013; Hedges et al. 2015; Torkkola et al. 2022). Recent genomic analyses support a novel topology comprising *Lerista*, *Ctenotus,* and the miniaturised skinks in the genus *Notoscincus* (Singhal et al. 2025), a topology also recovered by supermatrix phylogeny approaches (Pyron et al. 2013), although evidence for this relationship was not investigated in detail.

Generic taxonomy and boundaries also remain problematic for two assemblages of genera (hereafter the *Saiphos* and *Concinnia* groups) in a broader clade of Mesic-associated East Australian genera (hereafter the MEA clade, comprising *Anomalopus*, *Calorodius*, *Calyptotis*, *Silvascincus*, *Coeranoscincus*, *Coggeria*, *Concinnia*, *Gnypetoscincus*, *Nangura*, *Ophioscincus*, *Saiphos* and *Tumbunascincus*). These eleven genera comprise 29 species or ~ 10% of the total diversity in the sphenomorphines (~274 total species, Australian Society of Herpetologists, 2025). First, monophyly of the scansorial east coast genus *Concinnia* is unsettled with respect to the ecomorphologically unique cryptozoic and monotypic rainforest genus *Gnypetoscincus*, which is sometimes placed within *Concinnia* (Reeder, 2003; Skinner et al. 2013; Rabosky et al. 2014; Singhal et al 2018; Hoskin & Shea, 2018b; Camaiti et al. 2021). Second, for a clade of limb-reduced, largely fossorial MEA taxa (comprising *Coeranoscincus, Coggeria, Ophioscincus,* and *Saiphos*), analyses suggest *Ophioscincus* and *Coeranoscincus* are reciprocally polyphyletic (Pyron et al. 2013; Skinner et al. 2013; Rabosky et al. 2014; Singhal et al 2018; Torkkola et al. 2022; Singhal et al. 2025). To resolve this issue Skinner et al. (2013) suggested synonymizing this clade of four closely related but species-poor genera under the generic name *Saiphos*, but this has not been widely adopted. This clade ranges from tetrapodal to limbless with marked body size variation (max snout-to-vent length of 69 mm in *O. cooloolensis* to 291 mm in *C. reticulatus*, Greer & Cogger, 1985). Resolving these relationships will enable better understanding of the evolutionary origins of this morphological variation.

Molecular and morphological analyses of Australian reptile lineages have revealed that unrecognised and often morphologically cryptic species are pervasive (Oliver et al. 2009; Singhal et al. 2018; Melville et al. 2021; Prates et al. 2024). Species richness in the Australian Sphenomorphini has seen steady increase in the last twenty years with 37 species described (Australian Society of Herpetologists, 2025), mostly in the diverse *Lerista* and *Ctenotus* radiations (17 and 10 new species since 2005, respectively). Genetic evidence suggests additional species remain to be described from these two species-rich genera (Singhal et al. 2025), and from other genera such as *Eulamprus* (Pepper et al. 2018). A broader expert assessment of potential taxonomic issues in the Australian squamate fauna estimated that some ~18% (n = 48) of species of Australian Sphenomorphini may contain cryptic or undescribed diversity (Melville et al. 2021). However, lineage diversity in many species, and in some cases genera such as *Calyptotis* and *Notoscincus*, is yet to be assessed using molecular methods. Filling these gaps in knowledge will help to refine estimates of true species diversity in the Australian Sphenomorphini and improve future macroevolutionary analyses of this fascinating radiation.

Here we present a taxon-comprehensive phylogenomic assessment of the Australian Sphenomorphini. Our new phylogenomic hypothesis is built from a target capture approach that leverages genomic data with rigorous alignment filtering (to explore the impact of alignment information quality) and summary species-tree building approaches. We produce age estimates for the Australian radiation using Maximum-Likelihood and Bayesian Inference time tree methods, with both fossil and secondary calibrations. We use the resultant phylogenies to resolve outstanding issues in understanding the systematics of the major Australian Sphenomorphini clades, focusing on resolving uncertain intergeneric relationships, and to provide an estimate of species diversity based on the full spread of samples included in our analyses.

2. Methods

2.1. Sample selection and extraction

We compiled a list of Australian Sphenomorphini following taxonomy based on the Australian Society of Herpetologists Official List of Australian Species (Australian Society of Herpetologists, 2025), including recognised species and subspecies, adding candidate species and operational taxonomic units (OTUs) based on advice from experts in Sphenomorphini taxonomy and published literature (Rabosky et al. 2014; Hutchinson et al. 2021; Prates et al. 2024; Singhal et al. 2025). We collated tissues, DNA extractions, and compatible Squamate Conserved Loci (SqCL) and sequence-capture data from museum and research collections across Australia and the United States. Our final dataset included 508 total SqCL samples across 272 nominal species including 205 newly sequenced individuals, 29 Anchored Hybrid Enrichment (AHE) datasets for nine species (Pepper et al. 2018), and 15 non-Australian outgroups (see Table S1 for details).

2.2. Data collection

Genomic DNA was extracted by standard salt-precipitation or NucleoSpin Tissue kits (Macherey-Nagel). The SqCL (v2) dataset probes target 5,462 loci, including anchored hybrid enrichment (AHE) loci, ultra-conserved elements (UCE), and ~ 50 nuclear loci (GENE) typically used in reptile phylogenetic studies (Singhal et al., 2017). SqCL library preparation used the NextFlex Rapid DNA-Seq Kit 2.0 (Revvity) and largely followed Tiatragul et al. (2023). DNA samples were electrophoresed to assess shearing using the BioRad Gel Doc system (Bio-Rad, Hercules, CA) and quantified by dsDNA Qubit Kit (Mardis & McCombie, 2017). After normalizing concentrations, DNA was sonically sheared into 200–600 bp fragments using a Bioruptor NGS (Diagenode Inc.). Sheared samples were double-end size selected using SeraMag beads, first at 0.5x volume to remove unsheared fragments > 600 bp, then 0.7x volume to exclude small fragments < 200 bp. We washed, size-selected and bound SeraMag-DNA (200–600 bp) with 70% EtOH before eluting in nuclease-free water.

Eluted DNA samples were end-repaired and single-strand adenylated for adaptor site attachment before ligation with NEXTFLEX* Unique Dual Index Barcode adaptors. Adaptor-bound libraries were amplified with 8–12 PCR cycles in Applied Biosystems ProFlex thermocyclers then electrophoresed on the Revvity LabChip GXII Touch HT 5 K chip. Using the GXII results, all libraries were equimolar pooled and target hybridization was performed using biotinylated baits, specifically the SqCL probes, followed by several washes and 6–10 cycles of PCR (Innis et al. 2012).

To check that the target enrichment was successful, 4 ng of pre- and post-hybridisation libraries were used in qPCR reactions with primers for two on-target (SqCL) and two off-target (non-SqCL) genes. Libraries were then diluted to a 2 nM concentration, ready for sequencing on one lane of an Illumina NovaSeq6000 SP flow cell, 150 bp paired end, at the Australian National University's Biomolecular Resource Facility.

2.3. SqCL sequence assembly and gene tree inference

Raw SqCL reads were assembled via the *pipesnake* phylogenomics pipeline (Brennan et al. 2024a), written in Nextflow (Di Tommaso et al. 2017) and implemented on the Seqera platform using the Pawsey Setonix Supercomputer stack (Pawsey Supercomputing Research Centre, 2023). In brief, *pipesnake* collected our raw short-reads from the Illumina HiSeq platform and using a custom bash script (*concatenate_collate.sh*) identified sample-specific forward and reverse reads. BBMAP removed duplicates (*dedupe.sh*) (Bushnell 2014) before TRIMMOMATIC (Bolger et al. 2014) removed residual adapters and barcodes, and PEAR collated read pairs (Zhang et al. 2014). BBMAP then mapped reads against existing squamate SqCL alignments to remove off-target reads before contig assembly with SPAdes (Prjibelski et al. 2020). The resultant contigs are annotated to targets via reciprocal search in BLAT (Kent 2002).

From these mapped contigs, we generated Pseudo-Reference Genomes (PRGs) for each sample; singular fasta files for each sample containing all loci from the highest contig-to-target sequence matches. Individual loci from each PRG were then aligned in MAFFT with gap removal by GBLOCKS (block settings: b1 = 0.5, b2 = 0.85, b3 = 8, b4 = 10, b5 = h). Cluster alignments were then analysed using the Griffith University high performance cluster (GOWONDA), using custom Python scripts to run IQ-TREE 2.2.2 (Minh et al. 2020) with default settings in ModelFinder simultaneously to select best-fit molecular evolution models and produce locus-specific gene trees with 1000 ultrafast bootstrap replicates.

Examination in FigTree v1.4.4 (Rambaut, 2018) found abnormally long terminal branches in some gene trees. Inspecting associated alignments in Geneious Prime 9.1.8 (https://www.geneious.com) found sequence error at 5′ or 3′ alignment ends, typically ~ 20 bp with 50–100% polymorphic sites. These were largely eliminated using *TAPER* (version *correction_multi_aggressive.jl*), a two-dimensional likelihood-based outlier detection package implemented in *julia* programming language (Zhang et al. 2021) which computes divergences for each position in multiple sequence alignments and compares these across a sliding window to find outliers. Examination of the UCE alignments confirmed most 5′ or 3′ terminal errors were eliminated, and we manually removed remaining errors in Geneious Prime for smaller alignment datasets (the AHEs and GENEs). Cleaned alignments were used to regenerate gene trees in IQ-TREE as above.

2.4. Summary coalescent species tree inference and gene tree conflict

To infer a weighted-summary species tree, we used the ASTER* package (Zhang & Mirarab, 2022). Gene trees from trimmed and cleaned UCE (n = 4969), AHE (n = 377), and GENE (n = 30) alignments were used as input for the wASTRAL-hybrid algorithm, which weights the contribution of gene tree quartets by their relative support values, and calculates local posterior probability support (LocalPP, Supplementary Fig. S2a). As wASTRAL produces uninformative terminal branch-lengths of 1.0, we calculated branch lengths and support values using IQ-TREE, using the fixed topology from wASTRAL and a concatenated alignment of 87 Long Informative Loci (LIL, see below details). To visualize gene tree discordance, we used total cleaned alignment and gene tree datasets to calculate gene-concordance factors (gCF) and bootstrap support values using 1000 ultrafast replicates in IQ-TREE (Fig. 1, Supplementary Fig. S2b).

To assess concordance in phylogenetic relationships across different combinations of loci, we compared topology and concordance factors across species trees estimated using three subsets of the data selected using different filtering methods. First, we used PhyloConfigR (Hutter & Duellman, 2023, Supplementary Fig. S3, Supplementary Table S4) which subsets alignments by phylogenetic informativeness, missing data, and length, determining which subset contains the highest concordance between likelihood and coalescent trees (by calculating Robinson-Foulds distance between concatenated ML and coalescent species trees, which is expected to increase with gene tree incongruence, see Linkem et al. 2016; Chan et al. 2020). Second, we used MetablastR (Benoit & Drost, 2021) to identify Rapidly Evolving Long-Exon Capture (RELEC) loci, which show promise in resolving deep phylogenetic divergences (Karin et al. 2020). We aligned *Lerista edwardsae* reference RELEC loci (B. Karin, unpublished data) against our SqCL dataset, selecting loci with > 90% MetablastR weighted-grade match as our RELEC loci subset. Third, since SqCL loci were generally shorter than target RELEC loci, we used SEGUL (Handika & Esselstyn, 2024) to identify loci with desirable features of RELEC by targeting loci > 1500 bp in length, with > 25% informative sites, and < 5% missing data, which we call Long Informative Loci (LIL). A summary coalescent species tree was inferred for each subset of data: RELEC, LIL, and PhyloConfigR (see Fig. 2). We calculated gene-concordance factors (gCF) and site concordance factors (sCF) in IQ-TREE (Minh et al. 2020) and compared the topology and support values for each subset with our All-Loci species tree (Fig. 2a), especially among basal divergences, major clades, and genera. To determine if shorter branches show higher discordance across gene trees, we plotted a gCF against branch length (Supplementary Fig. S5).

2.5. Species delimitation

To generate estimates of total species richness based off sampling in our dataset we conducted species delimitation analyses in the PTP (Poisson Tree Process) server (https://species.h-its.org/ptp/). This software server applies both a Maximum Likelihood (ML-PTP) and Bayesian (bPTP) implementation of the Poisson Tree Process to estimate species boundaries (Zhang et al. 2013) (Table 1, Supplementary Table S6). As distant outgroups and rate variation can make species delimitation challenging (Zhang et al. 2013), we ran these analyses on

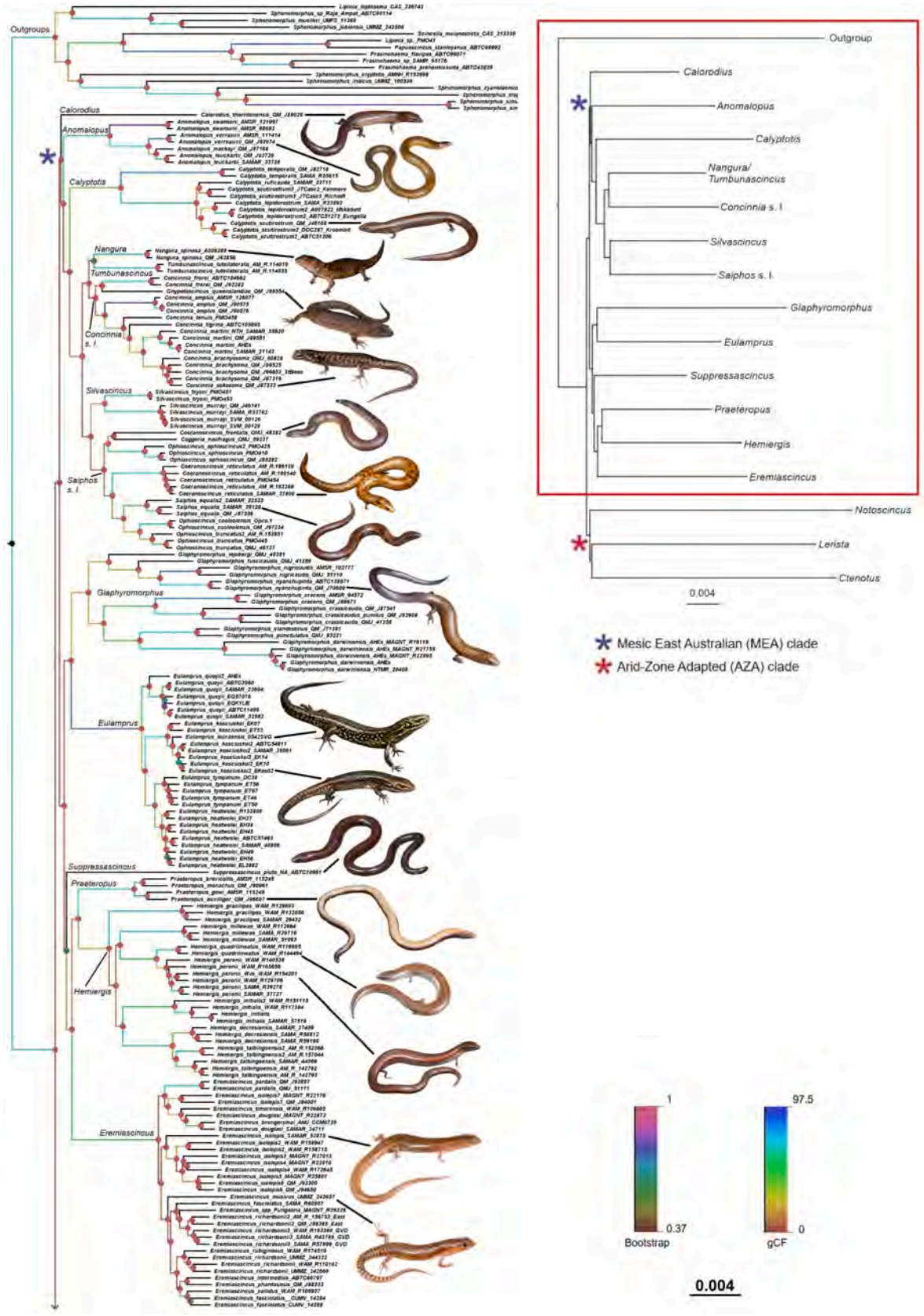

Fig. 1. Species tree for the Australian Sphenomorphini. Summary coalescent species tree topology estimated in wASTRAL from 5,298 independent gene trees. Branch colour indicates gene concordance factors (low = blue, high = red), and node numbers show Maximum Likelihood bootstrap support values from IQ-TREE. Labels a-q show crown nodes of genera or in two cases supra generic groups, asterisks indicate crown nodes for major radiations centred on distinct biomes. Inset with red box shows position of the figure within the overall species tree. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

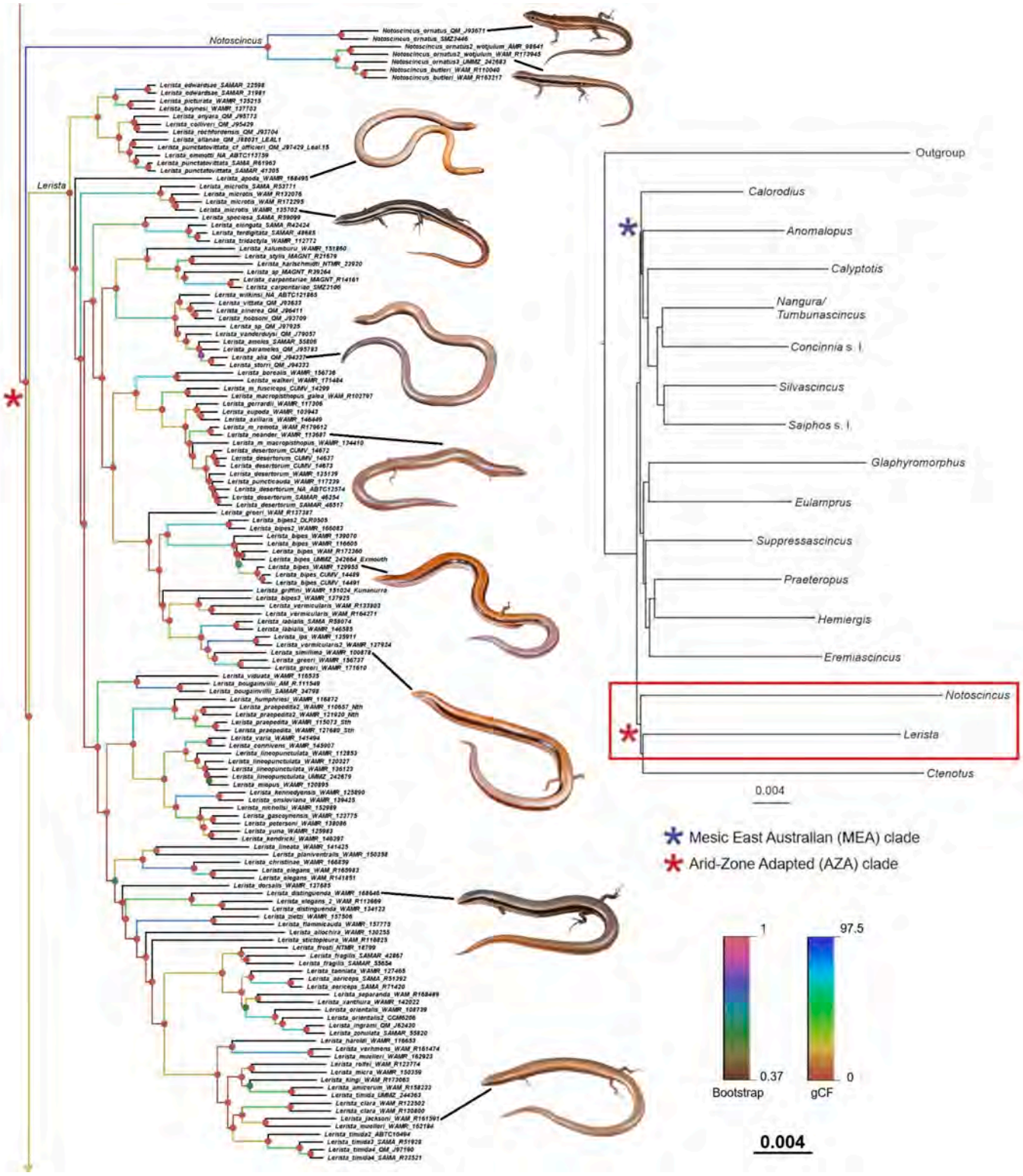

Fig. 1. (*continued*).

subsets of the final All-Loci species tree (Fig. 1), extracting clade/generic subtrees containing candidate lineages of interest – the *Concinnia* clade (including *Nangura* and *Tumbunascincus*), *Saiphos* clade (see below), the genera *Anomalopus, Calyptotis, Eremiascincus, Eulamprus, Glaphyromorphus, Hemiergis,* and *Notoscincus,* and 10 subtrees for *Ctenotus* and 12 subtrees for *Lerista* covering all major sub-clades in each genus. To gain an estimate of genetic divergence between candidate species and closest lineages we calculated Composite Maximum-Likelihood (CML) genetic distances in MEGA-X (Kumar et al. 2018) using our 87 LIL alignments. We emphasise that these species delimitation analyses are exploratory. PTP methods, while often applied to muti-locus data, were designed for analyses of single-loci (Luo et al. 2018). Our intraspecific sampling is also likely insufficient to delimit species from structured populations in many cases (Sukumaran & Knowles, 2017). Nevertheless, we include these analyses with the purpose establishing a framework to guide future taxonomic research and contribute new data towards

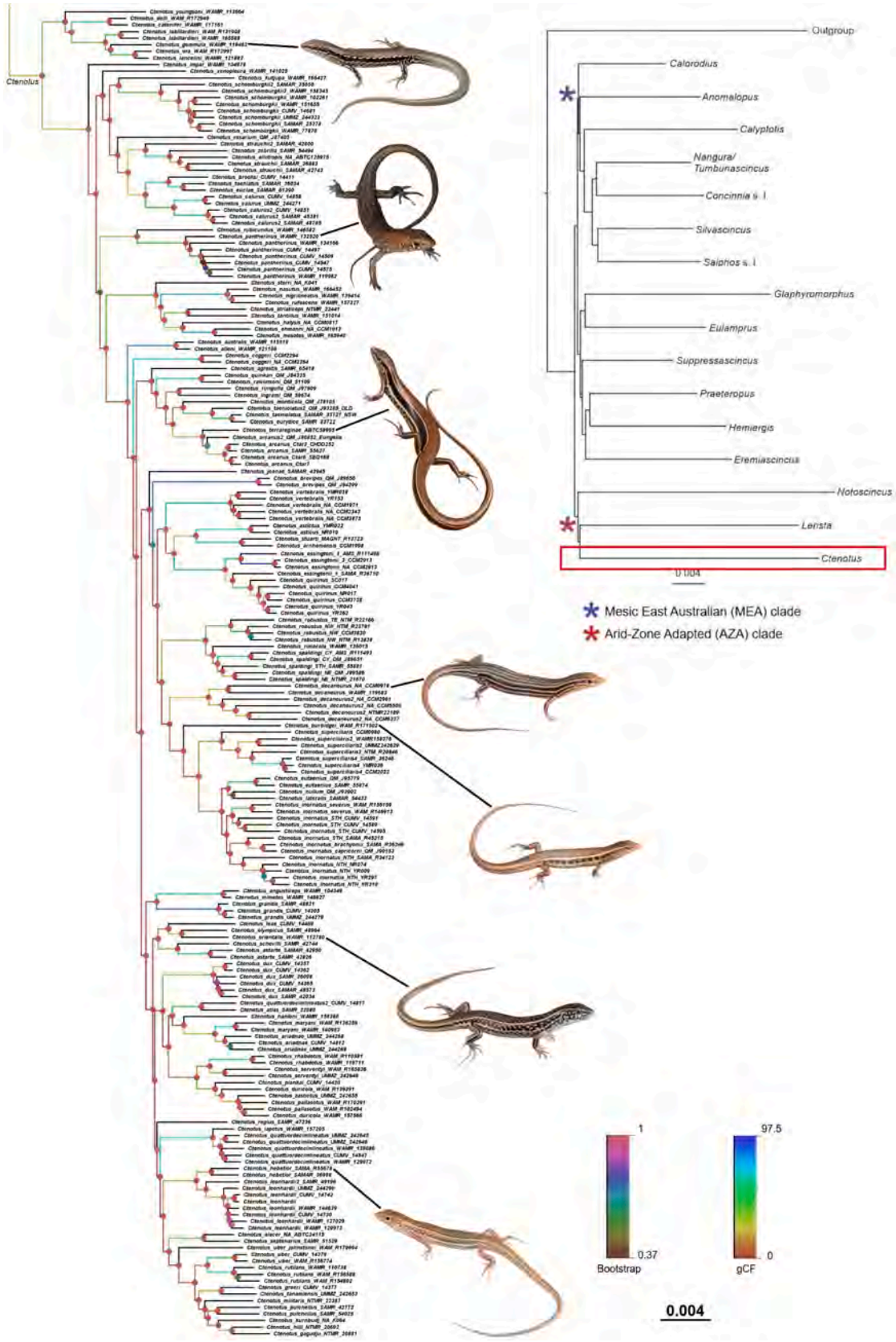

Fig. 1. (*continued*).

estimating species richness based on our sampling. Additional analyses and evidence are required to properly test the specific status of the candidate species identified.

2.6. Divergence dating analyses

To compare divergence dates under different dating methods, and

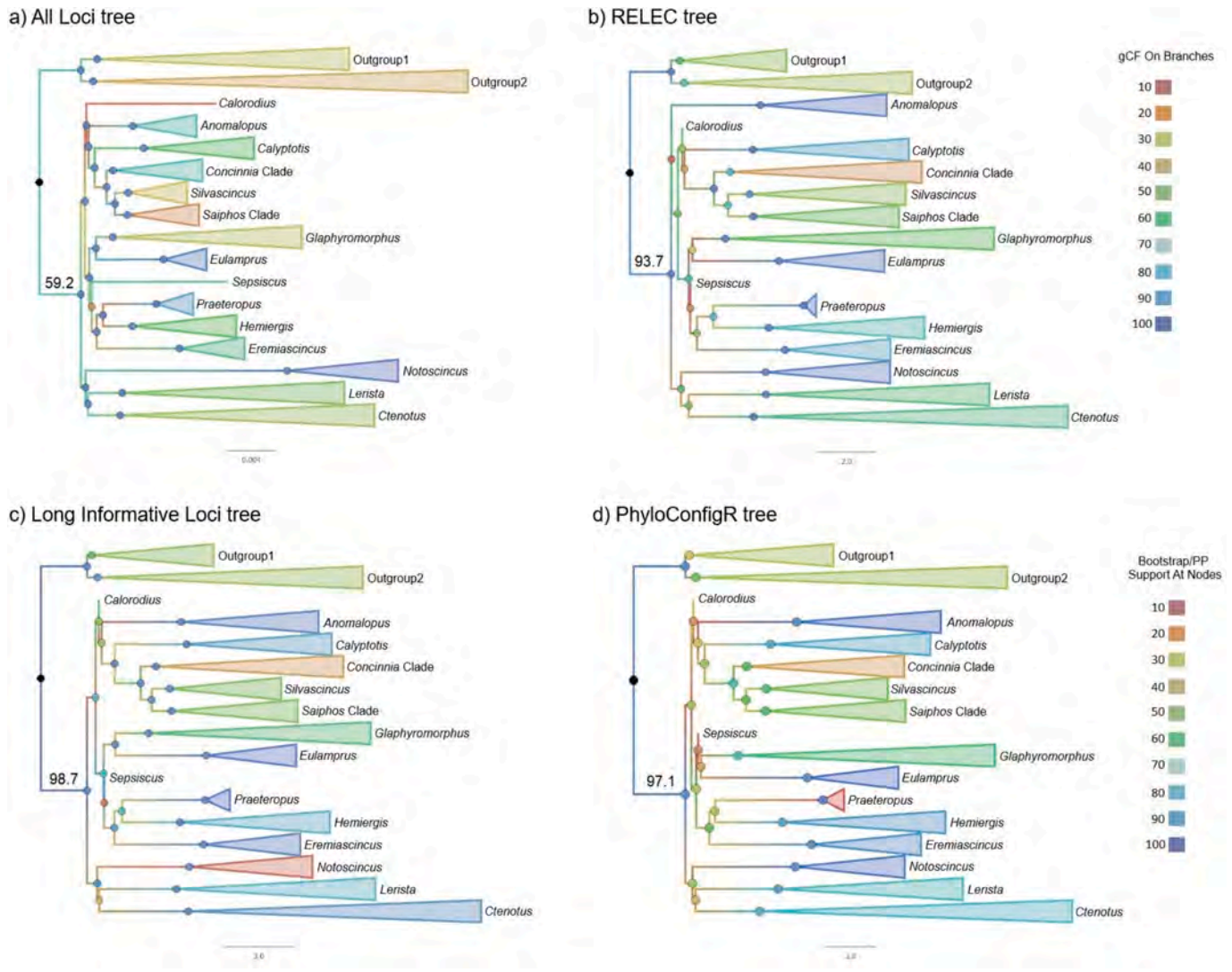

Fig. 2. Concordance Factors Across Filter Subsets. Gene concordance-factor (gCF) summary trees showing similarities across different subsets of loci and analyses in estimated relationship for the Australian Sphenomorphini. Branches coloured by gene-concordance factor and node values by 1000 ultrafast bootstrap scores from IQ-TREE: a) All loci gene tree dataset; b) best-matching Rapidly Evolving Long Exon Capture loci tree; c) Long Informative Loci subset tree; and d) highest gCF subset tree (PIS < 500) from PhyloConfigR. Numerical value indicates gene-concordance factor (gCF) at basal Australian node in each tree. Note strong concordance across trees with genera and major group inter-relationships largely stable, and discordant signal (red circles on nodes) limited to a small number of low diversity genera – *Suppressascincus*, *Calorodius*, and *Anomalopus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

test whether external fossil calibration alters estimated dates, we provide three divergence-time estimates using dated maximum-likelihood and Bayesian Inference time trees with calibration dates from previous phylogenetic dating studies (Skinner et al., 2011, 2013; Table 2). No fossils of unequivocal phylogenetic position are available for Australian Sphenomorphini, so for the first two analyses (see below) a prior constraint of 28 Ma with a broad normal distribution (Mean = 28 Ma, Σ = 4.75, 95% CI = 35.8–20.2 Ma) was used based on prior fossil-calibrated date estimates for the age of the Australian radiation (Skinner et al. 2013).

For the first dating analyses we used the Rel-ML tool for a RelativeRates maximum-likelihood analysis due to its low computational demand (Mello, 2018). We ran Rel-ML on our fixed topology species tree reduced to 310 taxa covering all species and candidate species, with 87 concatenated LIL alignments for sequence data. We used a General Time Reversible substitution model, Gamma distributed rate differences among sites, and Invariable rates (GTR + G + I) to estimate our Rel-ML time tree.

For the second dating analysis we estimated timescales of divergence using Bayesian Inference implemented in BEAST2 (Bouckaert et al. 2019) using a fixed topology from our wASTRAL species tree. We selected the longest 30 LIL alignments as input sequence data to reduce computation times in BEAST2. Taxon sampling was trimmed to include one representative per taxon. Counting subspecies and candidate OTUs we again included a total of 310 tips. We selected the longest 30 LIL alignments as input sequence data. We again applied a broad, normally distributed 28 Ma (95% CI = 35.8–20.2 Ma) prior for the Australian radiation (Skinner et al. 2013). We applied a simple strict-clock model with linked trees and linked HKY substitution model under a Calibrated-Yule process, running two MCMC chains of 25 million iterations, sampling every 2500th. Trace-files were read in Tracer 1.7.2 (Rambaut et al. 2018); chains rapidly converged with high effective sample sizes (ESS > 200) for all parameters at ~ 50,000 iterations onward, thus 10% were eliminated as burn-in. Trees were combined and resampled to n = 10,000 in LogCombiner 2.7.7 before Maximum Clade Credibility (MCC) tree estimation in TreeAnnotator (Drummond & Rambaut, 2007).

For a final dating analysis we used MCMCtree (Yang, 2007; Puttick, 2019) to estimate ages for major divergence events in the Australian

Table 1
Species Delimitation Summary by Genus/Clade. Species delimitation results summarised by genus or clade (Clade of Interest). Species richness counts include current estimates produced from the Australian Society of Herpetology (Current Taxonomy), Bayesian Poisson Tree Process (bPTP Taxa), Maximum-Likelihood Poisson Tree Process (ML-PTP Taxa), relative genetic distances (Genetic Distance), and our final combined estimate of species diversity (Operational Taxa).

Clade of Interest	Current Taxonomy	bPTP Taxa	ML-PTP Taxa	Genetic Distance	Operational Taxa
Calyptotis	4	7	6	6	6
Saiphos Group *(Saiphos-Coggeria)*	9	11	11	11	11
Concinnia Group *(Concinnia-Tumbunascincus)*	10	10	9	10	10
*Glaphyromorphus**	11	13	13	11	11
Eulamprus	5	24	10	7	7
Hemiergis	7	12	6	9	9
Eremiascincus	11	25	18	22	22
Notoscincus	3	5	2	4	4
Lerista1 (microtis)	2	1	2	1	1
Lerista2 (macropithopus-desertorum)	6	9	9	8	9
Lerista3 (griffini-bipes)	7	15	11	9	9
Lerista4 (wilkinsi-storri)	9	8	2	10	10
Lerista5 (humphreisi-praepedita)	2	4	2	3	3
Lerista6 (elegans-timida)	29	34	22	35	35
Ctenotus1 (kutjupa-schomburgkii)	2	4	3	4	4
Ctenotus2 (strauchii-calurus)	8	11	11	9	9
Ctenotus3 (arcanus-taeniolatus)	10	11	11	11	11
Ctenotus4 (spaldingi-quirinus)	6	8	7	7	7
Ctenotus5 (robustus-spaldingi)	3	8	7	6	6
Ctenotus6 (nullum-inornatus)	7	15	13	10	10
Ctenotus7 (rhabdotus-duricola)	6	9	6	6	6
Ctenotus8 (leonhardii)	2	9	4	3	3
Ctenotus9 (uber-hilli)	9	12	10	10	10
Ctenotus10 (decanuerus & supercilliaris)	2	9	11	6	6

Table 2
Divergence Dates for Crown Ages by Genus/Clade. Divergence dating analyses for crown ages of genera and clades/groups of interest. Dates for crown ages of groups and genera of interest given in millions of years before present for BEAST2 timetree analyses (BEAST2), Rel-ML timetree analyses (Rel-ML), MCMCtree analyses (MCMCtee) and StarBEAST analyses from Skinner et al. 2013 (Skinner *BEAST), with confidence intervals (95% HPD, highest posterior density) for each node, and variance in crown ages across analyses (Variance). * indicates groups not included in analyses (i.e. in MCMCtree where groups were often reduced to single representatives).

Group Node	BEAST2	95% HPD	Rel-ML 87	95% HPD	MCMCtree	95% HPD	Skinner *BEAST	95% HPD	Variance
Praeteropus	5.3	3.8–6.9	9.9	4.6–21.2	*	*	5.5	2.0–9.4	6.7
Sepsiscus	21.6	15.1–27.3	26.8	18.0–32.7	*	*	*	*	13.5
Eulamprus	6.0	4.3–7.8	8.8	4.4–17.6	*	*	5.7	3.0–8.8	2.9
Eremiascincus	8.4	6.0–10.8	10.9	5.7–20.8	*	*	9.6	6.2–13.5	1.6
Silvascincus	9.6	6.8–12.3	16.9	8.2–23.7	*	*	11.5	5.8–17.3	14.5
Anomalopus	11.3	7.9–14.4	15.7	18.1–30.3	*	*	12.9	7.8–18.3	4.9
Hemiergis	13.4	9.8–17.5	19.1	9.5–32.7	*	*	14.4	9.4–19.4	9.3
Saiphos Group	10.5	7.6–13.5	17.4	8.8–32.7	11.0	7.3–14.7	14.3	9.7–19.4	10.3
Calyptotis	14.0	9.9–17.9	17.6	9.5–32.6	*	*	15.4	9.3–21.4	3.3
Glaphyromorphus	19.6	13.9–24.9	22.7	13.8–32.7	*	*	18.2	12.7–24.3	5.2
Notoscincus	10.7	7.9–13.9	8.5	5.7–12.7	*	*	4.7	0.3–8.6	9.3
Concinnia Group	11.2	8.2–14.6	19.3	9.6–32.7	*	*	16.3	11.0–21.8	16.5
Ctenotus	23.0	16.5–29.4	20.8	13.5–31.9	17.5	10.4–24.6	13.6	9.0–18.8	16.6
Lerista	21.3	15.1–27.0	19.1	12.2–29.9	16.2	9.4–23.5	13.9	9.0–19.1	10.5
Saiphos–Silvascincus	12.5	9.0–16.0	20.0	10.6–32.7	13.6	9.7–18.1	16.9	11.6–22.8	11.6
Mesic eastern-Australian clade	22.1	15.6–28.1	26.8	19.3–32.7	23.9	18.1–31.1	21.2	14.8–28.3	6.0
Australian Sphenomorphus group	28.0	20.3–35.9	27.9	23.9–32.7	27.7	20.9–35.4	28.0	19.8–37.2	0.0
Tumbunascincus-Nangura Group	11.5	8.1–14.7	20.1	9.9–32.7	11.1	7.2–15.6	*	*	25.7
MEA + *Glaph-Hemi-Eulamp*	23.0	16.4–29.4	27.6	21.6–32.7	24.9	18.9–32.0	*	*	5.4
Arid Three (*Noto-Lerista-Ctenotus*)	27.8	20.1–35.6	26.1	21.8–32.4	25.4	19.1–32.8	*	*	1.5

Sphenomorphini based off a much broader sampling of squamates including multiple nodes where fossil calibration could be applied. We leveraged fossil evidence by combining our 377 AHE dataset with matching data for 17 outgroup taxa spanning major squamate groups, Rhynchocephalia, and a bird. We grafted these 17 external outgroup taxa to our sphenomorphine phylogeny, applying fossil calibrations from literature for six nodes (Aves, Sphenodontids, Gekkotans the Toxicofera, Xantusiidae, and crown Scincidae), using bounded, skew-Normal, and skewT distributed age prior calibrations (Supplementary Table S7). To reduce computational burden, we reduced sampling of Sphenomorphini to 29 representatives including all Australian genera (46 total tips, 17 outgroups). For these analyses we partitioned by 1st, 2nd, and 3rd codon position with independent log-normal rates, running 2,000,000 generations, discarding the first 10% as burn-in and sampling every 100th. Examining trace-files in Tracer 1.7.2 (Rambaut et al. 2018) showed convergence and high sample size (ESS > 200) for all parameters. Dates from MCMCtree (Supplementary Fig. S8) across major group nodes of interest were compared with those from BEAST2, Rel-ML, and prior estimates from Skinner et al. (2013) (Table 2).

3. Results

3.1. Sampling summary, sequence error, and data filtering

Following trimming and removal of low-quality alignments our final dataset contained 536 individuals comprised of SqCL data for 205

samples generated during this study, SqCL data for 302 samples generated by Singhal et al. (2025), and 29 samples with AHE-only datasets from Pepper et al. (2018). This sampling spanned 256 recognised Australian species (and an additional 18 subspecies) and 14 outgroup species from Melanesia and Southeast Asia. The edited dataset comprised of 5,376 loci including of 377 AHE-loci, 31 GENE-loci, and 4,968 UCE-loci (total 5,432 pre-cleaning). Sequence cleaning by TAPER and manual editing eliminated long terminal branches, reducing total sites by 0.09% (30,708 bases) and total characters by 0.17% (2,514,205 characters).

Alignment searching with MetablastR found 46 loci with > 90% weighted-grade matches to the RELEC data for *L. edwardsae*. SEGUL found 87 loci meeting our LIL criteria (>1500 bp in length, with > 25% informative sites, <5% missing data). PhyloConfigR found a subset of 104 trees with > 500 Parsimony Informative Sites (subset PIS_500) which outperformed others in terms of reducing anomaly zones and increasing gCFs and sCFs (Supplementary S4). Few loci were shared across these three subsets of the overall sequence dataset, with the highest similarity being between PhyloConfigR and LIL (subset overlaps: PhyloConfigR versus LIL = 57.7% or 60/104 alignments; PhyloConfigR versus RELEC = 16.4% or 17/104 alignments; RELEC versus LIL = 17.4% or 8/46 alignments).

3.2. Species tree topology and gene-concordance analyses

Our All-Loci species tree contained 536 tips based on 5,376 gene trees (Fig. 1, Supplementary Fig. S2). We found a deep divergence between an "Arid-Zone Associated" clade (*Notoscincus-Ctenotus-Lerista*, hereafter the AZA clade) and all other genera of Australian Sphenomorphini. While bootstrap values and posterior support were generally high, concordance factor analyses indicated areas of gene tree discordance (gCF < 0.75), including basal branches of the overall Australian radiation, within the MEA clade, the positions of *Calorodius*, *Anomalopus*, and *Suppressascincus*, relationships among lineages within *Eremiascincus*, and among basal branches of the AZA clade.

LIL and PhyloConfigR subsets showed a considerable improvement in gene-concordance for basal branches relative to the complete dataset (Fig. 2). Values for gCF (mean = 46.77, standard deviation = 31.1) and sCF (mean = 58.41, standard deviation = 20.3) were similar, suggesting that stochastic error and limited data are unlikely to impact tree inference in the PhyloConfigR summary tree. Gene-concordance scores for both LIL and PhyloConfigR subsets showed general increase across much of the tree relative to the All-Loci dataset, especially the base of the Australian radiation (gCF at Australian Sphenomorphini crown for All-loci = 59.2, and PhyloConfigR summary tree = 97.1, Fig. 2), although shorter branches continue to show relatively lower gCF (Supplementary Fig. S5). Despite these increases in gCF values, relationships between genera showed little difference across all subsets, aside from two genera, namely: *Anomalopus* was placed either inside the Mesic-associated East Australian clade or as a more basal member of the non-arid clades (see Fig. 2B); and *Suppressascincus* was placed basal to either the *Eremiascincus-Hemiergis-Praeteropus* clade or to the *Glaphyromorphus-Eulamprus* group (Fig. 2D).

3.3. Monophyly of genera

Most genera were monophyletic and well supported, however there were notable exceptions in two clades, namely in the *Saiphos* group including *Coeranoscincus, Coggeria*, and *Ophioscincus*, and in the genus *Concinnia* which includes *Gnypetoscincus*. Among the *Saiphos* group (Fig. 4C and 4D), *Coeranoscincus frontalis* was placed sister to the monotypic *Coggeria naufragus*, and these two taxa in turn were a sister lineage to *O. ophioscincus*. Conversely, *Coeranoscincus reticulatus* was placed sister to *S. equalis*, while *O. truncatus* plus *O. cooloolensis* formed a sister lineage to *Saiphos*. All of these relationships had IQ-TREE bootstrap and wASTRAL local posterior-probability support values of 1.0. Our analyses placed *Gnypetoscincus* within *Concinnia* and as sister to *C. frerei* (Fig. 4), both with strong wASTRAL posterior and ML-bootstrap support (Fig. 1, Supplementary Fig. S2).

3.4. Species delimitation and genetic distance analyses

A total of 49 lineages were identified as candidate species based on support from either one or both of ML-PTP and bPTP (Supplementary Table S6), and of these 40 were supported by both methods. Nineteen of the 49 candidate species were not identified in any prior analysis of the Australian Sphenomorphini (e.g. Singhal et al. 2025). Of the 49 candidate taxa 36 were divergent lineages within clades that correspond to a currently recognised species level taxon, while 13 were lineages that render the species that they are currently ascribed to paraphyletic with respect to one or more different recognised taxa (for example samples ascribed to *Calyptotis scutirostrum* are paraphyletic with respect to *C. ruficauda*). Species delimitation analyses also identified six recognised taxa that are not supported as distinct in one or more analyses, including four taxa not supported by either analysis (*Ctenotus delli*, *Ctenotus ora*, *Ctenotus taeniolatus*, and *Lerista macropisthopus remota*). Genetic divergence values (i.e. CML values with a potential range from 0 to 1) between candidate taxa vary greatly, with the lowest value calculated from the 87 LIL being 0.0031, ranging up to greater than 0.0100 for some candidate taxa of *Ctenotus* and *Lerista* (range of CML values = 6E-05–0.054). Conversely, all six recognised taxa that were not supported by one or more of the species delimitation analyses showed genetic divergences below 0.003.

3.5. Time tree analyses

As topology was constrained across time trees, we present only the BEAST2 dated phylogeny (Fig. 3) and a summary table of results across all three dating methods (Table 2). Our results suggest the Australian lineage diverged from its Southeast Asian/Melanesian ancestors (here the *Sphenomorphus muelleri-jobiensis* lineage) some 40.4 Ma (51.2–28.3; 95% HPD). We returned a crown age for the Australian Sphenomorphini of 27.7 Ma (35.4–20.9; 95% HPD) from our MCMCtree analysis, 28.0 Ma (35.9–20.3 Ma; 95% HPD) in BEAST2, and 23.8 Ma (30–19.2; 95% HPD) in Rel-ML. Our time trees showed overall similar date estimates for major groups and support a rapid initial radiation, with most generic level divergences occurring within 10 million years subsequent to the basal node for the extant Australian Sphenomorphini. The earliest split among Australian lineages was between the AZA clade and all other genera (BEAST2 estimate, 28 Ma), with rapid subsequent splits among *Notoscincus, Lerista,* and *Ctenotus* (diverging from one another prior to 27 Ma). *Lerista* and *Ctenotus* diversified considerably earlier than most other genera (21.2 and 22.9 Ma respective crown-ages). Nevertheless, there were some early splits between the non-arid groups, including crown ages of 22.1 Ma for the MEA clade and 22.3 Ma for the *Eulamprus-Eremiascincus* clade.

4. Discussion

Our species tree provides the most taxonomically complete phylogenomic framework for the Australian Sphenomorphini to date, with coverage spanning nearly 95% of recognised species. Inclusion of new taxa and additional phylogenetic analyses support the monophyly of most recognised genera but also identified three genera which are not monophyletic as currently circumscribed (*Coeranoscincus*, *Concinnia*, *Ophioscincus*). Short inter-node branch lengths at the base of the extant Australian radiation support the inference of explosive initial diversification. In the following sections we highlight and review the systematic insights provided by this new dataset and analysis.

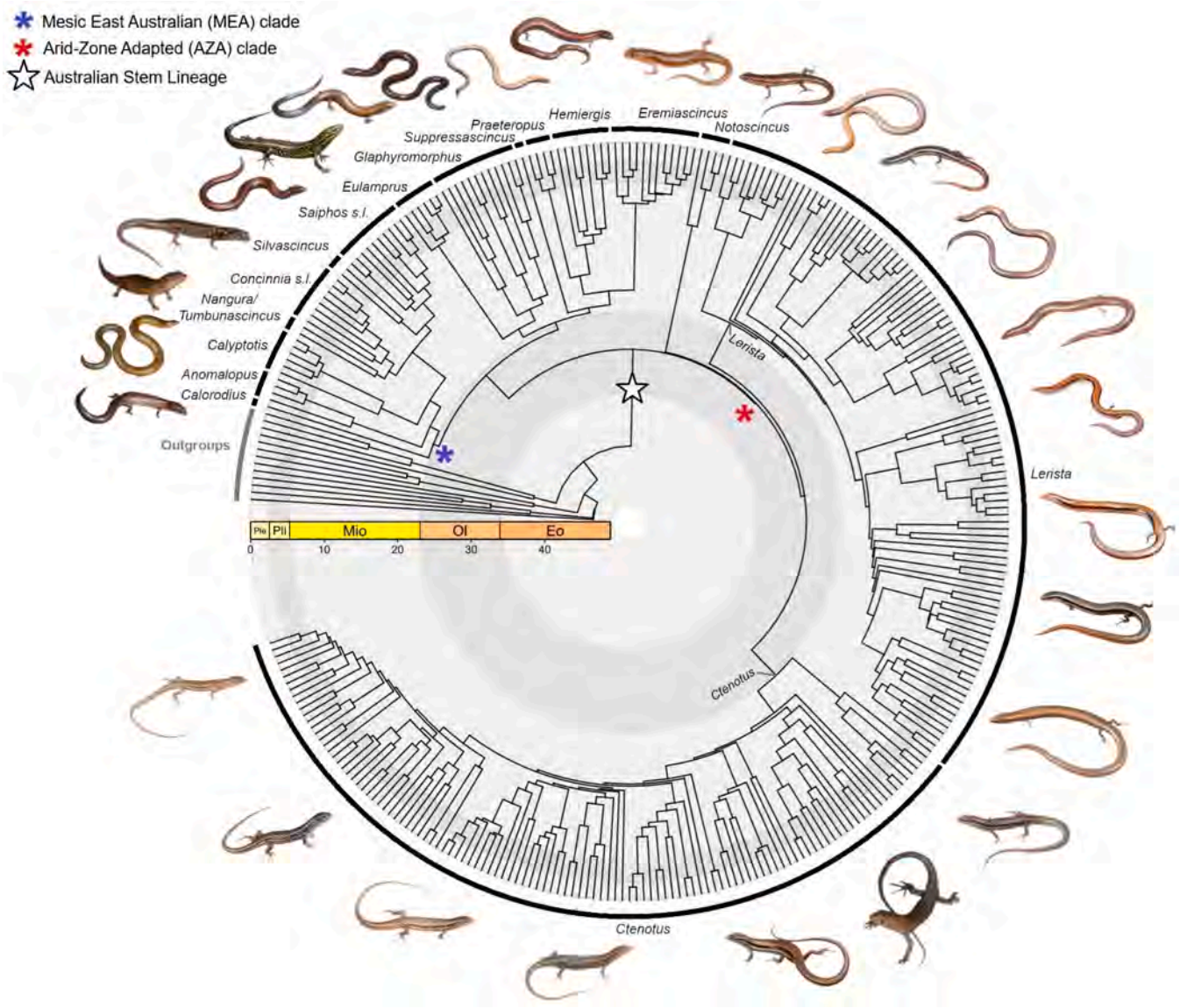

Fig. 3. Dated Bayesian Inference (BEAST2) SqCL Phylogeny of Australian Sphenomorphini. Phylogeny presented in radial layout with timescale in millions of years before present. Concentric shading shows relative position of Epochs (Pleistocene, Pliocene, Miocene, Oligocene, Eocene), as show in timescale. White star indicates stem of the Australian radiation. Images are representative examples starting from above outgroups – *Calorodius*, *Anomalopus*, *Calyptotis*, *Nangura, Concinnia*, *Saiphos, Eulamprus*, *Glaphyromorphus*, *Suppressascincus*, *Praeteropus*; *Hemiergis, Eremiascincus*, *Notoscincus*, species of *Lerista* including *L. apoda, L. microtis, L. alia, L. neander, L. bipes, L. simillima, L. distinguenda, L. jacksoni,* and species of *Ctenotus* including *C. gemmula, C. pantherinus, C. terrareginae, C. decaneurus, C. burbidgei, C. orientalis, C. hebetior.*

4.1. New phylogeny for Australian Sphenomorphini

In our estimated phylogeny for the Australian Sphenomorphini all early diverging nodes (excluding *Suppressascincus* and *Anomalopus*) are strongly supported by high local posterior-probability scores in wASTRAL and high bootstrap scores in IQ-TREE. Further, the topology of our total dataset (All-Loci) species tree overall is highly concordant with that estimated using our filtered datasets with improved gene-concordance (Fig. 2). This consistency across filtered and non-filtered datasets provides confidence in the inferred relationships of major clades and genera.

Our species tree for the Sphenomorphini is highly congruent with previous work by Skinner et al. (2013), Rabosky et al. (2014), and especially Singhal et al. (2025). All these studies recover the same generic and supra-generic clades. Differences between our topology and these other studies are most marked in the relative positions of two genera – *Anomalopus* and *Notoscincus*. The relationships of *Notoscincus* are discussed in more detail below in section 4.2.1. Our analyses place the limb-reduced fossorial eastern Australian genus *Anomalopus* within the MEA clade, with *Calorodius* at the base of the MEA clade (as per Singhal et al. 2025). Some earlier studies based on Sanger-sequencing datasets suggested *Anomalopus* diverged even earlier and is potentially sister to all other Australian Sphenomorphini, excluding *Notoscincus* (Skinner et al. 2013, Rabosky et al. 2014). In contrast our phylogenomic data strongly support expanding our concept of the MEA clade to include *Anomalopus*. The divergent position of *Calorodius* within the MEA clade also supports the recent removal of this taxon from the genus *Calyptotis* (Torkkola et al. 2022).

We also found some novel or unstable relationships among genera in the clade comprising *Eremiascincus*, *Eulamprus*, *Hemiergis*, *Glaphyromorphus*, *Praeteropus*, and *Suppressascincus*. In our analyses *Eulamprus* is sister to *Glaphyromorphus* and *Hemiergis* is sister to *Praeteropus* (as per Skinner et al. 2013; Hutchinson et al. 2021; Singhal et al. 2025), whereas Rabosky et al. (2014) found *Hemiergis* was sister to *Eulamprus*. This clade

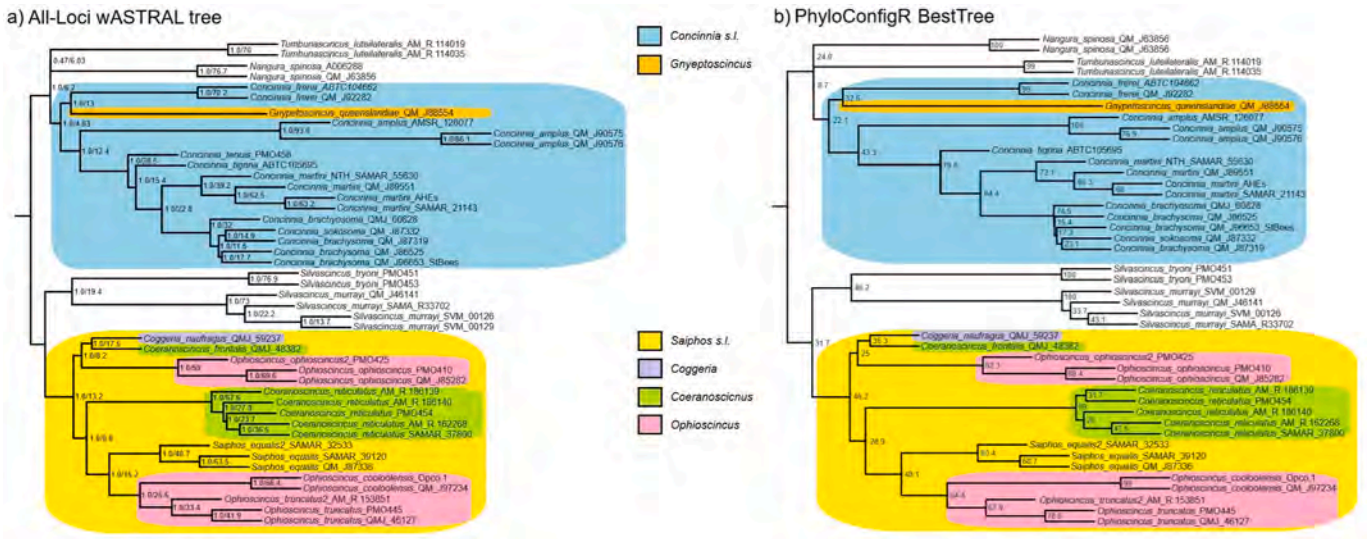

Fig. 4. *Concinnia* and *Saiphos* paraphyly. Relative positions of species across non-filtered (a) and filtered subset wASTRAL species trees (b). *Concinnia* group highlighted in blue with *Gnypetoscincus* in orange nested within. *Saiphos* group in yellow, with the taxa assigned to the genera *Coeranoscincus* in green, *Ophioscincus* in pink, and the montypic *Coggeria* in lilac. Node values in a show wASTRAL posterior probability/gene-concordance factors, node values in b show gene-concordance factors only. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

also includes the only genus, the monotypic *Suppressascincus,* for which relationships remain weakly supported in our tree. Three of our four phylogenomic analyses place this taxon as sister to the *Eremiascincus-Hemiergis-Praeteropus* clade, but with low phylogenetic support values (<0.75% bootstrap support). In our PhyloConfigR tree this monotypic genus is placed as sister to a clade *Glaphyromorphus-Eulamprus* clade (as per mitochondrial data in Hutchinson et al. 2021; Torkkola et al. 2022), but again with low support values (Fig. 2D). Singhal et al. (2025) found the former placement (*Supressascincus* sister to *Eremiascincus-Hemiergis-Praeteropus*) using a concatenated maximum-likelihood approach, but inferred the latter (sister to *Glaphyromorphus-Eulamprus*) using a coalescent approach. Regardless of data filtering efforts, uncertainty remains around the exact evolutionary relationships of the deeply divergent *Suppressascincus*. These challenges highlight how some Australian Sphenomorphini lineages may be in the "Anomaly Zone" whereby incomplete lineage sorting (ILS) may render confident inference of sister taxa relationships extremely difficult, if not impossible (e.g. incongruent gene tree topologies, Linkem et al. 2016).

Near simultaneous speciation events occurring in deep evolutionary history can produce 'hard' polytomies, as opposed to 'soft' polytomies due to insufficient data and limited phylogenetic signal (Suh, 2016; Koenen et al. 2020). Despite expanded genomic sampling, substantial efforts to filter data, and resultant overall improved phylogenetic resolution, we infer short internal branches in the Australian radiation of Sphenomorphini, highlighting the rapid radiation of this diverse clade. These consistently short basal branches, often associated with lower gCF (Supplementary Fig. S5), are indicative of a 'hard' polytomy producing anomalous gene trees near the base of the Australian Sphenomorphini phylogeny. For instance, crown ages for three major groups are under 1.7 million years apart, namely *Ctenotus* (22.9 Ma, 95% HPD = 29.4–16.5), *Lerista* (21.3 Ma, 95% HPD = 27.0–15.1), and the MEA-Clade (22.1 Ma, 95% HPD = 28.1–15.6). This diverse Australian Sphenomorphini show clear evidence for an explosive early-burst radiation sometime in the Late Oligocene-Early Miocene (Singhal et al. 2025). Similar early burst signals have been detected in other major Australian squamate groups (e.g. Brennan & Oliver 2017; Esquerré et al. 2022; Tiatragul et al. 2023; Brennan et al. 2024b), perhaps suggesting a shared signature of rapid initial radiation following late Oligocene climate change, turnover, and in some families, colonisation from Southeast Asia (Oliver & Hugall, 2017). Our age estimates suggest that Australian Sphenomorphini genera radiated after the early Miocene cooling event (~23 Ma), and marked environmental change around this time may have been a driver of both adaptive divergence and allopatric speciation (Byrne et al. 2011; Rabosky et al. 2014; Singhal et al 2025).

4.2. Genus level systematics

Our new phylogenomic framework and expanded taxon sampling for Australian Sphenomorphini provides an opportunity to revisit the relationships and content of problematic, unresolved genera, especially those for which there is evidence of non-monophyly. Before discussing relevant groups in detail, we also note that we are approaching the recognition of genera using phylogenetic classification principles *sensu* Hennig (1966); classification should reflect shared ancestry, mirroring evolutionary branching patterns, and only monophyletic groups (a common ancestor and all its descendants) are fit units for classification. In short, genera should represent well-supported monophyletic clades (De Queiroz & Gauthier, 1992; De Queiroz & Cantino, 2020). In practice however it is important to recognise that phylogeny should be one line of evidence among several when developing generic frameworks; morphological and ecological discontinuities between taxonomic groups should also be considered (Frost, 2000; Cicero et al. 2021; Vences et al. 2024). We also seek to encourage stability by minimising numbers of taxonomic changes and avoiding excessive proliferation of genera with few species. In cases where species, or low diversity lineages, show numerous morphological and ecological apomorphies, but are deeply embedded in clades lacking these characters, we favour the recognition of broader and more inclusive, if morphologically and ecologically variable, genera.

4.2.1. The Arid-Zone associated clade – Ctenotus, Lerista and Notoscincus

The vast majority of Australia Sphenomorphini species are concentrated in two species-rich genera with distributions centred on arid, semi-arid or seasonally arid environments – *Ctenotus* (113 species) and *Lerista* (104 species). The hypothesis that these two genera are sister taxa has received variable support, with some prior phylogenies showing non-sister relationships and low bootstrap values for these nodes (Skinner et al. 2013; Rabosky et al. 2014; Torkkola et al. 2022). However, an increasing number of studies have linked them together with strong support, and more recently also suggested that the species-poor

genus of the miniaturised *Notoscincus* may also be allied to these two genera (Pyron et al. 2013; Title & Rabosky, 2017; Singhal et al. 2025). We consistently recovered the AZA clade, comprised of *Ctenotus* and *Lerista* as sister taxa and this clade sister to *Notoscincus,* as a well-supported sister clade to all other Australian sphenomorphines (Figs. 1–2). Singhal et al. (2025) also recover these relationships using both concatenated maximum-likelihood and coalescent phylogenomic methods. It is possible that this relationship is artefactual, there is a long basal branch to the *Notoscincus* and the branches connecting the AZA genera are very short (Fig. 1), raising the possibility that anomalous gene trees or molecular evolution rates are confounding phylogenetic inference (Ritchie et al. 2022).

Morphological synapomorphies may provide another approach to assess support for the inferred AZA clade. Hutchinson et al. (2021) defined 50 derived morphological character states (absent in ancestral Asian lineages) that show variation in burrowing Australian sphenomorphines. These analyses did not identify characters that are both consistently shared across the AZA clade and absent in other taxa. Although AZA clade taxa do share a narrowed Meckellian groove and premaxilliary tooth count < 9, these features are also present in at least some other genera of Australian Sphenomorphini. One potential synapomorphy for the AZA clade is that the lower secondary temporal scale overlaps with the upper in all three genera, except where head shape is significantly modified i.e. cranially reduced *Lerista* (Greer, 2007). This temporal scale arrangement is a derived feature among *Lygosominae* (Greer, 2007) and is rarely present in other Australian Sphenomorphini, with the exception of a small number of distantly related lineages – *Concinnia martini*, *C. frerei*, *Coeranoscincus reticulatus*, *Calyptotis*, and *Coggeria*.

The distributions of most species in three genera putative AZA clade are also concentrated into arid desert or seasonally arid savannah regions, providing potential further evidence for their association with each other. Most remaining Australian sphenomorphine lineages (with the notable exception of *Eremiascincus*) are concentrated in relatively mesic, eastern, temperate, or southern regions (Cogger, 2014; Wilson & Swan, 2025). This pattern of deeply divergent sister clades of Australian Sphenomorphini with centres of diversity in differing biomes mirrors deep splits between primarily arid versus mesic lineages in some other widespread Australian squamates including agamids (Hugall et al. 2008; Tallowin et al. 2020) and carphodactylids (Oliver & Bauer, 2011). The mid-to-early Miocene emergence of these crown radiations of Arid-Zone associated lineages also adds to the growing body of evidence that arid environments in Australia date back well into the Miocene (Byrne et al. 2011). Niche conservatism is a significant driver of diversity patterns in some other broadly overlapping Australian radiations (Miller et al. 2013; Skeels & Cardillo, 2017; Tiatragul et al. 2024), and is a potential, but untested, explanation for this broadscale differentiation in the distribution of different lineages of Australian Sphenomorphini.

The contrasting species diversity of *Notoscincus* ($n = 2$, and two further candidate species) when compared with *Lerista* ($n = 97$) and *Ctenotus* ($n = 108$) (Uetz et al. 2025) is also notable. Estimated diversification rates in *Ctenotus* and *Lerista* by Singhal et al. (2025) double those of other Australian Sphenomorphini, and rates in *Notoscincus* significantly depart from the *Lerista-Ctenotus* superclade (Slowinski-Guyer test p-value = 0.014, Slowinski & Guyer, 1989). While this suggests differences in diversification dynamics, what underpins these rate differences is very difficult to test. Previous work hypothesised that adaptations to aridity may be a key innovation underlying increased diversification in *Lerista* and *Ctenotus* (Rabosky et al. 2007; Rabosky et al. 2014). One interesting possibility is that even though *Notoscincus* occurs in arid and seasonally arid areas, these relatively miniaturised species may be constrained to hydrically or thermally buffered microhabitats, and this may in turn have limited their scope for extensive diversification. Comparative physiological data are available for some *Ctenotus* species (Bradshaw, 2018), but ecological information is sparse across the Sphenomorphini. Filling in these knowledge gaps could provide information relevant to understanding contrasting patterns of diversification in these overlapping and potentially related arid-associated genera.

4.2.2. The Saiphos group

One residual problematic clade is the *Saiphos* group — a mesic and rainforest associated, generally limb-reduced, fossorial group within the MEA clade. Skinner et al. (2013) found support for a *Saiphos-Ophioscincus-Coeranoscincus-Coggeria* clade, and subsequent phylogenies (including ours) strongly support this grouping (Hutchinson et al. 2021; Singhal et al. 2025). However, as currently recognised, both *Coeranoscincus* and *Ophioscincus* are recovered as reciprocally polyphyletic, with *O. truncatus* (and now also *O. cooloolensis*) as sister to *C. reticulatus,* and *O. ophioscincus* sister to *C. frontalis.* Strikingly, our inclusion of *O. cooloolensis* brings the count of limbless species in this group to three, none with reciprocal sister relationships which implies that all three limbless species, including two *Ophioscincus,* have limbed sister taxa. Prior ancestral character estimation based on incomplete phylogenetic sampling (Camaiti et al. 2022) suggested limb-loss evolved some five times across Australian Sphjenomorophini, and though *O. cooloolensis* adds another independent limb-loss event, evolutionary patterns are yet to be mapped using this more complete phylogenetic framework.

To resolve reciprocal polyphyly in *Coeranoscincus* and *Ophioscincus,* Skinner et al. (2013) suggested assigning the name *Saiphos* to the entire *Coeranoscincus-Coggeria-Ophioscincus-Saiphos* clade. Based on our phylogeny, the only alternative option that would maintain monophyly of genera would be to recognise two additional genera, which would result in this broader clade of seven species comprising six genera, five of which are monotypic. Despite marked morphological diversity, especially in limb development, overall size and dentition (Greer & Cogger, 1985), this clade is relatively young (estimated 10.5 Ma crown age), especially when compared to more diverse arid-zone genera (*Ctenotus* 22.9 Ma, *Lerista* 21.3 Ma crown ages). Skinner et al. (2013) also emphasize the ecological similarity of the *Saiphos* group; all are elongated fossorial or species from mesic eastern habitats. While not entirely exclusive (some features also shared by members of *Anomalopus*, *Lerista, Praeteropus*), eight of Hutchinson et al. (2021)'s derived morphological characters are shared by all *Saiphos* group members: 1) external ear absent; 2) limbs reduced or absent; 3) loss of phalanges; 4) shaft of stapes diameter $>$ 50% stapes length; 5) stapes oriented laterally to anterolaterally; 6) alar crest of the prootic extending anteriorly and to semicircular canals; 7) elevated presacral vertebral count; and 8) complete inscriptional ribs > 2. All achieve trunk elongation via addition of presacral vertebrae (ranging from $n = 40$ in *S. equalis* to $n = 76$ in *C. reticulatus*, Camaiti et al. 2022). The nearest sister lineages, *Silvascincus* and *Concinnia*, are vastly different – fully limbed, non-elongate (presacral vertebrae $n = 26$, Greer, 1992), scansorial or arboreal scramblers. On basis of phylogeny, morphological similarities, and with the aim to avoid the proliferation of monotypic genera, we support the conclusions of Skinner et al. (2013) and synonymise the *Coeranoscincus–Coggeria–Ophioscincus–Saiphos* clade into the more cohesive *Saiphos*. Lumping these taxa into a single genus also emphasises the morphological and ecological plasticity of this clade, in a similar vein to how recognising *Lerista* as a single genus emphasises the remarkable plasticity in limb development in that clade (Skinner et al. 2013).

Saiphos comb. nov.

Type species: *Saiphos equalis* (Gray, 1825).

Type species: *Saiphos equalis* (Cogger, 1983) [=*Seps equalis* Gray, 1825].

Included species: *S. cooloolensis* (Greer & Cogger, 1985), *Saiphos equalis* (Cogger, 1983), *S. frontalis* (De Vis, 1888), *S. naufragus* (Couper et al. 1996), *S. ophioscincus* (Boulenger, 1887), *S. reticulatus* (Günther, 1873), *S. truncatus* (Peters, 1876).

Diagnosis: A clade of Australian Sphenomorphini group scincids that shows considerable variation in dentition, skull morphology and limb development, but share the following combination of character states:

trunk elongation (presacral vertebrae n ≥ 40); inscriptional rib count n > 2; external ears absent; and at least some limb-reduction (phalanges lost from manus or pes ≥ 1) (see Hutchinson et al. 2021). Further distinguished from other Australian Sphenomorphini that show limb-reduction, trunk elongation, and lack external ear openings as follows: from *Anomalopus* if limbed, by having more digits on the hindlimb than forelimb, or if limbless, by having recurved and relatively pointed teeth versus straight and relatively blunt; from *Prateropus* by having separated nasals (versus in broad medial contact); and from *Suppressascincus* by having the first supralabial separate from the nasal (versus fused).

Distribution: Tropical to subtropical rainforest, wet sclerophyll forest, and mesic heaths along eastern Australia from north Queensland south to around Sydney, New South Wales (see Cogger, 2014; Wilson & Swan, 2025).

Phylogenetic definition: *Saiphos* is a maximum crown-clade name referring to the clade originating with the most recent common ancestor of *Saiphos frontalis* and *Saiphos truncatus*, and including all species that share a more recent common ancestor with these taxa than with any of the type species of any other recognised genus.

4.2.3. The genus Concinnia and allied taxa

Concinnia is another historically unstable genus in the Australian Sphenomorphini. Skinks assigned to this genus are diurnal, scansorial, moderately-sized (max SVL 64–115 mm) and fully-limbed species from eastern Australia. Typical members (*C. amplus, C. brachysoma, C. martini, C. sokosoma, C. tenuis, C. tigrina*) form a strongly supported clade across datasets. The sister lineage to this clade of typical *Concinnia* is a clade comprised of two more deeply divergent lineages endemic to the Australian Wet Tropics region of north Queensland, namely the montane species *C. frerei* and the monotypic and highly apomophic "prickly skink" *Gnypetoscincus queenslandiae*. Our phylogeny places a clade comprised of the monotypic genera *Tumbunascincus* and *Nangura* as a sister-lineage to *Concinnia-Gnypetoscincus*. Based on our phylogeny, and other published work (Reeder, 2003; Skinner et al. 2013; Rabosky et al. 2014; Singhal et al. 2018; Singhal et al. 2025), recognition of *Gnypetoscincus* renders *Concinnia* polyphyletic.

The sister relationship between *C. frerei* and *G. queenslandiae* is notable for several reasons. They diverged some 10 Ma, providing further examples of divergent and low diversity lineages of cool climate relicts within the wet tropics region of north Queensland (e.g. *Calorodius thorntonenis* diverged ~ 22 Ma). They are notably different in morphology and ecology. *Concinnia frerei* is a smooth-scaled, diurnal, scansorial/arboreal species, and geographically restricted to small areas of cool, high elevation tropical uplands (>1210 m elevation, Hoskin & Shea, 2018a). *Gnypetoscincus queenslandiae* is a robust skink, with rugose, keeled scales, a very large ear opening, which is largely nocturnal, and lives in cool environments under rotting rainforest logs, extending into lowland areas (>100 m elevation, Hoskin & Shea, 2018b). Despite these differences, both species share an association with particularly cool and moist environments, one at the regional scale (cloud forest) and one at the microhabitat scale (rotting logs). An interesting potential area for physiological research is whether eco-morphological divergence of these two taxa may in part be linked to long-term conservatism in physiological tolerances (i.e. they are both dependent on cool and/or mesic conditions but access these conditions in very different ways).

There are three options for resolving polyphyly of *Concinnia*. First, we might erect a monotypic genus for *C. frerei*. This would add to the six monotypic genera throughout the MEA clade already. Second, *C. frerei* could be sunk into its sister group, *Gnypetoscincus*. This seems inconsistent – *C. frerei* resembles standard members of the *Concinnia* in that it is smooth-scaled, scansorial, diurnal basking, and would make this genus very hard to diagnose morphologically. Third, we could avoid the above issues by extending the *Concinnia* concept as per Skinner et al. (2013), sinking *Gnypetoscincus* into *Concinnia sensu stricto*. This third approach ("*Concinnia queenslandiae*") and has been followed by others (e.g. Hoskin & Shea, 2018b; Camaiti et al. 2022) and we also adopt this position with the taxonomy below to resolve these issues.

Concinnia. comb. nov.

Type species: *Concinnia martini* (Wells & Wellington, 1985).

Included species: *C. ampla* (Covacevich & McDonald, 1980), *C. brachysoma* (Lönnberg & Andersson, 1915), *C. frerei* (Greer, 1992), *C. martini* (Wells & Wellington, 1985), *C. queenslandiae* (Skinner et al. 2013), *C. sokosoma* (Greer, 2007), *C. tenuis* (Gray, 1831), *C. tigrina* (De Vis, 1888).

Diagnosis: A clade in the Australian Sphenomorphini group displaying the following combination of character states: pentadactyl limbs with phalangeal formula of manus 2.3.4.5.3; phalangeal formula of pes 2.3.4.5.4; midbody scales 28 or more; anterior ear lobules absent; supranasals usually absent (except in *C. amplus*); lower eyelid moveable and scaly; parietal scales in contact behind the interparietal; postmental in contact with two infralabials on both sides; third set of enlarged chin shield separated by three scales in a longitudinal series (except in *C. queenslandiae*); fourth toe much longer than third; and basal lamellae sometimes divided but all distal lamellae undivided. Greer (1992) also noted that species in *Concinnia* as defined here are characterised by inguinal fat bodies, and although this state may be pleisomorphic, it is nonetheless absent in some other outwardly similar and related genera in the MEA clade (e.g. *Silvascincus* and *Tumbanoscincus*).

Distribution: Tropical to subtropical rainforest, wet sclerophyll forest, and rocky boulder fields from north Queensland to southern New South Wales (see Cogger, 2014; Wilson & Swan, 2025).

Phylogenetic definition: *Concinnia* is a maximum crown-clade name referring to the clade originating with the most recent common ancestor of *C. queenslandiae* and *C. tenuis*, including all species that share a more recent common ancestor with these taxa than with any of the type species of other recognised genus.

4.3. Species diversity in the Australian Sphenomorphini

Like many diverse Australian lizard clades, new sphenomorphine species continue to be described with regularity (e.g. Rabosky et al. 2017; Amey et al. 2019; Hutchinson et al. 2021; Prates et al. 2022; Zozaya et al. 2024; Zozaya et al. 2025; Zimny et al. 2025). Broadly, our species delimitation analyses suggest that numerous additional species remain to be described. However, before discussing these results we highlight and acknowledge that species delimitation methods make assumptions about speciation, population, gene flow, and mutation processes, which are often violated in practice. Notably, branch-length based methods (as used here) assume Wright-Fisher panmixia (Zhang et al. 2013), and many delimitation tools can confound geographic structure with speciation (Sukumaran & Knowles, 2017). Each dataset presents unique challenges, thus assessing species boundaries with several methodologies is preferred (Carstens et al. 2013).

In the most comprehensive multilocus assessment of species richness in the Australian Sphenomorphini, Singhal et al. (2025) applied morphology, Fst (genetic fixation index), and divergence times to delimit species with more extensive sampling than available for our SqCL dataset. Here, we supplement these prior estimates with additional unsampled lineages, applying simple ML-PTP and bPTP branch-length based delimitations which require only an input tree (Zhang et al. 2013), and reinforce these with genetic divergence estimates. As noted above, we caution that these estimates, based solely on molecular data, are exploratory – many candidate species identified here (Supplementary Table S6) require more extensive geographic sampling, especially across contact zones (Cicero et al. 2021; Vences et al. 2024; Zozaya et al. 2024), before they can justifiably be considered more than geographically structured populations (Sukumaran & Knowles, 2017). There also remain under sampled areas, especially in northern Australia – a hotspot of lizard microendemism and cryptic diversity (Gambold & Woinarski. 1993; Rosauer et al. 2016) where targeted searches continue to discover novel taxa (Zozaya et al. 2024; Patykowski et al. 2025;

Zimny et al. 2025).

In our analyses, we delineated a maximum of 49 candidate species in addition to the 274 species currently recognised, of which 41 were supported by both ML-PTP and bPTP methods. This estimate includes several recognized subspecific taxa (included in our 49 candidate species) that may warrant elevation to species rank (e.g. *L. macrophisthopus galea, L. m. fuscipes, N. ornatus wotjulum, C. uber johnstonei*). Over half of the candidate taxa identified here have been documented in other studies, however our final count includes 19 candidate taxa not identified in prior estimates of species richness (e.g. Singhal et al. 2025). Our estimate of undescribed richness broadly matches earlier candidate species estimates based on genomic data (49 candidate species, Singhal et al. 2025) and on expert elicitation (48 recognised species needing taxonomic work, Melville et al. 2021). Candidate species are concentrated in diverse genera, especially *Ctenotus* (n = 23), followed by *Lerista* (n = 10), and *Eremiascincus* (n = 7), however we also provide molecular evidence for candidate taxa in some low diversity genera that have historically been overlooked such as *Calyptotis*, *Notoscincus* and *Saiphos* (sensu this paper). These analyses also suggested four named taxa that may need to be synonymised. Taking only the lineages supported by both species delimitation approaches would push estimates of Australian Sphenomorphini to just over 314 species.

While acknowledging the methodological caveats above, our results suggest that a slew of new species of Australian Sphenomorphini will continue to be described in coming years. However, based on available data it would also suggest that species richness of Australian Sphenomorphini is only moderately underestimated by contemporary taxonomy (~15% shortfall). Candidate species also tend to be allopatric and parapatric populations and lineages, rather than particularly divergent new taxa with overlapping ranges. As a corollary, we further suggest that better resolving species diversity in the Sphenomorphini will not necessarily change spatial estimates of alpha diversity for the group, but may lead to improved understanding of patterns of regional endemism and turnover.

4.4. Conclusions

The phylogenomic framework we present here helps clarify systematic relationships among Australia's most diverse squamate clade. Consilience with prior studies and topological support across filtered datasets with improving concordance values all contribute to our confidence in the novel topological arrangements presented here. Early divergence of the AZA clade comprising the genera *Ctenotus*, *Lerista* and *Notoscincus* against the remaining radiation of more tropical, mesic, or southern lineages, represents the main phylogenetic division in the Australian Sphenomorphini. We provide new generic rearrangements to resolve polyphyly in two problematic clades, now respectively lumped into *Saiphos* and *Concinnia*. Although species richness is not currently substantially underestimated, we estimate potentially as many as 49 lineages we have sampled represent candidate species, for an estimated total species diversity of 314 species. This is largely in agreement with results from recent phylogenomic estimates despite differing delimitation methods, though estimates derived from molecular data alone have many associated issues and we recommend viewing these delimitation analyses as a preliminary guide for targeting future taxonomic research. This genomic level phylogeny provides a robust framework for future studies of this diverse radiation, including more focused species delimitation efforts, and for modelling environmental niche and morphological trait evolution across the continent.

CRediT authorship contribution statement

Janne J. Torkkola: . **Sarin Tiatragul:** Writing – review & editing, Software, Methodology, Investigation. **Elizabeth S. Broady:** Writing – review & editing, Methodology. **Ian G. Brennan:** Writing – review & editing, Software, Methodology, Investigation. **J.Scott Keogh:** Writing – review & editing, Funding acquisition, Conceptualization. **Daniel L. Rabosky:** Writing – review & editing, Resources, Data curation, Conceptualization. **Sonal Singhal:** Writing – review & editing, Resources, Conceptualization. **Paul M. Oliver:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2026.108573.

Data availability

We have included a DOI link to the Zenodo data repository (https://doi.org/10.5281/zenodo.17541049) as part of the supplementary document.

Data will be made available on request.

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