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Repeated Mitochondrial Capture With Limited Genomic Introgression in a Lizard Group

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ABSTRACT

Mitochondrial introgression is common among animals and is often first identified through mitonuclear discordance—discrepancies between evolutionary relationships inferred from mitochondrial DNA (mtDNA) and nuclear DNA (nuDNA). Over recent decades, genomic data have also revealed extensive nuclear introgression in many animal groups, with implications for genetic and phenotypic diversity. However, the extent to which mtDNA introgression corresponds to nuDNA introgression varies. Here, we investigated historical and recent introgression in the *Gehyra nana-occidentalis* clade, a complex group of Australian geckos with documented cases of mitonuclear discordance suggestive of repeated mtDNA introgression. We hypothesised that mitonuclear discordance in this clade reflects mtDNA introgression with substantial nuclear introgression. Despite evidence of repeated mtDNA introgression, however, we found little to no evidence of historical nuDNA introgression using exon capture and genome-wide single nucleotide polymorphism (SNP) data. We also found no evidence of gene flow at modern contact zones and detected only a single early generation hybrid. Unsurprisingly, given these results, we found no evidence of transgressive, intermediate, or more variable morphological phenotypes in taxa with introgressed mtDNA. These findings suggest that hybridisation in this system has, at least in some cases, resulted in repeated mitochondrial introgression with little or no nuclear introgression. This pattern aligns with other studies showing limited nuDNA introgression in taxa with mitonuclear discordance, highlighting a potentially broader trend in animal radiations.

1 | Introduction

Hybridisation was once thought to occur rarely in animals (Mayr 1963), but modern phylogenomics has revealed extensive, post-divergence gene flow across many taxa (Abbott et al. 2013; Mallet et al. 2016). One potential outcome of hybridisation is the exchange of mitochondria between lineages, whereby 'lineage' can refer to a genetic lineage within a species or a species itself. This is known as mitochondrial introgression, which is now recognised as common across many taxa (Currat et al. 2008; Toews and Brelsford 2012). However, the extent to which matching nuclear introgression occurs can vary from extensive (e.g., Sarver et al. 2021; Ji et al. 2023) to limited or absent (e.g., Sloan et al. 2017; Grummer et al. 2018; Mao and Rossiter 2020). Mitonuclear discordance—where evolutionary relationships inferred from mtDNA differ to those inferred from nuDNA—is often the first indication of mtDNA introgression (e.g., Phuong et al. 2017; Pavón-Vázquez et al. 2024). In some cases,

mitonuclear discordance may also indicate a homoploid hybrid species, which form instantly via hybridisation; but these appear exceptionally rare (Schumer et al. 2014; Hill 2019). Species groups showing mitonuclear discordance offer valuable opportunities to examine levels of accompanying nuclear gene flow.

Introgression can have significant consequences for lineage divergence and phenotypic variation. If introgression is too frequent, it can swamp the genome, potentially reversing the speciation process (Rhymer and Simberloff 1996; Todesco et al. 2016). Alternatively, introgression may trigger or facilitate speciation (Edelman and Mallet 2021) by, for example, introducing adaptive variation (e.g., Staubach et al. 2012) or by altering phenotypes (Lamichhaney et al. 2015; Taylor and Larson 2019 and references therein). Introgressed populations may exhibit novel (transgressive) phenotypes through epistatic interactions or novel allelic combinations (Dittrich-Reed and Fitzpatrick 2013) or intermediate or more variable phenotypes driven by epistasis or heterozygosity for genes with incomplete dominance (Masello et al. 2019). Transgressive phenotypes are of particular interest in adaptive radiations as access to novel trait space may allow expansion into new niches, thereby facilitating rapid diversification (Pfennig et al. 2016; Wogan et al. 2023). Introgression, therefore, treads a fine line between promoting and inhibiting divergence and, thus, has important implications for understanding diversification (Cruickshank and Hahn 2014; Harrison and Larson 2014) and species boundaries (Hillis et al. 2021; Barley et al. 2024).

As the mitochondrial genome is effectively a single, non-recombining gene, mitonuclear discordance might not correspond to matching nuDNA introgression. So called 'massive discordance' may occur when a species' native mitochondrial genome is nearly or entirely replaced by mtDNA introgression without matching nuclear introgression (Bonnet et al. 2017). However, determining whether there has been mtDNA introgression based on contrasting mtDNA and nuDNA phylogenies is not straightforward; one must also consider incomplete lineage sorting (ILS) and tree estimation error (Larson et al. 2024). Indeed, identifying introgression in general—whether mtDNA or nuDNA—can be complicated by ILS and the loss of phylogenetic signal through time (Galtier and Daubin 2008). Model parameter misspecification (Cooper 2014; Huang et al. 2022) and failure to consider selection (Smith and Hahn 2024) can also mislead introgression estimates. Establishing confidence in introgression estimates therefore relies on comparing results across different methods of analysis (Hibbins and Hahn 2022).

We explored whether mitonuclear discordance corresponds to genomic introgression in a clade of *Gehyra* geckos from the Kimberley region of northern Australia. *Gehyra* is a genus of morphologically conservative geckos with a broad distribution across Australia, Wallacea, Melanesia, and southeast Asia (Heinicke et al. 2011). *Gehyra* diversity is highest in Australia, with 50 recognised species (Wilson and Swan 2020; Uetz et al. 2024) comprising two broad clades of Plio-Miocene origin: the typically small-bodied *punctata-variegata* group (Ashman et al. 2018) and the large-bodied *australis* group (Sistrom et al. 2009; Oliver et al. 2020). Several unresolved species complexes remain within the *punctata-variegata* group, including the *Gehyra nana* and *G. occidentalis* complexes of the Kimberley region (Oliver et al. 2016; Doughty et al. 2018; Lau et al. 2025), which we hereafter refer to as the *nana-occidentalis* clade. Phylogenetic analyses of the *nana-occidentalis* clade, using geographically dense sampling of mtDNA and exon capture sequencing, have identified eight lineages within this group (figure 1; Oliver et al. 2016; Moritz et al. 2018; Lau et al. 2025): *nana*1, *nana*2, *nana*4, and nanamulti in the *G. nana* complex; *occidentalis*-KL, *occidentalis*-OR, *occidentalis*-YI, and *G. multiporosa* (simply '*multiporosa*' hereafter) in the *G. occidentalis* complex. Lineages within each of the two complexes are morphologically similar and typically replace each other at parapatric boundaries, although *nana*4 and nanamulti occur in mosaic sympatry. In contrast, members of the smaller-bodied *nana* complex often co-occur with members of the *occidentalis* complex. Of particular interest in this clade is the strong evidence of mitonuclear discordance. One example is the nanamulti lineage that—while nested within the *nana* complex for nuDNA—has mtDNA that is interdigitated within *multiporosa* (Moritz et al. 2018; Figure 1), suggesting repeated mtDNA introgression between these distantly related lineages, rather than simple estimation error or ILS. The sympatry with nana4 and massive introgression for mtDNA suggests the hypothesis that nanamulti itself possibly arose via homoploid hybrid speciation. Further mitonuclear discordance is observed among lineages in the *occidentalis* complex (Figure 1; Oliver et al. 2016; Moritz et al. 2018; Lau et al. 2025), although here evidence of mtDNA introgression, rather than ILS, is less clear as each lineage is reciprocally monophyletic and phylogenetically within the same species complex (unlike nanamulti and *multiporosa*). Given such complex mitonuclear discordance, this group offers a good opportunity to investigate whether mitonuclear discordance corresponds to substantial nuclear introgression.

Here, we used exon capture and genome-wide SNP data to test for both historical and recent genomic introgression in the *nana-occidentalis* clade. We first performed hypothesis-based tests of historical introgression informed by cases of mitonuclear discordance, the results of which we then corroborated using D-statistics. We then assessed recent or ongoing introgression at two modern contact zones that include lineages with evidence of mitonuclear discordance. Finally, we assessed whether lineages with introgressed mtDNA exhibit transgressive, intermediate, or more variable phenotypes.

2 | Methods

2.1 | Exon Capture Sequence Data

We obtained published nuDNA exon capture sequence data spanning > 1000 loci to perform phylogenetic network analyses. Sequence data were acquired from Moritz et al. (2018) and Lau et al. (2025) for the following *Gehyra* species/lineages: *nana*1, *nana*2, *nana*4, nanamulti, *multiporosa*, *occidentalis*-KL, *occidentalis*-OR, and *occidentalis*-YI, with *G. paranana* used as the outgroup. These included 67 samples with 4–14 samples per focal lineage and a single sample of *G. paranana* (Table S1). Briefly, these data were produced using the exon capture approach described in Moritz et al. (2018), which targeted approximately 1900 single-copy exons. Sequences were processed, filtered, and aligned using the EAPhy pipeline (Blom 2015). Loci with ≥ 11

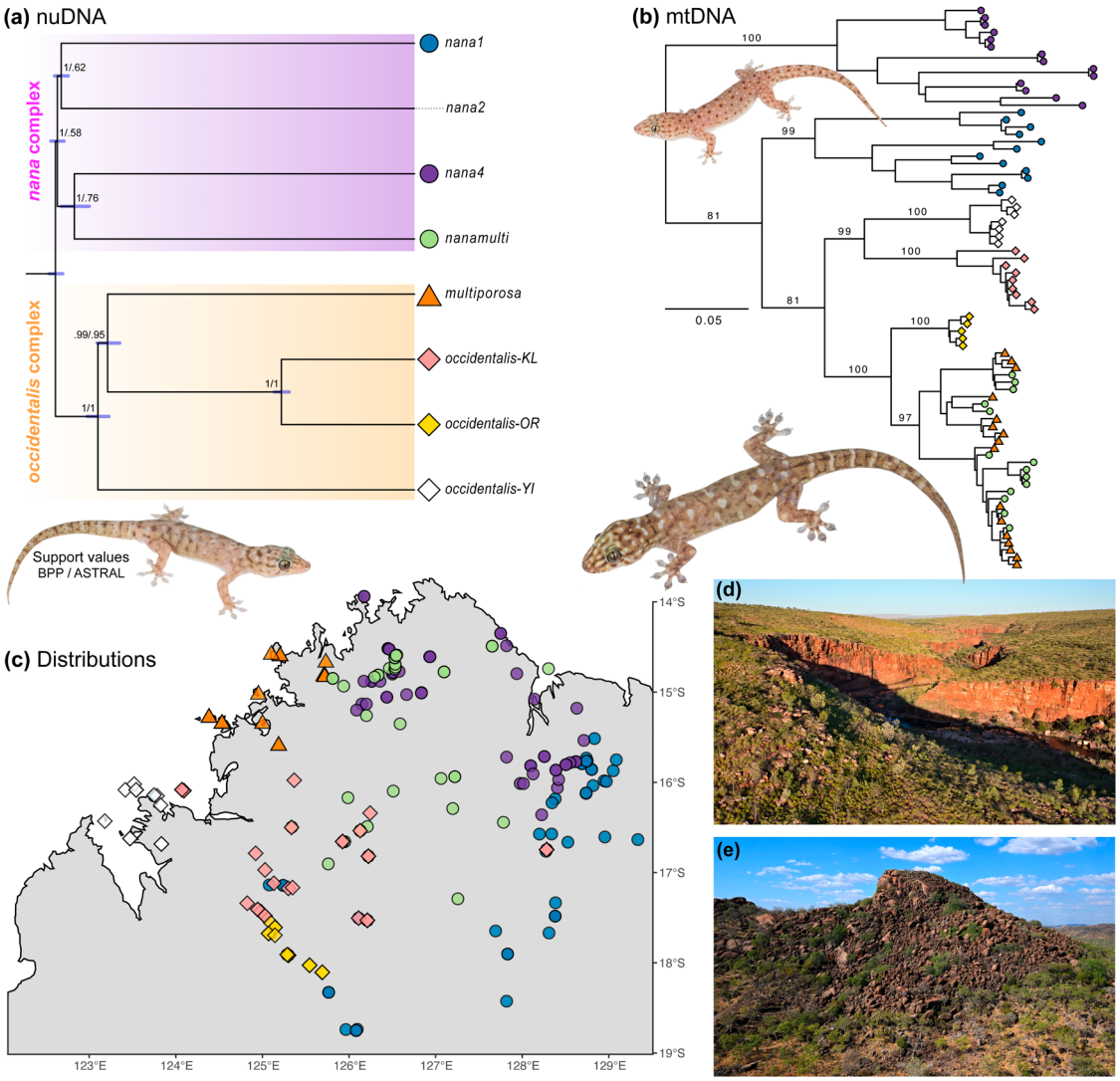

FIGURE 1 | Relationships and distributions of the *Gehyra nana-occidentalis* clade. (a) Species tree inferred from 1000 nuDNA exons using BPP, with support shown for both BPP and ASTRAL (identical topologies). Note that *nana*2 is included here but not elsewhere as it occurs outside the focal Kimberley region. (b) MntDNA relationships among focal lineages inferred with IQ-TREE, showing several cases of discordance with respect to nuDNA ancestry. Ultrafast bootstrap support values are shown for major branches. (c) Lineage distributions in Australia's Kimberley region based on samples with nuDNA data. (d,e) Typical habitat, showing sandstone gorges (d) and granite boulders (e). Gecko photos show *occidentalis*-OR (left), *nana*4 (top-right), and *occidentalis*-KL (bottom-right). Photos: Ian Bool (d,e); Scott Macor (geckos).

missing individuals (i.e., ≥15% missing data) were removed to maximise individual coverage while retaining ≥1000 loci. We then removed six individuals with ≥40% missing data and another two samples with uncertain locality data, retaining 58 samples for subsequent analysis (see Table S1). The final dataset comprised 1478 exonic loci, ranging from 108–2088 bp in length (mean = 334 bp; median = 228 bp), totalling 494,507 bp across all loci, with 20,517 parsimony-informative and 21,166 singleton sites. Alignments were manually inspected prior to subsequent analysis to ensure correct reading frames, with no missense mutations or unexpected stop codons within the respective exons.

2.2 | SNP Data

Genome-wide reduced-representation sequencing was done to obtain genome-scale SNP data to test historical introgression using *D*-statistics and to perform contact zone analyses. Contact zones were identified based on previously published data (Moritz et al. 2018; Doughty et al. 2018; Fenker et al. 2021; Lau et al. 2025). We used DArTseq via Diversity Arrays Technology (DArT; Canberra, Australia), which involves genome fragmentation with two restriction enzymes (PstI/HpaII) followed by filtering based on fragment size and subsequent Illumina short-read sequencing (Sansaloni et al. 2010; Kilian et al. 2012), yielding thousands of 60–80 bp sequence fragments. SNP calling and associated filtering is then done across all samples via DArT's proprietary pipeline. Newly generated DArTseq data ($n = 35$) were combined with data for relevant lineages from Fenker et al. (2021) and Lau et al. (2025). Our final dataset included 242 individuals sampled across lineage ranges and contact zones, including *G. paranana* as an outgroup (Table S2). DNA was extracted for newly sequenced samples using a Qiagen DNeasy Blood & Tissue Kit.

SNP data were filtered separately for each analysis to maximise the number of variant sites for each data subset. We used dartR v.2.9.7 (Gruber et al. 2018) to filter data in the following order: minimum read depth ≥ 6; maximum read depth ≤ 80 (resulting in no losses); reproducibility ≥ 0.99; call rate by locus ≥ 0.8; call rate by individual ≥ 0.5; minor allele count ≥ 3 (to ensure a given allele is present in at least two individuals); removal of monomorphic loci; and to retain only one variant site per locus (using method = "best" to retain the site with the highest PIC score). The final dataset of samples across all focal lineages contained 3966 variant sites. Before continuing, we used the *gl.pcoa()* function in dartR to perform a principal coordinates analysis (PCoA) on these data to confirm the lineage assignment of newly sequenced samples (Figure S1). After filtering, a total of 1828 variant sites were retained for the *multiporosa*/nanamulti contact zone, and 2192 variant sites were retained for the nanamulti/nana4 contact zone.

2.3 | MtDNA Data and Phylogenetics

Phylogenetic analysis of mtDNA sequence data was done to illustrate the mitonuclear discordance demonstrated in previous studies. For relevant lineages, we obtained sequence data for the 1038 bp *NADH dehydrogenase subunit 2 (ND2)* locus from previous studies (Doughty et al. 2012; Oliver et al. 2016; Moritz et al. 2018; $n = 468$). We then generated new *ND2* sequences for those samples with genomic data but lacking mtDNA data ($n = 132$) using the MinION barcoding method from Srivathsan et al. (2021). Methods followed those presented in Zozaya et al. (2024) except using the primers M112F (5′-AAGCTTTCGGGGCCCATACC-3′) and M1123R (5′-GCTTAATTAAAGTGTYTGAGTTGC-3′) from Sistrom et al. (2009). The resulting *ND2* sequences were aligned with those obtained from previous studies using MAFFT in Geneious Prime v. 2021.2.2, which yielded a final alignment of 1038 bp across 600 samples, including one *G. spheniscus* as the outgroup (Moritz et al. 2018). The alignment was inspected for gaps, unexpected stop codons, or frame shifts, followed by phylogenetic analysis using IQ-TREE v. 2.2.0 (Minh et al. 2020). The alignment was partitioned by codon position, with ModelFinder (Kalyaanamoorthy et al. 2017) used to determine the best partition scheme and substitution model and statistical support determined with 1000 ultrafast bootstrap (UFB) replicates (Hoang et al. 2018). The final partition and model scheme was 1st position (TIM + F + I + G4); 2nd position (TVM + F + G4); and 3rd position (GTR + F + I + G4). We also re-ran this analysis with a subset of 78 samples—chosen to represent mtDNA diversity in each lineage—to better visualise mtDNA relationships with fewer samples.

2.4 | NuDNA Phylogenomics

Our analyses of historical introgression depend on accurate knowledge of phylogenetic relationships. Given the varying phylogenetic relationships inferred for the *nana-occidentalis* clade, including variable support for the monophyly of lineages of *G. nana* itself in previous studies (Moritz et al. 2018; Ashman et al. 2018; Lau et al. 2025), we performed several phylogenomic analyses using exon capture sequence data to better understand relationships among the *nana-occidentalis* clade. Although it occurs outside our study area, we included the Northern Territory *nana*2 lineage in all phylogenomic analyses to test the monophyly of *G. nana* . All phylogenomic analyses used the exon capture dataset. We first performed maximum likelihood (ML) phylogenetic analysis on the concatenated 1478 exon alignment using IQ-TREE v2.2.2.6 (Minh et al. 2020) to confirm lineage assignment for all samples. The analysis was partitioned by locus with modelfinder (Lanfear et al. 2012; Kalyaanamoorthy et al. 2017) used to determine the best partition scheme (MFP + merge) and substitution models. We specified 1000 UFB replicates implemented via ufboot2 (Hoang et al. 2018) in addition to branch support metrics via a Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-aLRT; Guindon et al. 2010; Hoang et al. 2018) with 1000 replicates. We used genesite resampling to resample partitions and sites within partitions (Gadagkar et al. 2005; Seo et al. 2005). Next, we performed species tree analysis using the quartet-based algorithm implemented in ASTRAL-III v5.7.8 (Rabiee et al. 2019). ASTRAL requires gene trees as input, which were estimated for each of the 1478 exons using IQ-TREE v2.2.2.6, with modelfinder used to determine the best substitution model for each locus, with 1000 UFB replicates. Prior to ASTRAL analysis, gene tree branches with bootstrap support < 30 were collapsed using TreeCollapserCL4 (Hodcroft 2016) to improve species tree accuracy and branch support (Simmons and Gatesy 2021). Finally, we used BPP v4.7 (Flouri et al. 2018) to perform Bayesian multispecies coalescent phylogenetic analysis. We used the 1000 longest exons (180–2088 bp; mean = 418 bp; median = 333 bp) with a maximum of seven missing individuals, using 3–4 individuals with the least missing data from each lineage and with one *G. paranana* sample included as an outgroup (Table S1). The analysis was initially run as an A01, specifying the guide tree topology as inferred by ASTRAL-III. We assigned diffuse inverse-gamma priors for population size θ~InvGamma(3, 0.003) and tree height~InvGamma(3, 0.003). Units for both θ and represent the expected number of mutations per site. We ran the MCMC for 1000,000 iterations after a burn-in of 100,000 iterations, with sampling every two iterations for a total of 500,000 samples.

2.5 | Testing Historical Introgression Using Network Analysis

We conducted hypothesis-based tests of introgression using the multi-species-coalescence-with-introgression (MSCi) phylogenetic network analysis in BPP v.4.4.0 (Flouri et al. 2020) to specifically test for genomic introgression in cases where there is evidence of mitonuclear discordance (Figure 1). Specifically, we tested for introgression between (i) *multiporosa* and nanamulti; (ii) *multiporosa* and *occidentalis*-OR; and (iii) *occidentalis*-YI and *occidentalis*-KL. There is clear evidence of repeated mtDNA introgression from *multiporosa* to nanamulti, whereas there are two equivocal scenarios of mtDNA introgression within the *occidentalis* complex (see 3). BPP makes full use of the sequence data under the MSC, produces robust inferences even under model miss-specification (Huang et al. 2022), and is computationally efficient. Analyses used subsets of the same 1000 loci used for the phylogenomic analysis above. As BPP requires a user-specified phylogeny, analyses were run with three tips to avoid the uncertain

phylogenetic relationships and reduce computational burden. Three tips were used, rather than two, because the MSCi cannot estimate introgression when the lineages involved are sisters (Hibbins and Hahn 2022). The following relationships were specified for each combination of lineages: (i) (*multiporosa*, (nanamulti, *nana*4)); (ii) (*multiporosa*, (*occidentalis*-OR, *occidentalis*-KL)); and (iii) (*occidentalis*-YI, (*occidentalis*-KL, *occidentalis*-OR)). Each tip included 3–4 of the most data complete samples (Table S1). Three introgression scenarios—two unidirectional models and one bidirectional model—were run for each of these lineage combinations. For example, unidirectional introgression was tested from *multiporosa* to nanamulti and then from nanamulti to *multiporosa*, each as a separate analysis, and then a model was run with bidirectional introgression between the two lineages. Priors for population size (θ) and tree height () were both assigned as InvGamma(3, 0.003), while the prior for introgression probability (φ) was assigned as Beta(2, 4). Values for φ represent the proportion of the genome that traces its ancestry via the introgression edge (Flouri et al. 2020). Each analysis was run for 1000,000 iterations after a burn-in of 100,000 iterations, sampling every two iterations, for a total of 500,000 sampled iterations. All analyses were executed twice to check for convergent results, and posterior distributions were checked using TRACER v.1.7.2 (Rambaut et al. 2018). We assessed the statistical significance for each model by calculating Bayes factors (B_{10}) via the Savage-Dickey density ratio (Dickey 1971), which uses the MCMC sample to assess whether the posterior distribution of φ differs from what would be expected given the priors, with $B_{10} \geq 20$ indicating a strongly supported introgression event (Ji et al. 2023).

2.6 | Tests for Historical Introgression Using *D*-Statistics

We used the genome-wide SNP dataset to estimate *D*- and *f*-branch statistics using *Dsuite* (Malinsky et al. 2021). This method assesses all lineage combinations for introgression, except sister lineages, and then accounts for correlated allele frequencies among tips to identify introgression events on the internal branches of the tree (Durand et al. 2011; Patterson et al. 2012). We specified the topology recovered by both ASTRAL and BPP, again using *G. paranana* as the outgroup. P-values were calculated using the jack-knife method and, as more than three lineages were assessed, we applied the false discovery rate (FDR) correction to account for false positives due to multiple pairwise comparisons (Benjamini and Hochberg 1995) using the '*p*.adjust' function as suggested by Malinsky et al. (2021).

2.7 | Contact Zone Analyses

We analysed two contact zones, one between *multiporosa* and nanamulti, and another between *nana*4 and nanamulti. All analyses described below were run separately for each of these two contact zones, and SNP filtering (see above) was done separately for each to maximise the number of variant sites. We first used NewHybrids (Anderson and Thompson 2002) to test whether any individuals were F1, F2, or first-generation backcross (BC1) hybrids. This was done with the SNP dataset via the *gl.nhybrids()* in dartR using the 'AvgPIC' method, 100 sweeps, and a burn-in of 100. Next, we estimated the optimal number of ancestral populations (K) and individual admixture proportions using sNMF (Frichot et al. 2014) via the R package *LEA* (Frichot and François 2015). Genotypic clustering analyses can under- or over-estimate the optimal *K* value and thus admixture estimates, when there is strong population structure and sparse or uneven sampling (Puechmaille 2016; Lawson et al. 2018; Wang 2022). To mitigate the influence of within-lineage population structure, we excluded samples outside a 40–80 km radius (depending on the lineages included and sampling density; Table S3) centred on each contact zone. Each analysis was run with $K = 1$–5, alpha = 100, 100 repetitions, and masking = 0.05. We considered the optimal *K* value to be the one that produced the lowest average cross entropy (ce) score. Given the biases mentioned above, we verified both the *K* and admixture estimates using isolation-by-distance (IBD) plots (e.g., Prates et al. 2023; Zozaya et al. 2024), which plot pairwise geographic distance against genome-wide average pairwise F_{ST} (Wright 1943; Weir and Cockerham 1984; Weir and Hill 2002) among individuals at each contact zone. Pairwise geographic distances (km) were calculated using the *earth.dist()* function in *fossil* v0.4.0 (Vavrek 2011), and pairwise F_{ST} was calculated using the *calculate.all.pairwise.fst()* function in *BEDASSLE* v1.6.1 (Bradburd 2013). If there is no introgression at a given contact zone, we expect between-lineage pairwise F_{ST} to be relatively high and unrelated to the geographic distances among samples, whereas if there is recent or ongoing introgression, we expect between-lineage pairwise F_{ST} to decrease as geographic distances decrease. Finally, for each contact zone, we performed a PCoA using the *gl.pcoa()* function in dartR to further verify the optimal *K* value and visualise the major axes of genetic variation.

2.8 | Morphometric Analyses

Morphological data for relevant lineages were collected from adult genotyped specimens at the Western Australian Museum (WAM; Table S4). We measured 10 standardly used and ecologically relevant linear traits (Oliver et al. 2019; traits are illustrated in Figure S2) to the nearest 0.1 mm using Mitutoyo digital callipers: snout-to-vent length (SVL); head length (HL); snout length (SL); head width (HW); head depth (HD); orbit width (OR); width-between-eyes (WBE); inter-limb length (ILL); hindlimb length (HLL); and forelimb length (FLL). Sample sizes for each lineage are *multiporosa* = 15 (7 ♂, 8 ♀); *occidentalis*-KL = 45 (17 ♂, 28 ♀); *occidentalis*-YI = 13 (5 ♂, 8 ♀); *occidentalis*-OR = 5 (1 ♂, 4 ♀); nanamulti = 37 (17 ♂, 20 ♀); *nana*4 = 42 (21 ♂, 21 ♀); and *nana*1 = 22 (11 ♂, 11 ♀).

Using these data, we first tested for sexual dimorphism via a permutational multivariate analysis of variance (PerMANOVA) using the R package *RRPP* (Collyer et al. 2015). Sexual dimorphism was tested using three lineages for which we had the largest sample sizes (*occidentalis*-KL, $n = 45$; *nana*1, $n = 22$; and *nana*4, $n = 42$). All traits were log transformed prior to analysis. We used the *lm.rrpp()* function with the 10 log-transformed morphological traits as dependent variables and lineage, sex, and their interaction as predictor variables with 10,000 permutations and as a type III MANOVA for significance testing. Consistent with other

studies of *Gehyra* (Ashman et al. 2018), the effect of sex was not significant (df = 1/103, $F = 2.976$, $Z = 1.532$, $R^2 = 0.006$, $p = 0.064$; Table S5) and, therefore, was not considered in subsequent analyses. We then tested for morphological divergence among lineages. A PerMANOVA was performed using the 10 log-transformed traits as dependent variables with lineage as the predictor variable and 10,000 permutations for significance testing. We then ran pairwise contrasts using the *pairwise()* function for each lineage pair, followed by *p*-value adjustment using the *p*.adjust() function to account for inflated type 1 error with the FDR method (Benjamini and Hochberg 1995). We visualised morphological variation and divergence and identified traits associated with the greatest axes of variation, via a principal components analysis (PCA) using the *rda()* function (scale = T) in the *R* package *vegan* (Dixon 2003). Finally, we tested whether intraspecific phenotypic variation differed among lineages, which could reflect increased genetic variation due to introgression. We conducted a Fligner-Killeen test (Fligner and Killeen 1976), a non-parametric test that compares variances among multiple groups, even when the assumption of normality is violated, in this case by potential outliers of exceptionally large or small size. This is a univariate test and, as previous studies have established body size as the primary trait of variance in *Gehyra* (Sistrom et al. 2012; Ashman et al. 2018; Moritz et al. 2018), we assessed phenotypic variance using log-transformed SVL as a proxy for body size across all lineages.

3 | Results

3.1 | NuDNA Phylogenomics

All eight previously identified lineages were each recovered as monophyletic clades with strong support (IQ-TREE: UFB = 100; ASTRAL: posterior probability (pp) ≥ 0.99 for all; Figures S3 and S4). All three phylogenomic analyses recovered the *occidentalis* complex as a monophyletic clade with full support (Figures 1a, S3, and S4), with *occidentalis*-YI being the deepest branching lineage, followed by *multiporosa* and *occidentalis*-KL and *occidentalis*-OR as sister lineages. Relationships among the four lineages of the *nana* complex, however, differed between the concatenated and species tree approaches (Figures 1a, S3, and S4). The concatenated IQ-TREE analysis placed *nana*4 as sister to the remaining *nana-occidentalis* clade (UFB = 97, aLRT = 98.3), reducing the "*nana* complex" to a modestly supported clade (UFB = 87, aLRT = 75.2) with *nana*2 recovered as the first-branching lineage and *nana*1 and nanamulti as sister lineages (UFB = 89, aLRT = 91.6). In contrast, the *nana* group was recovered as monophyletic with low support in the ASTRAL analysis (pp = 0.58) and high support in the BPP (pp = 1) analysis. Both species tree analyses recovered *nana*4 + nanamulti and *nana*2 + *nana*1 as sister pairs, although ASTRAL inferred this with low support (pp = 0.76 for *nana*4 + nanamulti; pp = 0.62 for *nana*2 + *nana*1) compared to BPP (pp = 1 for both sister pairs). With respect to the *nana* complex (nana1, nana2, *nana*4, and nanamulti), all relationships are consistent with the 100-locus StarBEAST2 phylogeny from Moritz et al. (2018). Notably, low support for relationships within the *nana* complex is associated with very short internode lengths in the species tree analyses. What is important for our introgression analyses below—which require phylogenetic relationships to be pre-specified—is that the species tree methods each recover *nana*4 and nanamulti as sister lineages.

3.2 | MtDNA Phylogenetics

Five of the seven focal lineages are recovered as monophyletic mtDNA clades (Figures 1b and S5), while individuals of nanamulti are extensively interdigitated among *multiporosa*, often with very short branch lengths between samples of different nuDNA ancestry. All individuals assigned to nanamulti by nuDNA SNP analyses (Figure S1) have *multiporosa* mtDNA and are distributed across multiple, well-supported mtDNA clades within *multiporosa*. From these observations, we infer recent and repeated mtDNA introgression from *multiporosa* to nanamulti. *Gehyra occidentalis*-OR is recovered as sister to *multiporosa*/nanamulti with respect to mtDNA, despite *occidentalis*-OR having a close sister relationship with *occidentalis*-KL based on nuDNA. Furthermore, *occidentalis*-KL and *occidentalis*-YI are most closely related with respect to mtDNA despite *occidentalis*-YI being the first-branching lineage in the nuDNA phylogenies. These results suggest two possible cases of historical mtDNA introgression in the *occidentalis* complex—either from *occidentalis*-YI to *occidentalis*-KL resulting in their mtDNA clades being most closely related or from *multiporosa* to *occidentalis*-OR leading to close relationships of their mtDNA lineages.

3.3 | Historical Introgression

We used the MSCi in BPP to test introgression scenarios between *multiporosa* and nanamulti, *multiporosa* and *occidentalis*-OR, and *occidentalis*-YI and *occidentalis*-KL. Introgression was strongly supported ($B_{10} \geq 20$) only for unidirectional introgression from nanamulti to *multiporosa* ($\varphi = 0.0518$, 95% CI = 0.030–0.074; Figure 2 and Table 1). This estimate of ~5.18% nuDNA introgression is low and in the opposite direction to what we expected given evidence of repeated mtDNA introgression from *multiporosa* to nanamulti. The unidirectional model from *multiporosa* to nanamulti received only modest support ($B_{10} = 12.26$) with lower introgression estimates ($\varphi = 0.031$, 95% CI = 0.017–0.046). All other introgression scenarios were poorly supported ($B_{10} < 1$).

In contrast to the MSCi results, estimates of excess allele sharing using the ABBA-BABA approach via *Dsuite* found no support for introgression between nanamulti and *multiporosa* (Figure 3). Excess allele sharing was inferred between the *nana*1 branch and each of the three *occidentalis* lineages, with estimates of up to 7% excess allele sharing. However, following recommendations by Malinsky et al. (2021) to implement FDR *p*-value adjustment and using $p < 0.01$ as the threshold for statistical significance, no excess allele sharing scenarios were supported as statistically significant ($p = 0.017$–0.804; Table S6).

3.4 | Recent Introgression at Contact Zones

We detected only a single early generation hybrid using NewHybrids, which was between nanamulti and *nana*4 (F1 or

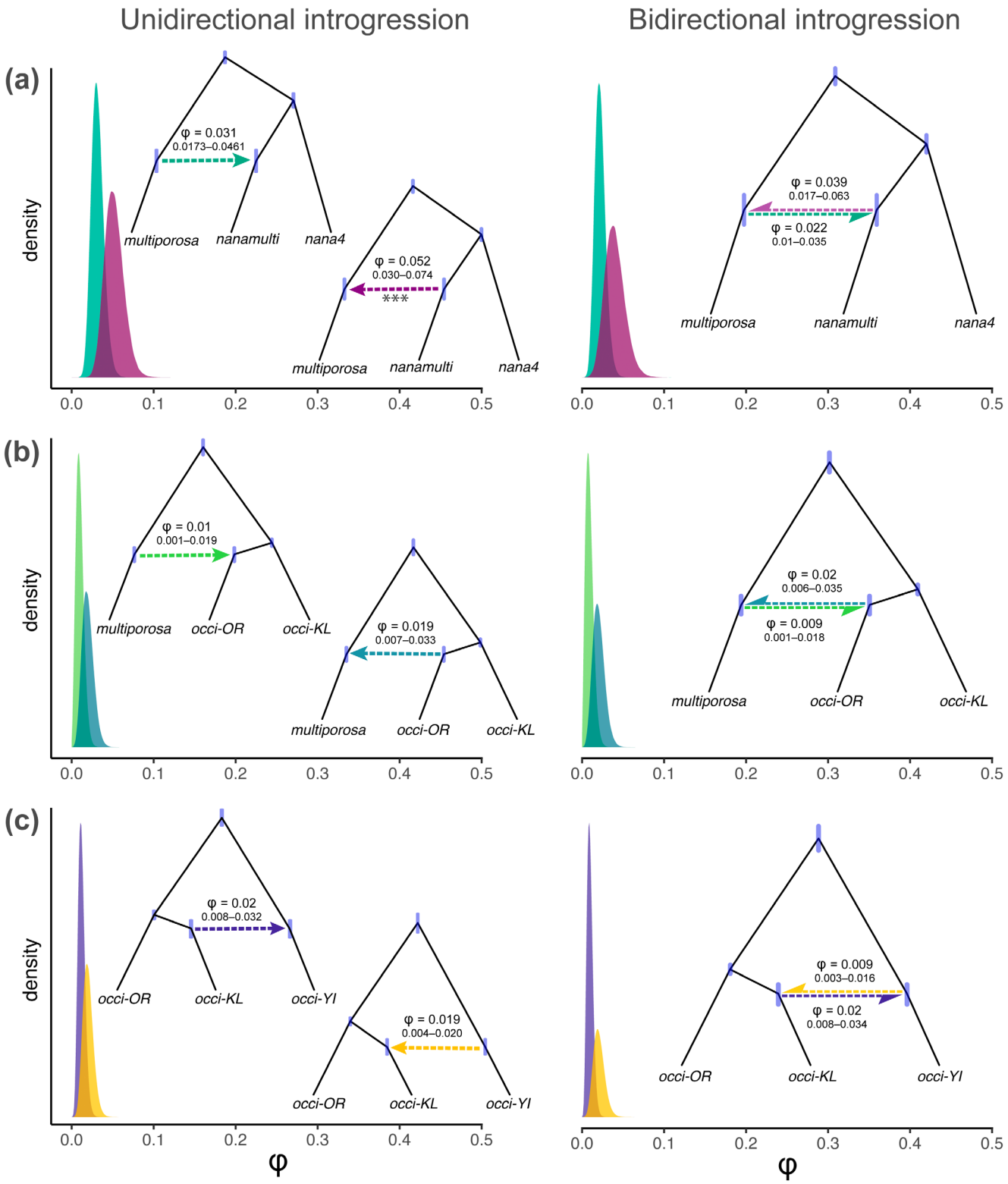

FIGURE 2 | Results of hypothesis-based tests of introgression using the MSCi model implemented in BPP. Each row (a–c) shows a different combination of lineages. The left column shows results for unidirectional models; the right column shows results for the corresponding bidirectional model. Trees within panels show the scenarios being tested, with coloured arrows matching the posterior distributions within the respective panel. Values show means and 95% credible intervals for introgression probability (φ), which reflects the proportion of the genome that traces its ancestry via the introgression edge. Only the unidirectional model from nanamulti to *multiporosa* (***) was strongly supported ($B_{10} \geq 20$; Table 1).

F2 hybrid; Table S2 and Figure S1), although the sample itself did not originate from our densely sampled contact zone for that lineage pair (as shown in Figure 4b). Using sNMF, optimum K values (based on lowest ce score; Figure S6) were $K = 3$ for the nanamulti/nana4 contact zone and $K = 2$ for the *multiporosa*/nanamulti contact zone. In the case of the *multiporosa*/

TABLE 1 | Results of MSCi phylogenetic network analysis using BPP.

Model	Donor	Recipient	φ	τ (10^{-3})	B_{10}
UDI	*multiporosa*	*nanamulti*	0.0315 (0.0173–0.0461)	1.255 (1.032–1.468)	12.26
UDI	*nanamulti*	*multiporosa*	0.0518 (0.0304–0.0746)	1.287 (1.092–1.499)	∞
BDI	*multiporosa*	*nanamulti*	0.0219 (0.0098–0.0349)	1.387 (1.157–1.606)	0.90
BDI	*nanamulti*	*multiporosa*	0.0397 (0.0171–0.0636)	1.387 (1.157–1.606)	0.06
UDI	*multiporosa*	*occidentalis-OR*	0.0099 (0.0015–0.0189)	0.861 (0.746–0.971)	0.00
UDI	*occidentalis-OR*	*multiporosa*	0.0198 (0.0069–0.0334)	0.896 (0.786–0.996)	0.01
BDI	*multiporosa*	*occidentalis-OR*	0.0089 (0.0009–0.018)	0.915 (0.814–1.01)	0.01
BDI	*occidentalis-OR*	*multiporosa*	0.0204 (0.006–0.035)	0.915 (0.814–1.01)	0.00
UDI	*occidentalis-YI*	*occidentalis-KL*	0.0197 (0.0043–0.0201)	0.8 (0.668–0.922)	0.00
UDI	*occidentalis-KL*	*occidentalis-YI*	0.02 (0.00816–0.0321)	0.652 (0.533–0.774)	0.02
BDI	*occidentalis-YI*	*occidentalis-KL*	0.0095 (0.003–0.0165)	0.742 (0.607–0.864)	0.02
BDI	*occidentalis-KL*	*occidentalis-YI*	0.0204 (0.0079–0.0339)	0.742 (0.607–0.864)	0.00

Note: The 'Model' column shows whether the respective analysis tested unidirectional introgression (UDI) or bidirectional introgression (BDI). Values are the posterior means and 95% credible intervals (in parentheses) for introgression probability (φ, proportion of the genome that traces its ancestry via the introgression edge) and introgression time (as the expected number of mutations per site), followed by Bayes factor (B_{10}) support. $B_{10} = \infty$ occurs if all φ values in the MCMC exceed the region of null effects (see Ji et al. 2023).

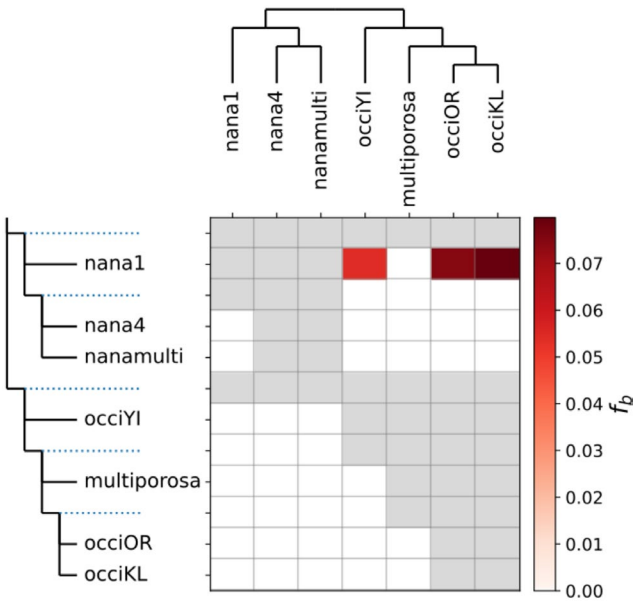

FIGURE 3 | Excess allele sharing in the *Gehyra nana-occidentalis* clade estimated using *f*-branch statistics implemented in *Dsuite*. Colours indicate the proportion of introgressed loci inferred between the lineage (*x* axis) and lineage branch (*y* axis). The *f*-branch metric accounts for correlated allele frequencies derived from ancestral introgression using internal branches on the *y*-axis (dotted lines). Grey cells represent duplicate or untestable relationships. Note that despite the *ca*. 5%–7% estimated excess allele sharing between *nana*1 and the three *G. occidentalis* lineages, these were not significant following *p*-value adjustment (Table S6).

nanamulti contact zone, however, $K = 2$ is likely favoured over $K = 3$ only because of the small sample size ($n = 2$) for what we refer to as the Mitchell plateau (MP) population of nanamulti (Figures 4a and S7). IBD plots show elevated pairwise F_{ST} between nanamulti samples from MP and the Theda Station (TS) population, with no indication that this is driven by introgression from *multiporosa*, which would be expected to result in relatively lower F_{ST} between some between-lineage pairs. Furthermore, the MP and TS samples form distinct clusters in the PCoA plot (Figure 4a). Considering these points, we opted to use $K = 3$ for this contact zone, under which sNMF inferred no admixed individuals. Similarly, there is no evidence of admixture at the *nana*4/nanamulti contact zone (Figure 4b), with IBD plots again showing no decrease in between-lineage pairwise F_{ST} as geographic distance decreases. At this contact zone, there is strong geographic structure within *nana*4, with one population restricted to the King Edward (KE) sandstones and another restricted to the Morgan River (MR) sandstones.

3.5 | Phenotypic Variation

There was significant morphological divergence among lineages (RRPP: df = 6/173 $F = 107.7$, $Z = 17.19$, $R^2 = 0.789$, $p < 0.001$), with lineage accounting for 79% of observed morphological variation. Subsequent pairwise comparisons between lineages found all lineage comparisons—with the exceptions of *multiporosa* + *occidentalis*-OR, *nana*1 + nanamulti, *nana*4 + nanamulti, and all *occidentalis* lineage comparisons—to be significantly different ($p < 0.05$; Table S7). Principal component (PC) axes indicate that body size is the main axis of morphological variation among lineages (Figure 5), with all traits loading heavily on PC1 (Table S8), which accounts for 95% of morphological variation. Body shape overlapped considerably among lineages (Figure 5). PC2 explained only 1.1% of variation, with head depth loading most heavily. PC3 explained 0.96% of variation, with (in descending order) width-between-eyes, forelimb length,

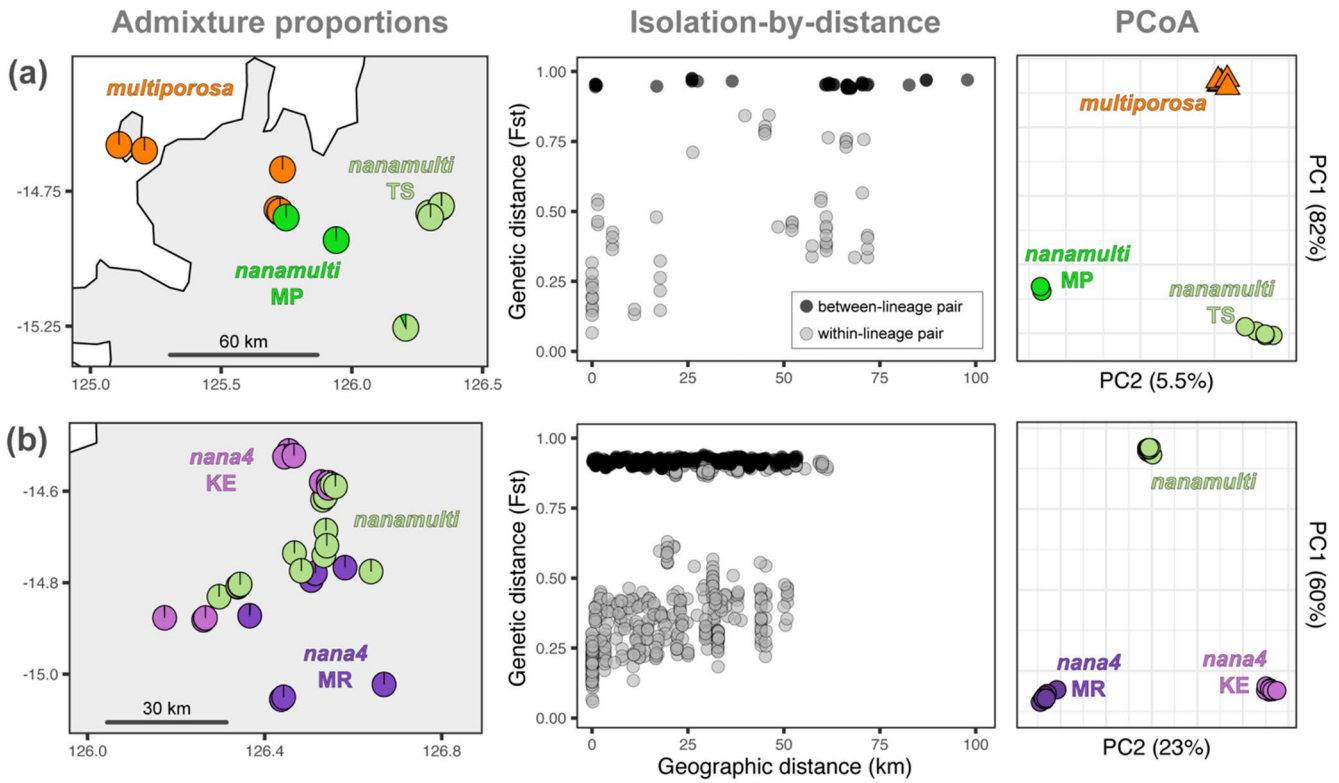

FIGURE 4 | Estimates of gene flow at contact zones between (a) *multiporosa* and *nanamulti* and (b) *nana4* and *nanamulti*. Maps (left column) show pie charts that reflect individual admixture proportions estimated by sNMF (some charts are slightly offset for visibility). Isolation-by-distance plots (middle column) illustrate within-lineage (grey) and between-lineage (black). Principal coordinates analysis plots (right column) illustrate the major axes of genomic variation for the respective samples. Note that one lineage at each contact zone is represented by two within-lineage populations, reflecting strong within-lineage geographic structure.

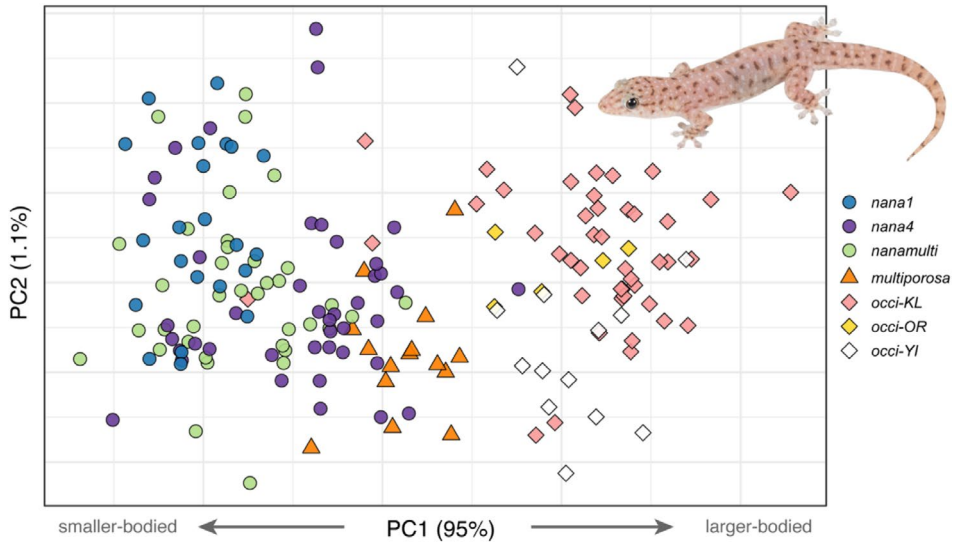

FIGURE 5 | Principal components analysis of morphological variation across focal lineages in the *Gehyra nana-occidentalis* clade. Individuals are coloured according to their nuDNA ancestry. Percent variation explained for each axis. An individual of *nana1* is shown (credit: Scott Macor).

and hindlimb length loading most heavily. A total of 98% of morphological variation was explained by PC1–3 (Table S8). Finally, while body size varied among lineages, there were no significant differences in body size variance among lineages (Fligner-Killeen test: $X^2 = 11.749$, df = 6, $p = 0.068$).

4 | Discussion

In this study, we found extensive, within-lineage mitonuclear discordance consistent with repeated mitochondrial introgression from *G. multiporosa* to nanamulti. We also confirmed

phylogenetic-scale mitonuclear discordance in the *G. occidentalis* complex that could reflect either of two equivocal scenarios of mtDNA introgression, although here mtDNA introgression, rather than ILS, is less certain than between *multiporosa* and nanamulti. Despite these cases of mitonuclear discordance, phylogenetic network analysis strongly supported only a single instance of modest nuDNA introgression—from nanamulti to *multiporosa* (Figure 2), in the opposite direction to mitochondrial capture—but with no congruent support from *D*-statistics. Furthermore, we found no evidence of recent or ongoing introgression between lineages at the two contact zones examined here (Figure 5), including between *multiporosa* and nanamulti where they currently co-occur; although we did detect a single early generation hybrid between *nana*4 and nanamulti. Finally, we found no evidence of novel, intermediate, or more variable morphological traits in lineages with mitonuclear discordance. Collectively, these results highlight a system with clear evidence of repeated hybridisation and mtDNA capture but with no overt evidence of other genotypic or phenotypic consequences. We note that our use of protein-coding exon data could have missed introgressed regions of the genome; however, we might still have expected our *Dsuite* analysis, which used genome-wide SNP data, to identify potential nuDNA introgression. Further studies in this system could use complete genome sequencing to compare nuDNA regions associated with mitonuclear interactions, as co-introgression of these alleles may be necessary to maintain mitochondrial performance (Ding et al. 2021; Nikelski et al. 2023).

4.1 | Mitonuclear Discordance but No Substantial Nuclear Introgression

Mitonuclear discordance is often an indicator of mtDNA introgression (Toews and Brelsford 2012) and frequently predicts matching nuDNA introgression (e.g., Sarver et al. 2021; Ji et al. 2023; Potter et al. 2024). However, widespread mtDNA introgression can also occur with comparatively low levels of nuDNA introgression (Chan and Levin 2005; Sloan et al. 2017). Here, our results add to a growing body of evidence demonstrating mtDNA introgression with little concomitant nuDNA introgression, which has been identified widely across taxa (e.g., Nevado et al. 2009; Boratyński et al. 2014; Good et al. 2015; Grummer et al. 2018; Mao and Rossiter 2020). However, complete, recurrent mtDNA replacement with no detected nuDNA introgression—as observed here for nanamulti—seems markedly rarer and, to the best of our knowledge, has only been reported in *Lissotriton* newts (Zieliński et al. 2013).

Mitochondrial genomes can easily cross species boundaries following hybridisation due to a lack of recombination and uniparental inheritance (Vargas et al. 2017; Zhang et al. 2019). Within the *nana-occidentalis* clade, mitonuclear discordance observed within nanamulti itself implies multiple, recent introgression events from *multiporosa*. Despite this, we detected only small amounts of nuDNA introgression (~5%) and in the opposite direction—from nanamulti to *multiporosa*—to what was expected given the direction of mtDNA introgression. The discordance within the *occidentalis* complex is more difficult to interpret and could be explained by mtDNA capture from *multiporosa* to *occidentalis*-OR or from *occidentalis*-YI to *occidentalis*-KL—or even by estimation error or incomplete lineage sorting. In this case, we found no evidence of nuDNA introgression to match either scenario of mtDNA introgression. Despite a general lack of nuDNA introgression shown here, repeated instances of mtDNA capture indicate that hybridisation is, or has been, relatively frequent in the *nana-occidentalis* clade. Phylogenies inferred from mtDNA are expected to achieve reciprocal monophyly more quickly than nuDNA due to the smaller effective population size and elevated mutation rates of mtDNA (Ballard and Whitlock 2004). This suggests that the mtDNA introgression events from *multiporosa* to nanamulti occurred only recently given the rampant mtDNA paraphyly within these lineages. Thus, nuDNA introgression was either swiftly purged or extremely limited following these introgression events.

Several factors may explain the lack of nuDNA introgression observed here. Adaptive introgression of mtDNA is frequently cited to drive asymmetrical patterns of mtDNA vs. nuDNA introgression (Toews and Brelsford 2012; Bonnet et al. 2017; Sloan et al. 2017) and has been identified in *Lepus* hares (Melo-Ferreira et al. 2014), *Drosophila* flies (Llopart et al. 2014), and *Myodes* voles (Boratyński et al. 2014), among other taxa. However, confident identification of adaptive introgression requires the demonstration of adaptive function, which is often difficult (Toews et al. 2013; Taylor and Larson 2019). Detection methods for positive selection (e.g., Suarez-Gonzalez et al. 2018) must be used with caution, as phenomena such as heterosis can mimic signals of adaptive introgression (Kim et al. 2017). Alternatively, demographic processes such as gene surfing—whereby markers more prone to drift, such as mtDNA, are fixed in populations undergoing rapid range expansion (Excoffier et al. 2009)—may have driven the fixation of *multiporosa* mtDNA in nanamulti, as there is evidence of range expansion in nanamulti (Lau et al. 2025). Similar introgression scenarios driven by range expansion have been detected in groups such as *Otospermophilus* ground squirrels (Phuong et al. 2017) and *Ursus* bears (Cahill et al. 2013). However, range expansion would not account for the fixation of *multiporosa* mtDNA over the entirety of the range of the nanamulti lineage, and demographic processes generally have been suggested to cause massive discordance only rarely (see Bonnet et al. 2017).

4.2 | Introgression and Morphology

Despite a growing number of studies demonstrating the potential role introgression can play in generating morphological variation (e.g., Lamichhaney et al. 2015; Taylor and Larson 2019), we found no association between introgression and phenotypic variation in the *nana-occidentalis* clade in terms of the morphometric characters we measured. However, given the lack of nuDNA introgression found here, it is not surprising that we found no evidence for transgressive, intermediate, or more variable phenotypes. In other cases where introgression has been suggested to influence morphology in squamates (e.g., Pavón-Vázquez et al. 2024; Wogan et al. 2023), the estimated proportion of introgression was significantly higher than what was found here. In line with other studies of *Gehyra* morphology (see Sistrom et al. 2012; Kealley et al. 2018; Moritz et al. 2018), our results highlighted body size as the main axis of among-lineage morphological variation in the *nana-occidentalis* clade. Considering

this, it is worth noting that *multiporosa* is somewhat intermediate in body size with respect to the *nana* and *occidentalis* complexes. This could have facilitated hybridisation with nanamulti or it could, conceivably, be the result of introgression; however, this is unlikely considering the modest nuDNA introgression estimated using the MSCi and the lack of introgression detected with *D*-statistics.

4.3 | Conclusions and Future Directions

Methods to infer genomic introgression have improved and diversified over the last two decades, and given the biases and limitations unique to each method, comparing the results of multiple analyses is often warranted to ensure that results are robust (Hibbins and Hahn 2022). Here, we used several such methods to understand the complicated evolutionary history of a clade of *Gehyra* geckos. These results highlight a system with repeated instances of asymmetrical mtDNA introgression with limited evidence of corresponding nuDNA introgression. Mitonuclear discordance and introgression have now been widely identified in squamates (e.g., Grummer et al. 2018; Prates et al. 2023; Wogan et al. 2023; Myers et al. 2024); however, in none of these instances has the disparity between levels of mtDNA and nuDNA introgression been so clearly demonstrated. More work in this and other systems is needed to understand whether such mismatches result from selection or non-adaptive factors. Such studies could also assess the potential for mtDNA introgression to drive speciation by providing adaptive benefit or by introducing mitonuclear interactions that reinforce RI between diverging lineages. Whole genome sequencing is more accessible than ever and will be needed to answer such questions (Combrink et al. 2025).

Author Contributions

W.J.R., S.M.Z., and C.M. conceived the study. W.J.R., C.C.L., and R.J.L. performed bioinformatics procedures. W.J.R., S.M.Z., and C.C.L. performed analyses. W.J.R. and S.M.Z. created figures. W.J.R. drafted the manuscript; all authors contributed to editing the final manuscript.

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Ethics Statement

Newly acquired samples were collected under Australian National University animal ethics approvals A2019/15 and A2022/07, Western Australia Regulation 25 scientific purposes permit FO25000338-3, and NT Parks and Wildlife Commission permit number 69132.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and R code are available for review at http://datadryad.org/stash/share/u83UGcbOwFLOV_YjZJ8TDfJ3hh3lspo36he34wURNMU.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.