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Genetic diversity in the American elephantfish (Chimaeriformes: *Callorhinchus callorynchus*) and among its congeners

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Abstract

Understanding genetic population structure and connectivity is essential for effective species-specific management and conservation strategies. The American elephantfish *Callorhinchus callorynchus* is targeted and retained as incidental catch in commercial and recreational fisheries in Chile and Argentina. Its wide-ranging distribution across southern South America may require transnational co-operation to ensure sustainable use, but its current population structure is not known. In this work, we analysed the levels of genetic diversity and differentiation within *C. callorynchus* in South America using two mitochondrial markers, the control region (CR) and the cytochrome oxidase subunit I gene (CO1). Moreover, we assessed levels of genetic diversity within, and divergence among, the three extant callorhinchids (genus *Callorhinchus*), a group that exhibits allopatric geographical distributions in the southern hemisphere. Overall, sequence analyses of the mitochondrial CR and the CO1 revealed extremely low levels of sequence variation both within and among *Callorhinchus* species. Genetic homogeneity was found throughout the range of *C. callorynchus* coupled to low-frequency haplotype sharing across spatially distant locations in Chile and Argentina, suggesting gene flow along the South American coast. Moreover, our analyses supported a scenario of recent population expansion of the species in South America. Given the absence of dispersive eggs or juvenile stages in chondrichthyans, gene flow is mainly mediated by actively swimming adults. Based on the available data, gene flow in callorhinchids appears to occur along continuous coastal regions, with deep oceanic waters serving as strong barriers. Findings here provide an important baseline for future research on dispersal and gene flow in holocephalans.

KEYWORDS
chimaeras, demographic history, genetic diversity, mitochondrial DNA, southern hemisphere

1 | INTRODUCTION

Chondrichthyes (elasmobranchs and holocephalans) are the most ancient and most evolutionary distinct lineage of jawed vertebrates (Dulvy et al., 2014; Stein et al., 2018), with holocephalans (i.e. chimaeras and ratfish) holding a very important phylogenetic position as a critical reference for our understanding of (genetic) evolution in vertebrates (Inoue et al., 2010). However, research on holocephalan genetic diversity and structure is scarce. The genus *Callorhinchus* Lacepède 1998 (Chimaeriformes: Callorhinchidae) houses three valid extant species of medium-sized chimaeroids, characterised by their plough-shaped snout, each with mutually exclusive geographical distributions in the temperate regions of the Southern Hemisphere (Didier, 1995). Specifically, the American elephantfish *Callorhinchus callorynchus* (L. 1758) is found in South America, the Cape elephantfish *Callorhinchus capensis* Duméril 1865 in southern Africa and the Australian elephantfish *Callorhinchus milii* Bory de Saint-Vincent 1823 is restricted to Australasia (Fricke et al., 2024). While most chimaeroids are known to be deep-water dwellers (i.e. occur below 200 m), the three species of *Callorhinchus* also inhabit shallower coastal waters (e.g. 0–600 m; López et al., 2000; Di Dario et al., 2011).

Callorhinchus callorynchus exhibits a continuous distribution in coastal waters (10–481 m) from Puerto López in Ecuador to the Brazilian state of Rio de Janeiro (Chirichigno & Cornejo, 2001; Cousseau & Perrotta, 2013; Di Dario et al., 2011; Finucci & Cuevas, 2020; López et al., 2000; Swing & Béarez, 2006). The species is a year-round target of handline, demersal gillnet, trawl and longline fisheries throughout its geographical range, but mainly in Argentina and Chile (Alarcón et al., 2011; Bernasconi et al., 2013; Chierichetti et al., 2017; Finucci & Cuevas, 2020). Moreover, it is often recorded as incidental catch (bycatch) in commercial fisheries and is reported as one of the most landed species of chondrichthyans across its distribution (e.g. Góngora et al., 2009; Hernandez et al., 2010; Jaureguizar et al., 2015; Lamilla et al., 2008; Ruibal Núñez et al., 2018). As with most chondrichthyans, chimaeroid abundance is highly sensitive to various anthropogenic pressures, attributable to their intrinsic conservative life-history characteristics such as slow growth, late sexual maturity, low fecundity and high longevity (Dulvy et al., 2014, 2021; Ferretti et al., 2010; Stevens, 2000). Without the implementation of adequate management, plough-nose chimaeras can undergo population decline (Francis, 1998). Evidence of population decline in the Southeast Pacific, combined with high distributional overlap with intensive fishing pressure, led to the species being assessed as Vulnerable by the IUCN Red List of Threatened Species (Finucci & Cuevas, 2020). There are some localised management actions in place for *C. callorynchus*, but its wide-ranging distribution across several countries may require transnational cooperation to ensure sustainable use (Finucci et al., 2021). Building a comprehensive understanding of the distribution and connectivity of population units is therefore fundamental to the establishment of appropriate management strategies and conservation priorities.

This work constitutes the first investigation into the genetic diversity of both the genus *Callorhinchus* and specifically of *C. callorynchus*, aiming to contribute to a better understanding of population structure and demographic processes of the latter. Based on the general trend of low genetic diversity reported for chondrichthyans (Martin, 1999; Martin et al., 1992; Martin & Palumbi, 1993; Mulley et al., 2009; Renz et al., 2013; Wang et al., 2008), analyses of mitochondrial genetic markers are expected to reveal low levels of genetic variation among specimens of *C. callorynchus* from different geographical regions in South America. For this purpose, the genetic diversity at two mitochondrial genetic markers often used for population-level genetic analyses was screened in sample collections obtained along the species´ geographic range. Given the distinct environmental features and geological histories of the Atlantic and Pacific coasts of the South American continent, shaping spatial divergence and genetic heterogeneity of species (Peterson and Whitworth, 1989; Camus, 2001; Acha et al., 2004; Spalding et al., 2007, Montecino & Lange, 2009; Miloslavich et al., 2011; Meuser et al., 2013; Artana *et al*., 2019; Orúe-Echevarría et al., 2021), the main question pertains to whether *C. callorynchus* forms a single population unit or, whether there are multiple population units throughout its distribution range. Moreover, we explored levels of intrageneric diversity and divergence within *Callorhinchus* by including samples of the congeners *C. milii* from New Zealand and Australia, and *C. capensis* from South Africa and Namibia in our genetic analyses.

2 | MATERIALS AND METHODS

2.1 | Sampling

Tissue samples of *C. callorynchus* were collected from specimens obtained at different sampling locations off the southeastern Pacific (Peru and Chile) and from the southwestern Atlantic (Argentina) year-round between 2021 and 2023 (Figure 1; see Table S1). Furthermore, specimens of *C. milii* were sampled off the coast of New Zealand in May 2014 and 2021, and July of 2023. Tissue samples of *C. capensis* were provided by the Two Oceans Aquarium, located in Cape Town, South Africa, and were collected from dead animals. All tissue samples were preserved in 100% ethanol and stored at −20°C until DNA extraction.

2.2 | Ethics Statement

Samples from Peru and Chile were obtained as target or bycatch species from commercial gillnet fisheries at the landing localities indicated in this manuscript (Figure 1; see Table S1). Specimens were dead at the moment of landing and thus sampling permits were not required since specimens were obtained directly in agreement with local fishers. Samples from New Zealand were collected during research trawl surveys and/or by fishers and did not need permits (see Table S1).

For samples from Argentina, collection permits were issued by the Secretaría de Pesca, Chubut Province, Argentina (permit no. 06/2023-DCPyA-SsP-SP). All protocols involving animal welfare were approved by the Institutional Committee for the Care and Use of Experimental Animals of the Centro Nacional Patagónico (permit no. 011).

2.3 | DNA isolation

Genomic DNA (gDNA) was isolated using the Qiagen DNeasy Blood & Tissue kit following the manufacturer's protocols. To test the quality of gDNA extractions, both elutions were visualised on electrophoresis on 0.8% agarose gel with GelRed (Biotium), run on 0.5X TAE buffer at 300 V.

2.4 | Mitochondrial DNA amplification

To analyse population genetic structure within *C. callorynchus* in South America, two mitochondrial markers were analysed. Newly designed oligonucleotide primers were used for the amplification of 506 base pairs (bp) of the control region (CR) and 458 bp of the cytochrome oxidase subunit 1 gene (CO1) (Table 1). Target fragments of the CR and CO1 were amplified via the polymerase chain reaction (PCR) consisting of an initial denaturation at 94°C for 3 min, followed by 35 cycles with 60 s of denaturation at 95°C, 60 s of primer annealing at 62°C and an elongation phase of 60 s for CO1 and 90 s for CR at 72°C, and a final extension step of 5 min at 72°C. The PCR mix had a total volume of 5 μL and contained 2.5 μL of autoclaved water, 2.5 μL of MyTaq™ HS Mix (Bioline), 0.2 μL of each primer (10 μM) and 0.6 μL of gDNA. Successful amplification was checked on 2% agarose gel electrophoresis (as described above) and purified with 0.5 μL of ExoSap-IT™ (Thermo Fisher Scientific) following the manufacturer's instructions. Purified amplicons were processed for Sanger sequencing in both directions using the Big-Dye™ Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific) following the manufacturer's instructions. Sanger sequencing was performed at CIBIO using an ABI 3500xL Genetic Analyzer (Thermo Fisher Scientific).

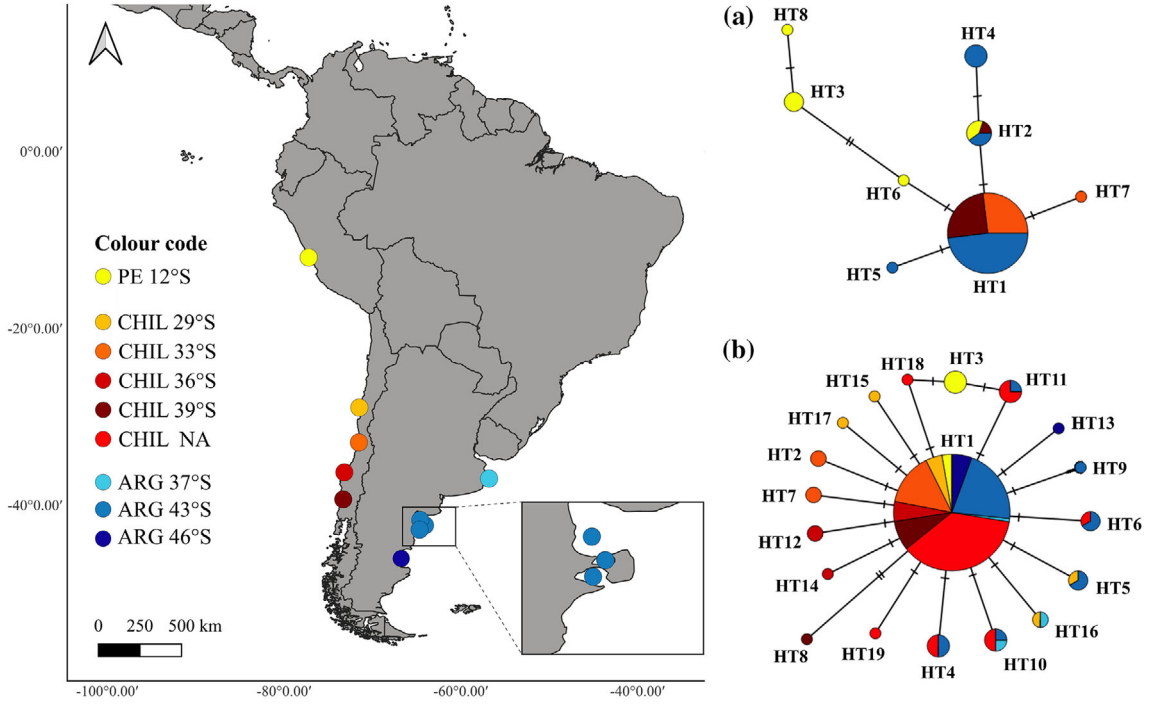

FIGURE 1 Map of South America with sample locations and TCS haplotype networks of *Callorhinchus callorynchus* (L. 1758) based on (a) 506 bp of the CR ($N = 68$) and (b) 458 bp of the CO1 gene ($N = 147$). Numbering of haplotypes (HT) is independent for each genetic marker (see Appendix S1 and Table S2). Circle sizes depict frequencies of haplotypes across all samples; numbers of mutations between haplotypes are visualised with hatch marks. Colour codes correspond to sampling locations: PE, Peru (latitude 12°S); CHIL, Chile (latitudes 29°S, 33°S, 36°S, 39°S); ARG, Argentina (latitudes 37°S, 43°S, 46°S); NA, latitude not available.

TABLE 1 New designed for the amplification of 516 bp of the mitochondrial control region (CR) and 458 bp of the cytochrome c oxidase subunit I gene (CO1) in *Callorhinchus*.

Marker	Primer	Sequence 5′→3′	bp	GC (%)	T_m (°C)	T_a (°C)
CR	CR-HF1	GYCCTGGTCTTGTAAACCARAG	22	50	60.3	62
	CR-HR1	RTGCGGAAACTTGCATGTGTAAG	23	46	59.8	62
CO1	CO1-CaF1	ATCATAAAGATATTGGCACCCTC	23	39	57.1	62
	CO1-CaR1	AGATTATACCGAAACCAGGTAGG	23	43	58.9	62

Abbreviations: bp, primer length in base pairs; F, forward primer; GC, guanine–cytosine content; R, reverse primer; T_m, primer melting temperature; T_a, temperature of annealing in the PCR temperature profile.

2.5 | Sequence data analysis

Chromatograms obtained from Sanger sequencing were proofread in Geneious Prime 2023.2.1 (https://www.geneious.com, accessed February 2024 and manually edited). The resulting nucleotide sequences were aligned using the built-in Geneious algorithm. Publicly available nucleotide sequences of CO1 from all three *Callorhinchus* species were retrieved from the BOLD database (v. 4; Barcode of Life Data System; https://www.boldsystems.org, accessed 28th August 2024) and aligned with the sequences obtained through PCR. Sequences of all haplotypes are available in the Supplemental files Data S1 for the CR and Data S2 for CO1. Haplotype identities of all samples included in this study are listed in Table S2.

2.6 | Genetic diversity analysis

The number of segregating sites (S), nucleotide diversity (π) and haplotype diversity (h) were estimated for each *Callorhinchus* species, sampling location and molecular marker using the 'pegas' package (v. 1.3; Paradis, 2010) in R 4.3.1 (R Core Team, 2023). Overall mean genetic distances based on the Kimura-2 parameter (K2P) method were calculated for each marker and species in MEGA (v. 11.0.13; Kumar et al., 2018). To explore divergence among species of the genus *Callorhinchus*, K2P distances were also calculated among *C. callorynchus*, *C. milii* and *C. capensis* using CO1 data as well as the whole mitogenome (GenBank accession nos HM147135, HM147136, and HM147137, respectively; www.ncbi.nlm.nih.gov/genbank/, accessed 28 August 2024).

The relationships among haplotypes in *Callorhinchus*, as well as their frequency and spatial distribution, were investigated for each molecular marker separately by the construction of haplotype networks using the TCS method (Clement et al., 2000; Templeton et al., 1992) implemented in the software PopArt (v. 1.7; Leigh & Bryant, 2015).

2.7 | Population genetic analysis

Because of the small sample size, the Peruvian samples ($N = 7$) were excluded from population genetic analyses. To estimate the levels of genetic differentiation between the different sampling collections of *C. callorynchus* based on haplotype diversity and frequency, a pairwise phi-statistic (Φ_{ST}) was performed using the R package 'haplotypes' (v. 1.1.3.1; Aktas, 2023). Statistical significance for $\alpha = 0.05$ was evaluated on correction for multiple testing using a strict Bonferroni correction (α/number of pairwise comparisons; Bonferroni, 1936). To test the null hypothesis of genetic homogeneity between *C. callorynchus* from the two coasts of South American (Pacific, CHIL; Atlantic, ARG), an analysis of molecular variance (AMOVA) (Excoffier et al., 1992) was conducted using the 'poppr' package (v. 2.9.6; Kamvar et al., 2014, 2015) in R, based on raw pairwise distances. The number of locations included in each group varied depending on the marker. Specifically, the CR dataset included two sampling locations in Chile (33°S and 39°S; Figure 1) and one in Argentina (43°S; Figure 1). In contrast, the CO1 dataset encompassed a broader range of locations, with four Chilean sampling sites (29°S, 33°S, 36°S and 39°S) and additional Chilean sequences without specific coordinates (NA). For Argentina, the CO1 dataset included three sampling locations (37°S, 43°S and 46°S; Figure 1). The significance of variance components and the derived Φ-statistic were estimated over 1000 permutations using the 'ade4' R package (v. 1.7–22; Chessel et al., 2004; Dray & Dufour, 2007; Dray et al., 2007; Bougeard & Dray, 2018; Thioulouse et al., 2018).

A scenario of isolation-by-distance (IBD) was tested using a generalised least square regression with correlated error structure between geographic and genetic distances using the R packages 'corMLPE' (v.1.0; Clarke et al., 2002) and 'nlme' (v. 3.1–162; Pinheiro & Bates, 2000; Pinheiro et al., 2024) to account for the non-independence of distance matrices. Pairwise genetic p distances among sample collections were calculated in MEGA (v. 11.0.13; Kumar et al., 2018). Geographic distances were calculated as least-cost distances between each pair of sampling sites in South America using the R packages 'marmap' (v. 1.0.10; Pante et al., 2023) and 'gdistance' (v. 1.6.4; Van Etten, 2017), with a resolution of 10 min. The least-cost distances were restricted to a bathymetric range between 1 and 500 m of depth, representing the typical range inhabited by *C. callorynchus*.

2.8 | Demographic analysis

To test spatial or demographic expansion, Tajima's D (Tajima, 1989), Fu's Fs (Fu, 1997) and Ramos-Onsins' & Rozas' R_2 (Ramos-Onsins & Rozas, 2002) statistics were estimated using the program DNAsp (v. 6.12.03; Rozas & Rozas, 1995; Rozas et al., 2017). The statistical significance of Tajima's D was tested for a significance level of $\alpha = 0.05$; Fu's Fs and Ramos-Onsins' & Rozas' R_2 values were estimated by generating 1000 random samples and the 95% confidence interval was calculated. All values were calculated based on an infinite-site model without recombination. Historical demographic patterns of both groups were further explored using mismatch distributions (Li, 1977) as implemented in DNAsp. Harpending's 'raggedness' index (r) (Harpending et al., 1993) was used to quantify the smoothness of the distributions as an indicator of population expansion.

2.9 | Phylogenetic relationship among haplotypes

To illustrate the evolutionary relationships among haplotypes, unique haplotypes in each marker dataset and including data from all *Callorhinchus* congeners were aligned using Geneious Prime 2023.2.1 (https://www.geneious.com, accessed February 2024). Sequences of the rabbitfish *Chimaera monstrosa* L. 1758 (used as an outgroup) were retrieved from GenBank (www.ncbi.nlm.nih.gov/genbank/, accessed

23 March 2025) and unique haplotypes were aligned with the dataset of *Callorhinchus*. Phylogenetic trees were estimated using the maximum likelihood method (Felsenstein, 1981) for each molecular marker separately, using the online version of PhyML software (v.3.0; Guindon et al., 2010) on the ATGC bioinformatics (http://www.atgc-montpellier.fr/phyml/, accessed 2 April 2025). The selection of the best-fitting substitution model of molecular evolution was done using the smart model selection in PhyML (Lefort et al., 2017) and Bayesian Information Criterion (BIC) as the selection criterion platform. Moreover, phylogenetic trees were constructed in MEGA (v. 11.0.13; Kumar et al., 2018) for each molecular marker separately, using the number of differences as a distance measure and the neighbour-joining method (Saitou & Nei, 1987). Branch support was calculated via 1000 bootstrap replicates to assess the reliability of the phylogeny (Efron, 1982; Felsenstein, 1985) (see Figure S1). Trees were edited in Inkscape (v. 1.3.2; https://inkscape.org).

3 | RESULTS

3.1 | Genetic diversity analyses

In total, 68 sequences were generated for the mitochondrial control region (CR) of *C. callorynchus* (506 bp) (see Table S2, Data S1). For the cytochrome c oxidase subunit, I gene (CO1), 61 sequences were generated (458 bp). Analyses of CO1 were complemented by 86 sequences retrieved from the BOLD database (https://www.boldsystems.org, accessed 28 August 2024) (see Table S2, Data S2). All COI sequences were translated to proteins and showed no stop codons.

TABLE 2 Genetic diversity indices for all sample collections of *C. callorynchus* based on sequence data of mitochondrial CR and CO1.

		N	*H*	*S*	*π*	*h*
CR		**68**	**8**	**8**	**0.0016**	**0.4096**
PE	Overall (12°S)	7	4	6	0.0047	0.8095
CHIL	Overall	29	3	2	0.0003	0.1355
	33°S	15	2	1	0.0003	0.1429
	39°S	14	2	1	0.0003	0.1429
ARG	Overall (43°S)	32	4	3	0.0012	0.3810
CO1		**147**	**19**	**18**	**0.0013**	**0.4483**
PE	Overall (12°S)	7	2	2	0.0025	0.5714
CHIL	Overall	98	16	16	0.0010	0.3987
	29°S	9	5	4	0.0019	0.7222
	33°S	20	3	2	0.0008	0.3579
	36°S	9	3	2	0.0013	0.5556
	39°S	10	2	2	0.0009	0.2000
	NA	50	7	6	0.0009	0.4419
ARG	Overall	42	9	8	0.0012	0.4901
	37°S	3	3	2	0.0029	1.0000
	43°S	32	7	6	0.0012	0.4839
	46°S	7	2	1	0.0006	0.2857

Note: Individuals are grouped into sample collections according to latitude of capture. Bold values mark the indices for the whole marker.
Abbreviations: *π*, nucleotide diversity; ARG, Argentina; CHIL, Chile; *h*, haplotype diversity; *H*, number of haplotypes; *N*, number of individuals; PE, Peru; *S*, number of segregating sites.

Overall, the genetic diversity at each marker was very low, as indicated by the low values of nucleotide diversity (π), number of haplotypes (H) and segregating sites (S) (Table 2 and Figure 1). However, diversity levels were not equal among sampled sites: haplotype diversity (h) showed high location-dependent discrepancies for CR and CO1 (Table 2 and Figure 1). Despite the small sample size, the Peruvian sample (PE) showed the highest genetic diversity values compared to the Chilean (CHIL) or Argentinean samples (ARG), in terms of both π and h, while CHIL revealed the lowest genetic diversity at both markers.

The haplotype networks for the CR (Figure 1a) and CO1 (Figure 1b) showed a star-shaped conformation, with a predominant central haplotype shared by most individuals across the different sample collections with several low-frequency derived haplotypes (Figure 1). Both molecular markers revealed low levels of haplotype divergence, generally characterised by one to two substitutions between haplotypes, with the maximum being four.

In total, the CR network comprised eight distinct haplotypes (Figure 1a) and showed higher haplotype diversity in the small Peruvian sample collection ($N = 7$; Table 2). Except for the two specimens sharing haplotype 2 (HT2) with one specimen from CHIL and two from ARG, all specimens from PE had exclusive haplotypes (HT3, 6, 8). These specimens were separated from the most common haplotype (HT1) by one to four mutations while other haplotypes in the network were separated from the central haplotype by one or a maximum of two mutations. In the CO1 network (Figure 1b), we observed 19 haplotypes in total, which all differed from the central haplotype by one or a maximum of two mutations. Unlike in the CR network (Figure 1a), some individuals from PE shared the most common haplotype (HT1) with the rest of the sample collections. All locations displayed low-frequency derived haplotypes. Additionally, six of these derived haplotypes were shared between CHIL and ARG (HT4, 5, 6, 10, 11, 16).

3.2 | Population genetic analysis

The pairwise comparison of the genetic diversity between the Chilean (CHIL) and Argentinean (ARG) sample collections based on Φ_{ST} (Table 3) revealed no significant genetic differentiation among sampled sites of *C. callorynchus* on correction for multiple tests.

For the AMOVA, sample collections were grouped into two regions corresponding to the Atlantic (ARG) and Pacific coasts (CHIL) to test the null hypothesis of genetic homogeneity between the two continental margins of South America (Table 4). The differences within sample collections constitute the main source of variation in our data (CR 95.725%, CO1 100.379%). Genetic differentiation

TABLE 3 Pairwise phi-statistics (Φ_{ST}) based on mitochondrial sequence data from five sample locations of *C. callorynchus*.

	CHIL 29°S	CHIL 33°S	CHIL 36°S	CHIL 39°S	ARG 43°S
CHIL 29°S	–	NA	NA	NA	NA
CHIL 33°S	0.0479	–	NA	0.0002	0.0690
CHIL 36°S	0.0357	0.0925	–	NA	NA
CHIL 39°S	0.0045	0.0279	0.0549	–	0.0129
ARG 43°S	0.0080	0.0300	0.0587	0.0012	–

Note: Above diagonal, CR; below diagonal, CO1. No value was significant on strict Bonferroni correction for multiple tests ($p < 0.005$).
Abbreviations: ARG, Argentina; CHIL, Chile.

TABLE 4 Analyses of molecular variance (AMOVA) based on CR and CO1 sequence data of *C. callorynchus* between the Atlantic (Argentina) and Pacific (Chile) coasts of South America.

Marker	Source of variation	*df*	Sum Sq	Variance component	Variance (%)
CR	Between regions	1	0.624	0.012	4.275
	Within regions	59	15.606	0.265	95.725
CO1	Between regions	1	0.331	−0.002	−0.379
	Within regions	138	58.769	0.426	100.379

Abbreviations: *df*, degrees of freedom; Sum Sq, sum of squares.

TABLE 5 Estimated demographic parameters Tajima's *D*, Fu's *Fs*, and Ramos-Onsins and Rozas' R_2 based on mitochondrial sequence data (CR, CO1) of *C. callorynchus* (including all samples from Chile and Argentina together).

Marker	Tajima's *D*	Fu's *Fs*	Ramos-Onsins' and Rozas' R_2
CR	−1.1658	−2.491*	0.0608*
CO1	−2.3221*	−24.020	0.0182*

Note: Asterisks indicate significant values.

between the Atlantic and Pacific coasts was not statistically significant for either of the two markers, corresponding to $\Phi_{ST} = 0.043$ and −0.004 for the CR ($p = 0.1$) and CO1 ($p = 0.59$), respectively.

Additionally, the IBD analysis based on least-square regression of distance matrices indicated a tendency for genetic distances to increase with geographic distances among sampling locations based on the CO1 marker. However, this relationship was not significant as the 95% confidence interval of correlation estimate included zero (estimate 0.33; 95% CI −0.48–1.14).

3.3 | Demographic analysis

Given the genetic homogeneity among sample collections as described above, the results of Tajima's *D*, Fu's *Fs* and Ramos-Onsins' & Rozas' R_2 tests were calculated for a group including all samples of *C. callorynchus*, with exclusion of the Peruvian samples ($N = 7$). Estimates of Tajima's *D* and Fu's *Fs* were negative for both molecular markers (Table 5), but only the values of Tajima's *D* for CO1 and Fu's *Fs* for CR were statistically significant. Ramos-Onsins' & Rozas' R_2 statistics, which are more robust for small sample sizes, showed statistically significant positive values for both markers, pointing towards population expansion.

The mismatch distributions of the CR (Figure 2a) and CO1 data (Figure 2b) revealed a mostly smooth distribution of pairwise nucleotide differences, characteristic of recent population expansion, in line with the results from the neutrality tests (Table 5). The observed mismatch distribution based on the CR (Figure 2a) showed a slight deviation from the neutrality expectation. However, the raggedness statistic of mismatch distribution analyses (*r*) was low for both markers, confirming the fit of the data to a unimodal distribution.

3.4 | Phylogenetic relationships among haplotypes

The phylogenetic trees based on CR (Figure 3a) and CO1 (Figure 3b) showed the existence of one highly supported main clade of *Callorhinchus* haplotypes (bootstrap support [BS] 100%), however, internal resolution was weak, as indicated by low bootstrap support values. CR haplotypes do not form monophyletic clusters for each of the three species of *Callorhinchus* (Figure 3a), pointing towards incomplete lineage sorting in the CR data. Only haplotypes from *C. capensis* form a visible subcluster with high bootstrap support (BS 91%) nested within the rest of *Callorhinchus* haplotypes. The haplotypes exclusive to PE (HT3, HT6, HT8) form a separate cluster within *C. callorynchus* (BS 84%). *Callorhinchus* COI haplotypes also form a highly supported monophyletic group (BS 100%; Figure 3b), but the pattern is distinct from the one observed for the CR. CO1 haplotypes from *C. callorynchus* and *C. capensis* each form monophyletic clades with high bootstrap support (97% and 85%, respectively). No spatial structure was evident for *C. callorynchus* in the tree. In contrast, *C. milii* does not form a monophyletic group but, interestingly, haplotypes were spatially structured: those exclusive to Australia (HT27, 28) formed a highly supported subgroup (BS 97%). A similar pattern was observed using the neighbour-joining method, revealing a lack of monophyly in *C. milii* and providing further support for the divergence of specimens from New Zealand (see Figure S1).

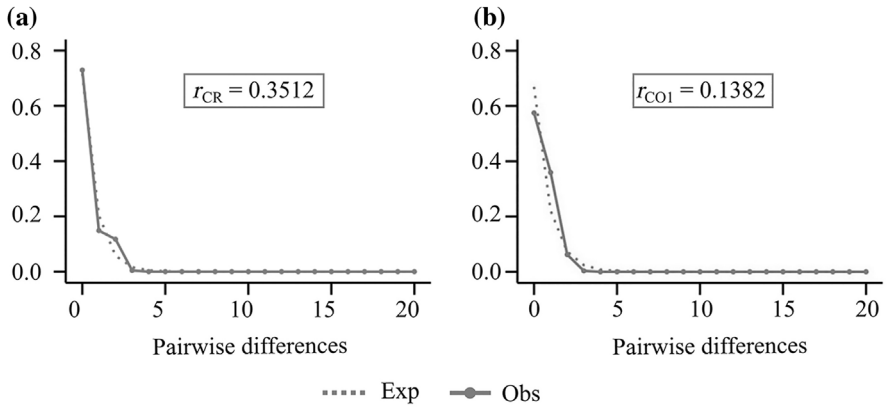

FIGURE 2 Mismatch distributions and Harpending's raggedness index (*r*) of *Callorhinchus callorynchus* (L. 1758) (including all samples from Chile and Argentina together) based on (a) CR and (b) CO1. The *x* axis shows the number of pairwise differences and the *y* axis shows the frequency of the pairwise comparisons. Exp, expected frequencies under the population expansion model; Obs, observed frequencies.

3.5 | Interspecific comparisons

Sequence data for CO1 show higher genetic diversity in *C. capensis* and *C. milii* compared to *C. callorynchus*, in terms of both higher haplotype (*h*) and nucleotide diversities (π), and despite their considerably smaller sample sizes (Table 6). The higher diversity in the CO1 dataset of *C. milii* was particularly evident in the comparison among congeners.

The K2P overall mean distances (Table 7) between individuals within *C. callorynchus* equalled 0.16% and 0.13% for CR and CO1, respectively, reflecting the low intraspecific diversity observed before (Table 1). Overall mean distances in *C. milii* and *C. capensis* were considerably higher compared to *C. callorynchus*, confirming the results of Table 6. *Callorhinchus milii* showed the highest diversity between individuals, with K2P distances being equal to 0.20% for CR and 1.53% for CO1. Among species, K2P distances ranged between 1.92 and 2.62% based on CO1 and between 1.34 and 1.82% based on the mitogenome, demonstrating the overall low levels of diversity between each pair of species within *Callorhinchus*.

The *Callorhinchus* CO1 haplotypes revealed four distinct haplogroups separated by six to seven mutations each and corresponding to the three currently accepted species (Figure 4). Haplotypes of *C. milii* were further divided into two geographically distinct groups: one consists of haplotypes found exclusively in Australia, while the other includes only haplotypes from New Zealand specimens. The divergence observed within *C. milii* is marked by a minimum of seven mutations, which is therefore as pronounced as the separation between *C. callorynchus* and *C. capensis* haplotypes.

4 | DISCUSSION

4.1 | Low genetic diversity and weak population structure in *C. callorynchus*

This study is the first to provide insight into the patterns of population genetic diversity and differentiation of *C. callorynchus* across its distribution, based on analyses of two mitochondrial markers. Our results identify remarkably low genetic diversity in *C. callorynchus*, as shown by the low number of differences among sequences and low nucleotide diversity in both the CR and CO1 (see Table 2). The Chilean specimens consistently showed the lowest level of diversity for each marker, in terms of both nucleotide and haplotype diversities, while the highest values were observed in the Peruvian specimens (Table 2). However, the high diversity levels in the Peruvian specimens should be interpreted with caution in light of the limited sample size ($N = 7$). We therefore decided to exclude it from further analyses to avoid potential biases in the results. Future studies should aim to adequately sample locations on the northern-most edges of the species distribution on both coasts of South America because they may exhibit unique genetic diversity and distinct population units. Nevertheless, overall variation in the mtDNA of *C. callorynchus* is evidently very low, even among *Callorhinchus*, as further supported by the low mean K2P distances (see Table 3). The results of our AMOVA (Table 4), the observed haplotype sharing among all sampling locations (Figure 1), and the unresolved phylogenetic relationships among haplotypes (Figure 3), moreover suggest that the distribution of the genetic variation among samples of *C. callorynchus* is not spatially structured. Most importantly, it suggests the absence of significant genetic differentiation between the samples from the Atlantic and Pacific coasts. Together, these results point towards the presence of a single population comprising samples from both Chile and Argentina, suggesting that coastal connectivity is crucial for maintaining gene flow in *C. callorynchus*. Species-specific management implementations are currently limited to some gear restrictions, recreational bag limits and daily catch limits in some regions of the Argentinean Sea (Finucci & Cuevas, 2020; Venerus & Cedrola, 2017). However, in Chile, the species is still unregulated and there are no catch limits (Aedo et al., 2010). Since *C. callorynchus* has been listed as "Vulnerable" showing decreasing population trends as reported by the IUCN Red List (Finucci & Cuevas, 2020), transnational cooperation on fisheries management measures for *C. callorynchus* may be required. Moreover, coastal areas that serve as breeding and recruitment areas (Bernasconi et al., 2015; Di Giácomo, 1992) should be identified and protected from commercial fishing to mitigate effects on juveniles within the population in the future.

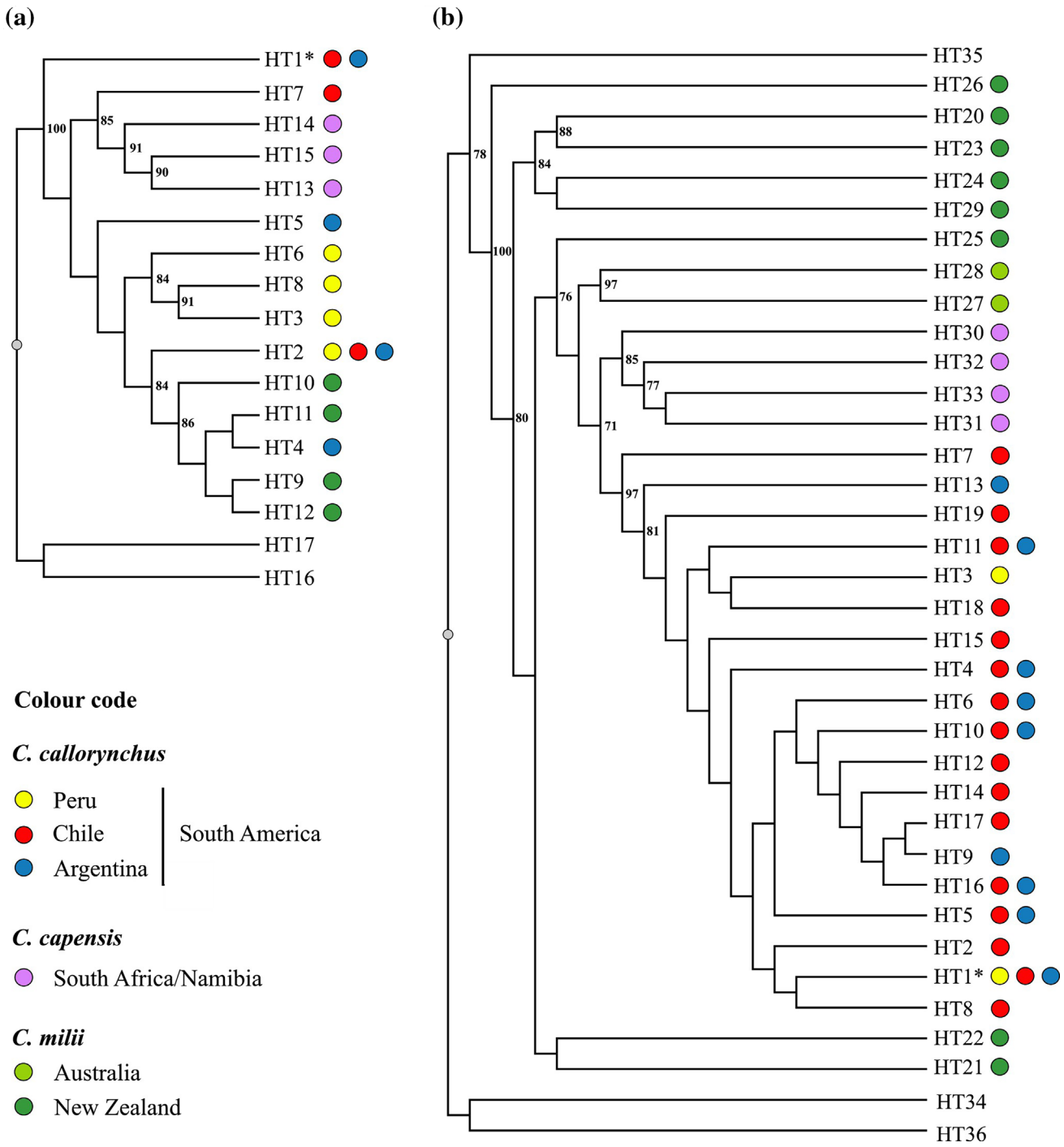

FIGURE 3 Maximum-likelihood trees of *Callorhinchus* Lacepède, 1798 based on (a) CR (506 bp, $N = 68$) and (b) CO1 (458 bp, $N = 147$). Colours indicate sampling location: PE, Peru; CHIL, Chile; ARG, Argentina. HT numbering and colour code of sampling locations correspond to haplotype networks in Figure 1. HT1 represents the most common haplotype. (a) HT16-17 and (b) HT34-36 are haplotypes of *Chimaera monstrosa* L. 1758 serving as outgroups. Bootstrap support values >50 are shown to the right of their respective nodes.

4.2 | A phylogeographic perspective on *C. callorynchus* population structure

Previous studies collectively underscored the complex interaction of various ecological and environmental factors demarcating marine biogeographic provinces along the South American coast (e.g. Camus, 2001; Spalding et al., 2007), providing a foundational framework for understanding the spatial organisation and distribution of species. Since *C. callorynchus* is an oviparous species, depositing and attaching eggs on bottom substrates, it is likely that dispersal and gene flow are mediated by actively swimming adults, as already reported in *C. milii* (Barnett et al., 2019). Given our limited knowledge

on the putative barriers to gene flow in holocephalans in general, and *Callorhinchus* in particular, it could be hypothesised that known biogeographic breaks would match areas of genetic differentiation in coastal marine species as *C. callorynchus*. However, the genetic homogeneity observed in *C. callorynchus* throughout its distribution in temperate and austral South America suggests that soft environmental barriers, such as climatic phenomena and mesoscale variabilities affecting ocean temperature, salinity and productivity, do not significantly restrict gene flow. Comparison of these results with those of other marine organisms with similar distributions are difficult because marine biogeographical studies throughout the area are limited, and most species analysed have a planktotrophic dispersal stage in their life cycle (e.g. Barahona et al., 2019; Brante et al., 2012; Cárdenas et al., 2009; Hernández et al., 2005; Lancellotti & Vásquez, 2009; Lara et al., 2019; Moreno et al., 2006).

TABLE 6 Genetic diversity indices for the three species of *Callorhinchus* based on sequence data of the mitochondrial gene CO1.

Species	*N*	*H*	*S*	*π*	*h*
C. callorynchus	147	19	18	0.0013	0.4483
C. capensis	10	4	6	0.0032	0.5330
C. milii	23	10	16	0.0137	0.7708

Abbreviations: *π*, nucleotide diversity; *h*, haplotype diversity; *H*, number of haplotypes; *N*, number of individuals; *S*, number of segregating sites.

4.3 | Recent demographic expansion in *C. callorynchus*

The extent of the genetic structure of a species is not solely determined by the amount of past and/or current gene flow but by the impact of historical and demographic factors. Our genetic data exhibits several key characteristics that suggest a recent and rapid demographic expansion of *C. callorynchus* in South America. The star-like topology of the haplotype networks (Figure 1) highlights a central most common haplotype surrounded by many low-frequency derived variants. While the sharing of the central haplotype across all sampled

TABLE 7 Summary of Kimura-2-parameter (K2P) genetic distances (%) calculated for different markers and taxonomic levels.

Taxonomic level of comparison	Taxon name	Marker	K2P
Within species	*C. callorynchus*	CR	0.16
		CO1	0.13
	C. capensis	CR	0.29
		CO1	0.35
	C. milii	CR	0.20
		CO1	1.53
Between species	*Callorhinchus*	CO1	1.92–2.62
		Full mitogenome	1.34–1.82

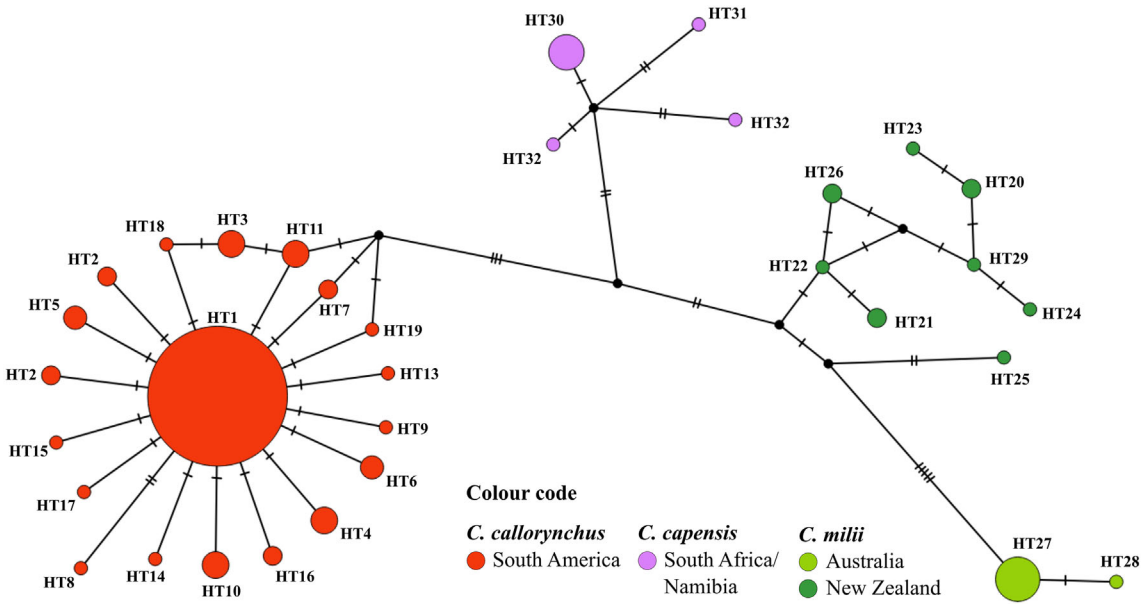

FIGURE 4 TCS haplotype network based on CO1 sequence data of *Callorhinchus* Lacepède, 1798. Circle sizes depict frequencies of haplotypes; numbers of mutations between haplotypes are visualised with hatch marks. Haplotype numbering of *C. capensis* and *C. milii* corresponds to the tree in Figure 3b; colour codes correspond to sampling locations.

locations of both the Atlantic and Pacific coasts suggests a common widespread ancestral population, the many low-frequency derived haplotypes are consistent with a recent evolutionary origin from the common one during a population expansion event. This scenario is also supported by the smooth and unimodal pattern of the mismatch distributions (Figure 2) and the neutrality tests (Table 5). The lack of statistical significance in some of these tests, combined with discrepancies between test results between the two markers, are potentially attributed to the few nucleotide differences among haplotypes noted in the previous diversity assessments. However, Ramos-Onsins and Rozas (2002) demonstrated that the power of R_2 is comparably higher when the number of segregating sites is low. Taken together, the integration of these results supports a scenario of a recent expansion of a single widespread population along the South American coast.

Dynamics associated with the Last Glacial Maximum (LGM) were powerful drivers in shaping the genetic and ecological diversity of many species. Under LGM conditions (19,000–23,000 cal yr. ago), a massive extra polar ice sheet, known as the Patagonian ice sheet (PIS), stretched along the crest of the Andes between ~38°S and 55°S (Davies et al., 2020; Hulton et al., 2002). Habitat loss and fragmentation, as well as changes in temperature and salinity, caused by the advance and subsequent retreat of the PIS likely forced coastal species such as *C. callorynchus* northwards and/or into glacial refugia. Since the Argentinean and Peruvian coastlines were not covered by the PIS, Argentinean and Peruvian ancestral populations of *C. callorynchus* could have been able to persist throughout the LGM, isolated from each other by the PIS. When subsequent deglaciation caused suitable habitats to expand, these populations may have undergone rapid spatial expansion. The observed genetic homogeneity between Chilean and Argentinean specimens points towards a potential recolonisation event from Argentina to Chile after the LGM. Combined with a comparably high diversity observed in even a small sample size from Peru, distinct refugial *C. callorynchus* populations along the Peruvian coastline might have been isolated from the rest of the species for an extended period, harbouring significant genetic variation, as has been hypothesised for other species such as the longfin squid *Doryteuthis gahi* (A. d'Orbigny, 1835) (see McKeown et al., 2019). However, since we cannot accurately date back demographic expansion in *C. callorynchus*, this or comparable scenarios remain highly speculative. Given this uncertainty, it would be valuable to further investigate the genetic and ecological diversity of *C. callorynchus* populations along northern Chile and Peru.

4.4 | Identifying barriers to gene flow in holocephalans

The sharing of low-frequency derived COI haplotypes among distant sampling locations (Figure 1) and the absence of genetic differentiation between regions in the AMOVA (Table 4) indicate the presence of gene flow in *C. callorynchus* along the South American coast ranging from Argentina to Chile. In short, similar to *C. milli* (see Barnett et al., 2019), *C. callorynchus* seems to be capable of dispersing over long distances alongshore. On the other hand, the results showed a tendency for genetic distances to increase with geographic distances, although the signal was not strong enough to allow definitive conclusions. Future studies are needed to ascertain whether this relationship is robust by adding more sampling locations and possibly larger sample sizes.

In contrast, the intraspecific divergence observed between Australian and New Zealand specimens of *C. milii* suggests that the deep oceanic waters in the Tasman Sea likely serve as significant barrier to dispersal and gene flow, as has been shown in several coastal marine species (Grewe et al., 1994; Ward & Elliott, 2001). This is consistent with the distinct species distributions in the genus, with each species inhabiting mutually exclusive geographic regions. As noted, *C. callorynchus* is confined to the South American coasts, *C. capensis* is found solely along the South African and Namibian coasts, and *C. milii* is exclusive to the coasts of southern Australia and New Zealand. These regions are all separated by deep open ocean waters that are not traversed by shallow coastal species of small to medium size, such as *Callorhinchus*. These observations highlight the role of deep oceanic waters as barriers to gene flow, driving species divergence in *Callorhinchus*.

In contrast to *Callorhinchus*, the majority of the extant holocephalans occur in deep waters (>200 m) and thus may differ in the patterns and drivers of population structure. For instance, studies on the rabbitfish *Chimaera monstrosa* L. 1758, the only holocephalan for which population-level genetic studies have been conducted so far, revealed marked intraspecific genetic heterogeneity attributed to geographical isolation consistent with the presence of shallow water barriers such as the Strait of Gibraltar (Carugati et al., 2024; Catarino et al., 2017). Notably, there are no shared haplotypes between the Atlantic Ocean and the Mediterranean Sea, as well as significant spatial divergence within the Tyrrhenian basin (Carugati et al., 2024; Catarino et al., 2017). Consequently, distribution of *C. monstrosa* is confined to deeper waters, with shallow areas being suggested to act as natural barriers to gene flow.

Overall, this suggests that shallow-water coastal species like *Callorhinchus* are limited in their ability to cross deeper oceanic zones but may move long distances along continuous suitable coastal habitats, while deep-water holocephalans, such as *C. monstrosa*, cannot traverse shallow-water regions. To identify barriers to gene flow in holocephalans, it is therefore imperative to consider the distinct characteristics pertaining to the ecology of the species.

4.5 | Callorhinchids exhibit low genetic diversity at mitochondrial markers

All species of *Callorhinchus* exhibited low genetic diversity values (Table 3), with *C. milii* showing slightly higher diversity compared to *C. callorynchus* and *C. capensis*. Such low levels of intraspecific genetic diversity are accompanied by low interspecific genetic divergence among *Callorhinchus* congeners. Indeed, the haplotypes of the three recognised extant species of *Callorhinchus* exhibit overall high genetic

similarity, with a low number of nucleotide differences separating them (Figure 4) and low overall mean K2P distance among species (1.92%–2.62% and 1.34%–1.82% based on CO1 and the whole mitogenome respectively; Table 3). These observations are remarkable as the three congeners are separated by vast expanses of open ocean waters that are unlikely to be traversed by *Callorhinchus*.

In comparison, other chondrichthyans that show genetic divergence across ocean basins in the Southern Hemisphere (e.g. short-tail stingray *Bathytoshia brevicaudata* (Hutton 1875), see LePort & Lavery, 2012; school shark *Galeorhinus galeus* (L. 1758), see Hernández et al., 2015; Bester-van der Merve et al., 2017) exhibit similarly low numbers of differences between mtDNA haplogroups. However, for these species, the observed genetic differences are considered to represent distinct regional populations within the same species, whereas in *Callorhinchus* speciation has occurred even with relatively limited genetic divergence.

Recent isolation and speciation may lead to low genetic differentiation among species, including incomplete lineage sorting (Maddison & Knowles, 2006). When examining the mitogenome tree presented in Inoue et al. (2010), the three *Callorhinchus* species exhibited notably short branches compared to other holocephalans, suggesting recent divergence of the species. Indeed, recent speciation was also supported by the phylogenetic trees here showing incomplete lineage sorting between *C. callorynchus* and *C. milii* (Figure 3). Given the current disjunct distribution of *Callorhinchus* species in South America, southern Africa and New Zealand–Australia waters, one could hypothesise that speciation was due to allopatric isolation associated with separation of continental landmasses in the Southern Hemisphere. However, the timing of such geological events would point to a relatively old speciation, ~50–130 mya, which appears inconsistent with the low levels of interspecific divergence observed among *Callorhinchus*.

One alternative explanation may be the extremely slow mutation rate of the mitogenome in *Callorhinchus* compared to other holocephalans. In fact, low genetic diversity at mitochondrial genes appears to be a feature of the family Callorhinchidae: *C. milii* has been noted to have the slowest-evolving genome of vertebrates (Venkatesh et al., 2014). Our results indicate that the mitogenome of *C. capensis* and *C. callorynchus* is likely to exhibit similarly low mutation rates given the observed low interspecific genetic divergence, as well as the overall genetic homogeneity within *C. callorynchus*. On the other hand, similarly low levels of genetic variation in the CO1 gene were found in *C. monstrosa* (Carugati et al., 2024; Catarino et al., 2017), albeit focusing on a smaller geographical range.

The bulk of the evidence gathered so far suggests that holocephalan taxa may exhibit low genetic variation at mitochondrial markers. This observation is consistent with the low levels of molecular evolution detected in chondrichthyan species (Martin & Palumbi, 1993; Sendell-Price et al., 2023). Indeed, elasmobranchs, the closest living relatives of holocephalans, are well known for their particularly low mitochondrial nucleotide substitution rates (Martin, 1999; Martin et al., 1992). This feature underlines the necessity for using multilocus datasets (e.g. Inoue et al., 2010; Stein et al., 2018) as well as other sources of information to accurately reconstruct phylogenies, such as morphological, distributional and ecological data (Naylor et al., 2012; Ward et al., 2007, 2008).

4.6 | Considerations for future studies

This work is the first to use the mitochondrial CR for population genetic analyses of a holocephalan, providing a comparative analysis between two widely used mitochondrial markers (CR and CO1). In general, the CR yielded lower genetic diversity values than CO1, with higher discrepancies between diversity values observed among sampling sites. Moreover, CR haplotypes of *C. milii* cluster in the same clade as haplotypes of *C. callorynchus* in the phylogenetic tree (Figure 1a), pointing towards incomplete lineage sorting in the CR data. However, while the CR is widely recognised for its notably fast evolutionary rate (McMillan & Palumbi, 1997; Meyer, 1993) and polymorphic nature (Ghatak et al., 2016) in comparison to the rest of the mitogenome, previous studies on elasmobranchs suggest that it may evolve slower than other mitochondrial coding genes (e.g. Domingues et al., 2018; Dudgeon et al., 2009; Feutry et al., 2014) consistent with our findings for *C. callorynchus*. The surprisingly low variability in our sequence data of the CR in *Callorhinchus* makes it a less powerful marker for intraspecific and intrageneric analyses of genetic differentiation and may overlook key elements of population structure. Therefore, despite the ease of using mtDNA as a molecular tool, combining mtDNA with other approaches seems appropriate to enhance the power of molecular data for hypotheses testing. Future studies should aim to screen many nuclear markers, e.g. via RAD-sequencing or whole genome shotgun sequencing, to increase the power of detecting genetic differentiation in a potentially low diversity group of taxa. Additional tagging studies could help to assess whether genetic results match movement patterns of individuals, thereby aiding in the validation of genetic findings and providing a more comprehensive understanding of the ecological and evolutionary processes shaping the population structure.

Moreover, the results shown here may have suffered from incomplete geographic coverage and small sample sizes; to increase the statistical power of future studies, larger and more balanced sample sizes covering the whole geographic range of the species should be pursued to enhance the robustness and reliability of the analyses. Notably, Ecuador, Brazil and Uruguay, where sightings and catch rates are particularly low, have not been included in our sampling efforts thus far, and future studies should aim to incorporate these regions to ensure a more comprehensive representation of the species' geographic range and genetic diversity. In addition, ensuring a more equal representation by balancing numbers of the different geographical groups would be crucial for a more comprehensive understanding of the species' population structure.

Finally, future studies should address the observed spatial structure in *C. milii* between Australian and New Zealand specimens. This result raises questions on the possible existence of markedly diverged populations of *C. milii* or even the existence of an undescribed cryptic species since the intraspecific divergence is as pronounced as interspecies differences between the other two congeners (Figure 4).

5 | CONCLUSIONS

This work contributes important information on the patterns of population genetic diversity and divergence in a data-deficient group of cartilaginous fish, the Holocephali. Overall, our findings reveal low genetic diversity levels in the mitochondrial genome, both within and among *Callorhinchus* species (Tables 6 and 7), which limits the power to detect intraspecific genetic differentiation. However, analyses of the CO1 gene in *C. callorynchus* support a scenario of a recent population expansion in South America. Moreover, the observed uniformity in haplotype distribution and the lack of distinct genetic separation between regions suggest putative gene flow across the sampled geographical range. Gene flow is likely to be mediated by actively swimming adults that disperse along coastal regions but are limited in their ability to traverse deep oceanic waters. Our findings suggest coastal connectivity is crucial for maintaining gene flow in shallow-water holocephalans such as *C. callorynchus*, whereas shallow-water regions may act as significant barriers to dispersal and gene flow in deep-water holocephalans. Therefore, our results provide valuable information supporting the implementation of trans-national fisheries management measures for *C. callorynchus*, as well as establishing an important baseline for future research on dispersal and gene flow in other holocephalan taxa.

AUTHOR CONTRIBUTIONS

F.Co., C.A., B.F. and A.V. conceived the study and obtained funding. F. Co., C.A., B.F., A.B.G.-C., F.Cr. and C.S. performed sample collection. C.P.E. executed laboratory work and data analysis, and wrote the paper. A.V. contributed to data analysis and manuscript writing. F.Co., C.A., B.F., A.B.G.-C., F. Cr. and C.S. provided edits on the paper.

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