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A Chromosome-Scale Genome Assembly and Annotation of the Antarctic Pearlwort *Colobanthus quitensis* (Caryophyllaceae)

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Accepted: July 09, 2026

Abstract

Colobanthus quitensis (Caryophyllaceae) is one of only two vascular plants native to Antarctica and a model species for studying adaptation to extreme environments. We report a chromosome-scale reference genome generated from PacBio HiFi and Hi-C sequencing. The final assembly spans 887.1 Mb and resolves into 40 chromosome-scale scaffolds ($2n = 80$), with a scaffold N50 of 20.4 Mb and a maximum scaffold length of 35.1 Mb. Assembly completeness was high, with 99.0% of Embryophyta BUSCOs recovered, the majority as duplicated (95.7%), consistent with the species' putative tetraploid origin. The genome exhibits a GC content of 36.3%. We further assembled the complete chloroplast genome (151,314 bp; 113 genes) and a draft mitochondrial assembly comprising two partial contigs totaling ~289 kb. Repeat annotation identified 69.9% of the genome as repetitive, with long terminal repeat retrotransposons

as the dominant class (34.8%), primarily of the Ty1/Copia and Gypsy/DIRS1 superfamilies. A total of 40,762 protein-coding genes were predicted, of which 95% were functionally annotated. Combined with transcriptomic resources, this genome enables functional annotation and comparative studies. This is the first chromosome-scale assembly for an Antarctic angiosperm and a resource for investigating polyploidy, genome organization, and adaptive evolution in polar environments. The *C. quitensis* genome will also support ecological and applied studies, including the development of crops resilient to cold and other abiotic stresses.

Key words: chromosome-scale genome assembly, Caryophyllaceae, polyploidy, Antarctic angiosperm, *Colobanthus quitensis*.

Significance

Colobanthus quitensis is one of only two flowering plants native to Antarctica and a model for understanding how vascular plants establish and persist in extreme polar environments. We present the first chromosome-scale reference genome for this species, resolving its genome into 40 chromosome-level scaffolds ($2n = 80$). This assembly enables studies of polyploidy, genome organization, and chromatin architecture in a high-latitude angiosperm. With 99.0% BUSCO completeness and strong contiguity metrics, the genome supports comparative research within Caryophyllaceae and across polar taxa. It also enables investigation of the molecular basis of cold tolerance and stress adaptation. The *C. quitensis* genome also supports applied research on crop resilience and on the mechanisms of plant survival under extreme conditions.

Introduction

The flora of Antarctica has low species richness with only two native angiosperms, *Deschampsia antarctica* Desv. (Poaceae) and *Colobanthus quitensis* (Kunth.) Bartl. (Caryophyllaceae). Caryophyllaceae is a large angiosperm family, with ~3,000 species, primarily Holarctic in distribution but found worldwide (Harbaugh et al. 2010). *Colobanthus quitensis*, also known as Antarctic Pearlwort, exhibits a pan-American and Antarctic distribution, ranging from México to the Antarctic Peninsula (Moore 1970; Convey et al. 2011). Molecular work has revealed *C. quitensis* as a recent migrant to Antarctica, probably in the late Pleistocene (<1 Mya; Biersma et al. 2020), and most studies have centered on the ecophysiology and adaptive traits of this plant, for example, cold, drought, and UV tolerance.

Colobanthus quitensis exhibits sexual and asexual reproduction, though the former is the primary mode of establishment in natural populations (Zúñiga et al. 2009; Giełwanowska et al. 2011). Antarctic populations of *C. quitensis* form dense cushions and thick amphistomatic leaves that aid with water conservation and cold tolerance (Ramírez et al. 2024). Additionally, they exhibit seed heteromorphism, characterized by dark brown seeds with higher germination and salinity tolerance, thereby aiding establishment under stress (Ontivero et al. 2024). Physiologically, Antarctic populations of *C. quitensis* are better adapted to freezing and cold temperatures, are more efficient at photosynthesis, and possess antioxidant, photoprotective, and osmoprotective mechanisms (Gianoli et al. 2004; Cho et al. 2018; Min et al. 2025). It is believed that many of these traits are regulated by fungal endophytes, epigenetic modifications, and stress-induced gene expression (Cho et al. 2018; Barrera et al. 2020; Hereme et al. 2020; Acuña-Rodríguez et al. 2024; Egas et al. 2025). The molecular underpinnings of these traits are largely unknown, relying primarily on marker genes and reference-free de novo gene expression analyses.

Colobanthus quitensis is tetraploid (2C ~ 2.0 pg) with a known diploid population in Conguillío National Park, Chile (Cuba-Díaz et al. 2016; Pascual-Díaz et al. 2020) (2C ~ 1.0 pg). Its chloroplast genome has been sequenced and contains 112 genes (78 protein-coding, 30 tRNA, and four rRNA), with a genome structure highly congruent with that of *C. apetalus* (Kang et al. 2016). *Colobanthus quitensis* de novo transcriptome has been reported with more than 47,000 functionally annotated transcripts (Cho et al. 2018). *Colobanthus quitensis* populations have high genetic differentiation and low gene flow, where isolation by distance shapes genetic structure (Cuba-Díaz et al. 2017; Koc et al. 2018; Biersma et al. 2020).

We present the reference genome assembly of *C. quitensis* from the Maritime Antarctic region. This chromosome-level assembly is highly contiguous, with most chromosomes resolved from telomere to telomere, and includes annotated gene models. It will facilitate the study of trait variation within *C. quitensis* populations, help identify genes responsible for adaptation to extreme environments, and improve the precision of experiments assessing changes in gene expression under different conditions.

Results and Discussion

Genome Assembly

The assembly resolved into 40 chromosome-level scaffolds (93.8% of total length; Table 1; Fig. 1a), spanning 887.1 Mb (consistent with the flow-cytometry estimate of 1C ~1 pg) with a scaffold N50 of 20.4 Mb and a maximum scaffold of 35.1 Mb. Assessment against the Embryophyta OrthoDB v12 dataset ($n = 2{,}026$ genes) yielded 99.0% BUSCO completeness (C:99.0% [S:3.3%, D:95.7%], F:0.3%, M:0.6%); most recovered genes (95.7%) were classified as duplicated, a pattern diagnostic of the species' tetraploid origin ($2n = 80$). K-mer completeness reached 98.4%, and the gap density of 2,075 gaps/Gbp represents a 10-fold improvement over the prior unpublished scaffold-level assembly (KOPRI_Coqu_10Xv1; Table 1), which achieved a scaffold N50 of only 2.3 Mb and 22,587 gaps/Gbp. This assembly, POLARIX, meets Earth BioGenome Project quality tier 6.7.Q30 (Table 1). Telomere identification using Quartet revealed that 29 chromosomes possess both telomeres, ten chromosomes contain one telomere, and one chromosome lacks detectable telomeric sequences (Fig. S5).

Table 1 Assembly statistics and quality assessment of the *Colobanthus quitensis* genome

Genome assembly	Current study	Previous reference
Assembly name	POLARIX	KOPRI_Coqu_10Xv1 (PRJNA1100813)
Assembly level	Chromosome	Scaffolds
Assembly size (bp)	887,064,685	905,644,381
Number of contigs	2,678	48,598
Number of scaffolds	626	28,143
Longest scaffold	35,143,692	13,269,416
GC content (%)	36.3	32.64
EBP quality standard	6.7.Q30	5.6.Q59
Contigs NG50	801,095	49,700
Scaffolds NG50	21,037,107	2,310,145
Gaps/Gbp (1,811 gaps)	2,075.16	22,587.23
Consensus quality QV	29.75	58.65
K-mer completeness	98.4%	95.5%
Assembly: BUSCO (Embryophyta_odb12: 2,026 BUSCO genes)	C:99.0% [S: 3.3%, D:95.7%], F:0.3%, M:0.6%	C:98.1% [S:8.1%, D:89.9%], F:1.0%, M:0.9%
Genome masked	69.98%	…
LINEs(L1/CIN4)	5.58%	…
LTR (Gypsy/DIRS1 + Ty1/Copia)	34.84%	…
DNA transposon	3.55%	…
Unclassified repeats	26%	…
Number of proteins-coding genes	40,762	54,342
Genes with associated GO terms	24,789	…
Genes with PFAM annotation	36,082	…
Genes with description	38,724	…
Annotation: BUSCO (Embryophyta_odb12: 2,026 BUSCO genes)	C:93.3% [S:14.1%, D:79.3%], F:0.8%, M:5.9%	90.0% [S:36.8%, D:53.3%], F:5.9%, M:4.0%
Annotation: OMArk (Pentapetalae: OMA/All.Jul2023, 9,983 conserved HOGs)	C:87.17% [S:12.64%, D:74.53%], M:12.83%	C:93.27% [S:21.01%, D:72.26%], M:6.73%

Assembly metrics for the primary contigs generated with hifiasm (PacBio HiFi reads) and the chromosome-scale scaffolds obtained after Hi-C–based scaffolding with YaHS. Assembly length, contiguity metrics (N50, L50, N80, L80), and GC content are shown. BUSCO assessment was performed against the Embryophyta 12 dataset ($n = 2{,}026$ genes), indicating 99.0% completeness in the final assembly, with only 0.6% of genes missing. The scaffolded assembly spans ~887 Mb across 626 scaffolds (≥10 kb), with an N50 of 20.36 Mb, demonstrating near-complete, chromosome-scale resolution.

Repeat Annotation

Repeat annotation identified 69.9% of the *C. quitensis* genome as repetitive, with LTR retrotransposons constituting the dominant class at 34.8% of the total assembly (Table 1; Table S3). Ty1/Copia (21.6%) and Ty3/Gypsy (12.3%) dominated this class; LINEs and DNA transposons contributed 5.6% and 3.6%, respectively, with 26% unclassified by RepeatModeler (Table S3). The predominance of LTR retrotransposons in *C. quitensis* is consistent with patterns observed in other angiosperm genomes, in which, the Gypsy and Copia superfamilies, organized into phylogenetically conserved lineages across eudicots (Neumann et al. 2019), are the principal drivers of genome-size variation and chromosomal restructuring. Whole-genome duplication can trigger retrotransposon activation by relaxing epigenetic silencing, with LTR eruptions documented in autopolyploids following chromosome doubling (He et al. 2022). Furthermore, the extreme abiotic conditions characteristic of Maritime Antarctica, sustained subzero temperatures, intense UV irradiance, and repeated freeze–thaw cycles, are recognized activators of stress-responsive retrotransposons in plants (Papolu et al. 2022). Ongoing polar environmental pressures may therefore continue to shape the transposable element content of *C. quitensis* independently of its polyploid origin.

Gene Functional Annotation

Gene prediction yielded 40,762 protein-coding gene models, of which 95.0% received functional annotations from eggNOG-mapper, including GO terms for 24,789 genes, PFAM domain assignments for 36,082 genes, and functional descriptions for 38,724 genes (Table 1; Table S4). BUSCO assessment of predicted proteins

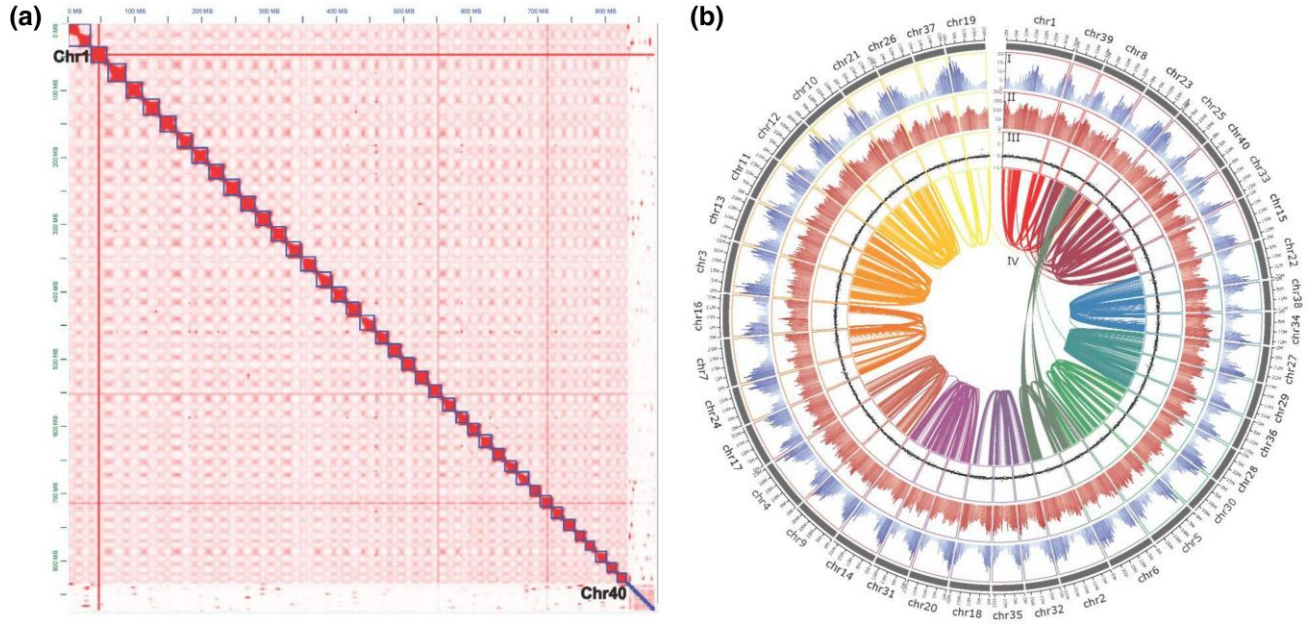

Fig. 1. Chromosome-scale Hi-C contact map of the *Colobanthus quitensis* genome assembly. a) Hi-C interaction heatmap of the *C. quitensis* genome assembled from PacBio HiFi long reads and scaffolded with Hi-C data. Interaction frequencies are shown on a red–white scale, with stronger contacts along the diagonal. The map reveals 40 discrete chromosome-scale scaffolds, sorted and named by length from chr1 to chr40, each visible as a distinct square along the diagonal, indicating successful reconstruction of the haploid chromosome set. Off-diagonal contact patterns reflect long-range chromatin interactions within and between chromosomes. The uniformity and sharpness of the contact map demonstrate the high contiguity and accuracy of the final assembly, spanning ~900 Mb. b) Chromosome-scale ideogram of the *C. quitensis* genome assembly. Chromosomes were ordered based on the number of intrachromosomal connections from MCScanX. I: gene density shown in blue, II: transposon density shown in red, III: GC skew, IV: intrachromosomal synteny relationships calculated from MCScanX; ribbons of the same color represent clusters of chromosomes that share the highest number of connections among themselves compared to the rest. Ideogram generated in 100 kbp windows.

against the Embryophyta OrthoDB v12 dataset yielded 93.3% completeness, with 79.3% of recovered genes classified as duplicated, a pattern that mirrors the assembly-level BUSCO signal and is consistent with the retention of homeologous gene copies across the two subgenomes of this tetraploid species. OMArk assessment of Pentapetalae-conserved Hierarchical Orthologous Groups (HOGs) corroborated these results, with 87.2% of conserved gene families represented in the annotation (Table 1). The gene count of ~40,700 is broadly comparable to other polyploid Caryophyllaceae: the chromosome-level genome of *Gypsophila paniculata*, which has undergone two rounds of WGD, was annotated with approximately 86,000 gene models (Li et al. 2022) and 54,342 models in the reference genome KOPRI_Coqu_10Xv1 (Table 1). Furthermore, while our annotation shows a higher duplication rate (79.3% in BUSCO) compared to the reference (53.3%), this difference reflects our stringent filtering pipeline, which reduced the initial 51,156 candidates (Table S4) to 40,762 high-confidence models to minimize false positives. This conservative approach effectively removed fragmented sequences, as evidenced by increases in mean gene length (from 3,361 to 3,897 bp) and mean CDS length (from 1,203 to 1,372 bp). This reduction did not compromise the biological completeness of the annotation. While the raw annotation showed higher BUSCO (C:97.7%) and OMArk (C:93.49%) scores, our filtered set maintained robust levels (BUSCO C:93.3%; OMArk C:87.17%). The high proportion of duplicated genes (79.3% in BUSCO) across both sets supports the validity of the retained homeologous copies in this polyploid species and yields a high-confidence dataset for downstream evolutionary analyses. This pattern is relevant to cold adaptation: ancient WGD events in Caryophyllaceae have been linked to gene family expansions enriched for ubiquitination and stress-response functions, with duplicated copies in cushion plant lineages, including *Colobanthus*, proposed as contributors to the colonization of cold climatic niches (Feng et al. 2024).

Genome Architecture

Interchromosomal synteny analysis revealed that most chromosomes maintain connections with at least two others, reflecting retention of ancestral genomic architecture consistent with one or more WGD events in the lineage (Table S5; Fig. 1b). Seven chromosomes displayed

connections with more than three partners (Table S5), suggesting complex reorganization following polyploidization. Syntenic blocks were predominantly collinear, indicating that large-scale chromosomal rearrangements have been limited since the most recent WGD, with gene order broadly preserved across subgenomes. These findings are consistent with the documented paleopolyploid history of Caryophyllaceae, in which at least 15 putative ancient WGD events have been inferred from transcriptomic data, including events predating the family-level divergence (Feng et al. 2024), and multiple WGDs have been associated with shifts into colder climatic occupancies across the Caryophyllales (Yang et al. 2015; Smith et al. 2018). Reads not assigned to *C. quitensis* yielded 113 high-quality metagenome-assembled genomes (MAGs) spanning 13 bacterial phyla, serving as a companion resource for studying the plant-associated microbiome (Table S8; Figs. S3 and S4).

Chloroplast and Mitochondrial Genomes

Assembly of organellar genomes from HiFi reads yielded one complete plastid genome and two partial plastid contigs, as well as two partial mitochondrial contigs. The complete plastid genome spans 151,314 bp and encodes 113 genes (Fig. S1, Table S6), closely matching the size and gene content of other Caryophyllaceae plastomes, which range from approximately 150,224 bp in *Silene capitata* to over 152,000 bp in *Lychnis wilfordii* (Kang et al. 2017). Regarding the additional partial plastid and mitochondrial contigs, their significantly lower read coverage (~50×) compared to the complete plastid genome (~1,000×) indicates that these sequences might be assembly artifacts or exogenous contaminants rather than genuine structural variants of the *C. quitensis* genome. The mitochondrial assembly comprised two partial contigs totaling ~289 kb and encoding six protein-coding genes each (Fig. S2, Table S7). The fragmented mitochondrial assembly is consistent with the highly dynamic and recombination-prone mitochondrial genome architecture characteristic of angiosperms, and particularly of Caryophyllaceae, which exhibit elevated rates of mitochondrial gene loss and genome restructuring compared to most other plant families (Sloan et al. 2010). Consequently, these partial mitochondrial contigs should be interpreted with caution, as their reduced coverage suggests that they may represent nontarget sequences captured during assembly.

Materials and Methods

Sample Collection and DNA Extraction

Plant material was collected in King George Island, South Shetland Archipelago, Antarctica (Puchalski Point; Arctowski Polish Antarctic Station; −62.162, −58.471). DNA extraction was carried out from a single individual of *C. quitensis*, collected in a UV-radiated sterile plastic bag and frozen until processing. Sample collection and export were authorized by the Instituto Antártico Chileno (INACH), in accordance with the Protocol on Environmental Protection to the Antarctic Treaty. DNA extraction was conducted using the QIAGEN Genomic DNA Purification procedure.

PacBio Library and Sequencing

DNA samples were quantified on a Qubit 4.0 (Thermo Fisher) and assessed on a Femto Pulse (Agilent) prior to library preparation. QC-passing DNA was sheared on a MegaRuptor 3 (Diagenode) to 15 to 18 kb and then prepared with the SMRTbell Prep Kit 3.0 (Pacific Biosciences). Adaptor-ligated libraries were size-selected with AMPure PB beads or on a BluePippin (Sage Science) and sequenced on a Revio SMRT cell (25 M) for 24 h.

Dovetail Omni-C Library Preparation and Sequencing

Dovetail Omni-C libraries were prepared following the manufacturer's protocol: in-nucleus formaldehyde crosslinking, DNase I digestion, ligation of a biotinylated bridge adapter, proximity ligation, crosslink reversal, and DNA purification. Sequencing libraries were prepared with NEBNext Ultra enzymes and Illumina-compatible adapters, enriched after streptavidin pull-down of biotin-containing fragments, and sequenced on an Illumina HiSeqX at 30× coverage.

Read Filtering and Decontamination

Omni-C Hi-C reads were processed using Trim Galore! v0.6.10 (Krueger 2019) (https://github.com/FelixKrueger/TrimGalore) with parameters "-q 28 –length 100 --paired" to remove adapters and low-quality sequences. To isolate *C. quitensis* reads from potential contaminants, a decontamination blacklist was generated. Taxonomic identification of contaminants was performed using the sendsketch.sh script from BBMap v39.45, which identified eight bacterial and arthropod contaminant genomes (Table S2). Reference genomes were retrieved from NCBI and concatenated with the existing *C. quitensis* reference genome (GCA_041430805.1) to create a combined reference file. PacBio HiFi reads were then aligned against this combined reference using minimap2 v2.3r1287 (Li 2018) with options "-p 0.7 -N 50 --cs." Reads whose primary alignment, highest identity, and CIGAR score corresponded to *C. quitensis* (GCA_041430805.1) scaffolds were selected from the resulting SAM file.

These selected reads were further validated using Kraken2 (Wood et al. 2019) v2.17.0 against the PlusPFP database (updated October 2025) with the option

"--minimum-hit-groups 5." Reads classified within the Viridiplantae taxonomic group (taxid: 33090) were extracted using extract_kraken_reads.py from KrakenTools (Lu et al. 2022) v1.2.1 with the parameters "-t 33090 --include-children." Viridiplantae and unclassified reads formed the final *C. quitensis* dataset; remaining reads were assigned to the plant-associated microbiome.

Genome Assembly and Scaffolding

Filtered Hi-C and HiFi reads were assembled using Mabs (Schelkunov 2023) v2.28 with the parameters "--local_busco_dataset eudicots_odb10.2024-01-08.tar.gz --number_of_busco_orthogroups all --ploidy 2 --genome_size 1G." Reads from the filtered Omni-C library were mapped to the assembled primary contigs using bwa (Li 2013) v0.7.19-r123 and subsequently filtered using pairtools v0.3.0, following the Omni-C protocol published online. The resulting data were utilized in YAHS (Zhou et al. 2023) v1.1.2 for scaffolding. Finally, the scaffolds were manually corrected using Juicer, JuicerTools, and Juicebox. (Durand et al. 2016). Additionally, telomeres were identified using Quartet v.1.2.5r3 with the TeloExplorer function (Lin et al. 2023).

Genome Annotation

Transposable and repetitive elements were annotated using reasonaTE (TransposonUltimate pipeline; Riehl et al. 2022). Repetitive elements were classified using RepeatClassifier from RepeatModeler (Flynn et al. 2020) v2.0.7 and used to mask the genome with RepeatMasker (Tempel 2012) v4.2.1 ("-xsmall -nolow -no_is -norna -qq -gff -e rmblast"). The masked genome was annotated using BRAKER v3.0.8 supported by 29 mRNA-seq datasets from various *C. quitensis* experiments (Table S9), 3,185 Viridiplantae proteins from Swiss-Prot, and annotated proteins from 23 Caryophyllales species from NCBI (Table S10). The BRAKER (Gabriel et al. 2024) annotation was filtered using AGAT v1.5.0 to remove mono-exonic genes lacking functional or PFAM annotations, genes with mRNA lengths <150 bp, and secondary isoforms. Prior to BUSCO assessment of the predicted proteome, a single representative protein per locus was retained by keeping only the longest isoform using agat_sp_keep_longest_isoform.pl (AGAT v1.5.0). Functional annotation used eggNOG (Cantalapiedra et al. 2021)-mapper v2.1.12 against EggNOG 5.0 (Table S11). Genome assembly completeness was assessed with Merqury v1.3 and BUSCO v6.0.0 (Embryophyta OrthoDB v12), while the completeness of the filtered protein-coding annotation was evaluated using BUSCO v6.0.0 (Embryophyta OrthoDB v12) and OMARk (Nevers et al. 2025) v0.3.0. Organellar genomes were assembled using PMAT (Bi et al. 2024) v1.5.3 and annotated with GeSeq (Tillich et al. 2017) v2.03, using *Silene latifolia* (NC_014487) and *C. quitensis* (NC_028080) as mitochondrial and plastid references, respectively.

Synteny Analysis

An all-against-all BLASTp (Camacho et al. 2009) v2.17.0 alignment ("-evalue 1e-10 -outfmt 6 -num_alignments 5") of annotated proteins was analyzed with MCScanX (Wang et al. 2012) v1.0.0 ("-b 1") to identify intrachromosomal syntenic blocks.

Metagenomic Assembly and Binning

HiFi reads that were not classified as belonging to the *C. quitensis* genome were assembled using hifiasm-meta v0.3.1. (Feng et al. 2022). The resulting contigs were processed with the HiFi-MAG-Pipeline (Portik et al. 2024) (from pb-metagenomics-tools) to generate high-quality MAGs. Only MAGs exhibiting >70% completeness, <10% contamination, and a maximum of 20 contigs were retained for further analysis.

Supplementary Material

Supplementary material is available at Genome Biology and Evolution online.

Funding

This study was funded by ANID Anillo ACT192057 and ANID Anillo ATE250008.

Data Availability

The raw sequencing data, assembled genome, and organelle sequences have been deposited in the NCBI Sequence Read Archive (SRA) under BioProject accession PRJNA1457453. The genome assembly is available at GenBank accession JBXXPJ000000000. Annotated gene models, repeat libraries, and organelle assemblies are accessible via Zenodo (https://doi.org/10.5281/zenodo.19741749). Supporting transcriptome datasets are available under BioProject PRJNA388703.

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Associate editor: Vincent Castric