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Genome of elegance coral *Catalaphyllia jardinei* (Euphylliidae)

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Coral reefs are under stress throughout the world. To better understand the molecular mechanisms underlying coral biology and their genomic evolution, here we sequenced the genome and transcriptomes of elegance coral *Catalaphyllia jardinei* (Euphylliidae). This monotypic genus stony coral is widespread but rare, being found across the Indo-West Pacific, from the northern Indian Ocean, Australia, Philippines, to the South China Sea. Due to its popularity among aquarium hobbyists, it is an overexploited species collected in large quantities from the wild for aquarium trade. The assembled genome is ~ 651.3 Mb in total length and of high physical contiguity with a scaffold N50 size of 28.9 Mb. The gene copy numbers of abiotic stress regulator (heat shock protein family genes) and neuropeptides (GLWamide, GRFamide, PRGamide and HIRamide) are similar to other sequenced anthozoans, and we have also identified the first set of sesquiterpenoid biosynthetic pathway genes in coral. Sequencing of small RNAs allows us to identify 35 microRNAs in *C. jardinei* and update the number of conserved microRNAs in cnidarians. This study established a foundation for further investigation into the roles of sesquiterpenoids and microRNAs in development of coral and understand their responses to climate change. Due to the easiness to culture *C. jardinei* in reef tanks and the established resources in this study, we propose this species be adopted as a new laboratory model in environmental and ecological experiments aiming to understand coral biology and responses to environmental stressors.

KEYWORDS
coral, genome, *Catalaphyllia*, microRNA, sesquiterpenoid

Introduction

The elegance coral *Catalaphyllia jardinei* was first described as *Pectinia jardinei* found in the shallow water on the reefs at the Warrior Reef (latitude 9° 45' S), Thursday Island (latitude 10° 35' S), and Albany Pass (latitude 10° 45' S) (Saville-Kent, 1893). Based on the morphological and color identification, the species was later determined to be a new genus under Euphylliidae (Yonge and Nicholls, 1931; Catala, 1964). Given that its skeleton is homomorphic to that of *Euphyllia*, and in recognition of Catala's contribution to tropical marine fauna, *Pectinia* was changed to *Catalaphyllia* (Wells, 1971). Today, the genus *Catalaphyllia* is considered monospecific with *C. jardinei* as its only member (Fujii et al., 2020).

Coral reef ecosystems are important in providing a favorable habitat for its associated organisms (Bellwood et al., 2004). Throughout the world coral reefs are under stresses that include habitat destruction (Yeung et al., 2021), overexploitation (Jackson et al., 2001; Pandolfi et al., 2003), pollution (Williams et al., 2002; McCulloch et al., 2003), diseases (Harvell et al., 2002), predation (Qiu et al., 2014), and climate change (Wilkinson, 2002; Hughes et al., 2003; Gardener et al., 2003; Schlager, 1981; Dullo, 2005; Xie et al., 2020). The reef-building coral *C. jardinei* has a broad geographical distribution and can be found both in the Indian Ocean and Pacific Ocean (Veron and Stafford-Smith, 2000), including Australia, Indonesia, Japan, Maldives, Malaysia, Papua New Guinea, Philippines, Seychelles and Vietnam (UNEP, 2005). Nevertheless, given its small population size and overexploitation, it is considered by the IUCN Red List as having a "Vulnerable" status (IUCN, 2020).

Since the late 1980s, the popularity of keeping live corals at home has increased rapidly (Delbeek, 2001). Large-scale culture of *C. jardinei* is a current business in Indonesia and corals are exported globally (Akbar and Asadi, 2021). In addition to its appearance as described in its common name, *C. jardinei* is a popular coral species due to its easiness to culture *ex situ*. Naturally found in deep flats (greater than 35 meters) with sandy/silty bottoms, lagoons, and nearshore mudflats (Richard, 2005), *C. jardinei* can tolerate and survive in fluctuating or less favorable environmental conditions (Richard, 2005; http://www.edgeofexistence.org/species/elegance-coral/), making it a potential new model in the laboratory to study coral biology and their responses to environmental stressors.

To facilitate the use of *C. jardinei* to study the molecular mechanisms underlying coral biology, this study sequenced and provided the first genome and transcriptomic resources of this coral species.

Materials and methods

Sample collection and genome sequencing

Adult *Catalaphyllia jardinei* (Euphylliidae) (Figure 1A) were purchased from mainland China (original source from Indonesia) and Hong Kong suppliers (original source from Australia), and were cultured in an aquarium tank with circulating artificial seawater (salinity: 30-35 ppt) at around 23 ± 1°C and other equipment to simulate pristine waters at The Chinese University of Hong Kong. Corals were allowed to acclimatize under the laboratory conditions for 15 days prior to be used for DNA and RNA extraction.

Sample for genome sequencing originated from tentacles from a single individual (Figure 1A). Genomic DNA (gDNA) was extracted using the QIAamp DNA minikit (Qiagen, Hilden, Germany) following the manufacturer's instructions. Extracted gDNA was subjected to quality control using a Nanodrop spectrophotometer (Thermo Scientific) and gel electrophoresis. Qualified samples were sent to Novogene and Dovetail Genomics for library preparation and sequencing. The resulting library was sequenced on an Illumina HiSeq X platform to produce 2×150 paired-end sequences. The length-weighted mean molecule length was 17.9 Kb, and details of the sequencing data were highlighted in Supplementary Information S1.

Dovetail Omni-C library preparation and sequencing

For each Dovetail Omni-C library, chromatin was fixed with formaldehyde and extracted. Fixed chromatin was digested with DNase I, and chromatin ends were repaired and ligated to a biotinylated bridge adapter followed by proximity ligation of adapter containing ends. After proximity ligation, crosslinks were reversed and the DNA was purified. Purified DNA was treated to remove biotin that was not internal to ligated fragments. Sequencing libraries were generated using NEBNext Ultra enzymes and Illumina-compatible adapters. Biotin-containing fragments were isolated using streptavidin beads before PCR enrichment of each library. The library was

A

B

Common name	Elegance coral
Species name	*Catalaphyllia jardinei*
Accession number	JAEMPF000000000
Number of scaffolds	38,168
Assembly size	651.363 Mb
Gap content (N)	5.56%
GC content	38.99%
Contig N/L50	8,242 / 20.569 Kb
Scaffold N/L50	9 / 28.948 MB
Number of genes	44,407
Complete BUSCOs	88.05%

C

Metazoa odb10 (n=954)	assembled genome sequence	protein-coding genes
Complete BUSCOs (C)	88.05%	82.18%
Complete and single-copy BUSCOs (S)	84.28%	77.78%
Complete and duplicated BUSCOs (D)	3.77%	4.40%
Fragmented BUSCOs (F)	6.60%	9.01%
Missing BUSCOs (M)	5.35%	8.81%

FIGURE 1
(A) Picture of elegance coral *Catalaphyllia jardinei*; **(B)** Genome assembly statistics of C *jardinei*; **(C)** BUSCO scores.

sequenced on an Illumina HiSeqX platform to produce 196.9 millions of 150 bp reads, and the raw data were listed in Supplementary Information S1.

Transcriptome sequencing

Total RNA, including messenger RNA and small RNA, from tentacles from single individual was isolated using mirVana™ miRNA Isolation Kit (Ambion) according to the manufacturer's instructions, and subjected to quality control using a Nanodrop spectrophotometer (Thermo Scientific), gel electrophoresis, and Agilent 2100 Bioanalyzer (Agilent RNA 6000 Nano Kit). Qualified samples underwent library construction and 150 bp paired-end (PE) sequencing at Novogene; polyA-selected RNA-Sequencing libraries were prepared using TruSeq RNA Sample Prep Kit v2. Insert sizes and library concentrations of final libraries were determined using an Agilent 2100 bioanalyzer instrument (Agilent DNA 1000 Reagents) and real-time quantitative PCR (TaqMan Probe) respectively. Small RNA was submitted to BGI Hong Kong for HiSeq Small RNA library construction and 50 bp single-end (SE) sequencing. Details of the sequencing data can be found in Supplementary Information S1.

Genome assembly

K-mers of the HiseqXten 150PE (Chromium WGS) were counted using jellyfish version 2.2.5 (Marçais and Kingsford, 2011) with k-mers = 21, and estimation of genome size, repeat content, and heterozygosity were analyzed based on a k-mer-based statistical approach in the GenomeScope2 webtool (Ranallo-Benavidez et al., 2020, Supplementary Information S3). Kraken2 (Wood et al., 2019) (k2_standard_20210517 (kraken2 standard database) from https://benlangmead.github.io/aws-indexes/k2, which contains archaea, bacteria, viral, plasmid, human1, UniVec_Core) was used to mark and remove the contamination from the gDNA and transcriptome reads, 3.75% and 0.29% of contaminated reads were removed respectively. Processed Chromium WGS reads were used to construct a *de novo* assembly using Supernova (v 2.1.1) with default parameters (raw coverage = 78.86x), which generates phased, whole-genome *de novo* assemblies from a Chromium-prepared library (Weisenfeld et al., 2017) (https://support.10xgenomics.com/de-novo-assembly/software/pipelines/latest/using/running). The supernova output pseudohap assembly were used to generate the dedupe assembly by dedupe.sh (version 19Feb, 2020) of BBMap (Bushnell B. - sourceforge.net/projects/bbmap/), and then scaffolded using Dovetail Omni-C library reads by HiRise, a software pipeline designed specifically for using proximity ligation data to scaffold genome assemblies (Putnam et al., 2016). Dovetail Omni-C library sequences were aligned to the draft input assembly using bwa (https://github.com/lh3/bwa). The separations of Dovetail Omni-C read pairs mapped within draft scaffolds were analyzed by HiRise to produce a likelihood model for genomic distance between read pairs, and the model was used to identify and break putative misjoins, to score prospective joins,

and make joins above a threshold. To further check for potential symbiotic contamination, 11 symbiodinium genomes were downloaded from NCBI (Supplementary Information S2) and BLASTN (Altschul et al., 1990) were carried out on the assembled genomes (e-value 1e-3). Scaffolds with alignment lengths >= 500 bp were further searched on nt database with BLASTN, and no symbiotic contamination was found in the final assembly genome.

Gene model prediction

Gene models were predicted as described in the jellyfish genomes (Nong et al., 2020). Briefly, the gene models were trained and predicted using funannotate (v1.8.9, https://github.com/nextgenusfs/funannotate) (Palmer and Stajich, 2020) with the following parameters: "–protein_evidence uniprot_sprot.fasta –genemark_mode ET –busco_seed_species fly –optimize_augustus –busco_db arthropoda –organism other –max_intronlen 350000". In the "funannotate predict" step, GeneMark-ES v4.32 (Lomsadze et al., 2005) was used for ab initio gene prediction and Augustus (Keller et al., 2011) was trained using BUSCO. The gene models from the prediction sources "Augustus", high-quality Augustus predictions (HiQ) with exon evidence, "pasa" (Haas et al., 2008)_, "snap" (Korf, 2004), "GlimmerHMM" (Majoros et al., 2004), and "GeneMark" were passed to Evidence Modeler (EVM Weights: {'GeneMark': 1, 'HiQ': 2, 'pasa': 6, 'proteins': 1, 'Augustus': 1, 'GlimmerHMM': 1, 'snap': 1, 'transcripts': 1}) to generate the final annotation files. Finally, followed by PASA to update the EVM consensus predictions, and add UTR annotations and models for alternatively spliced isoforms. Protein-coding genes were searched with BLASTP against the nr and SwissProt databases by diamond (v0.9.24) (Buchfink et al., 2015) with parameters "–more-sensitive –evalue 1e-3", and mapped by HISAT2 (version 2.1.0) (Kim et al., 2019) with transcriptome reads. Gene models with no similarity to any known proteins and no mRNA support were removed from the final version. The gene models were screened by CGAT (Sims et al., 2014) and only the longest genes were retained.

Synteny analysis

Orthologues and orthogroups in *C. jardinei* and other 33 cnidarians proteomes were identified and inferred using OrthoFinder v2.5.2 (Emms and Kelly, 2019) with "-M msa" activated and default values to other parameters. To symbolise the gene families, the longest protein of each gene was taken as the representative in orthologues analysis. The species tree was constructed with fasttree using STAG algorithm and *Hydra vulgaris* was identified as the best outgroup species to construct the rooted tree using STRIDE method by OrthoFinder (Emms and Kelly, 2017; Emms and Kelly, 2018). Tree supporting value were the proportion of species tree derived from gene tree supporting each bipartition. The species tree was then converted into divergence tree using r8s (Sanderson, 2003). The tree structure and annotations were visualised using R package 'ggtree' (Wickham, 2016; Yu et al., 2017) in R v4.1.2 (R Core Team, 2022). Orthologues anchored by mutual best Diamond blastp hits (e-value cut-off 0.001) between *C. jardinei* and other 33 cnidarians as mentioned above were used in macrosynteny analyses. Oxford synteny plot were generated following previously described methods (So et al., 2022; Yichun, 2022). Detailed analytical scripts and materials were distributed at https://github.com/xieyichun50/coral_genome_Catalaphyllia_jardinei.

microRNA annotation

Adaptor sequences were trimmed from small RNA sequencing reads and Phred quality score less than 20 were removed. Processed reads of length within 18 bp and 27 bp were then mapped to the genomes using mapper.pl module of the mirDeep2 package (Friedländer et al., 2012). To identify known miRNA, the predicted coral microRNA hairpins were compared against metazoan microRNA precursor sequences from miRBase (Kozomara and Griffiths-Jones, 2014) using BLASTN (e-value <1e-2). For miRNAs with no significant sequence similarity to any of the miRNAs in miRBase were then checked manually. Novel microRNAs were defined when they fulfilled the criteria of microRNAs (Fromm et al., 2020). The expression levels of different arms of a miRNA were calculated based on the number of sequencing reads mapped to the respective arm region in the predicted miRNA hairpin by bowtie. In addition to the above, the precursor sequences of microRNAs from other corals in previous studies (Liew et al., 2014; Praher et al., 2021) were also used to carry out BLASTN searches for identification of any missed microRNA annotations.

Annotation of sesquiterpenoid pathway and neuropeptide genes

17 gene sequences involved in the sesquiterpenoid biosynthetic pathway retrieved from *Nematostella vectensis* and 4 gene sequences of neuropeptide (GLWamide, GRFamide, PRGamide and HIRamide) sequences from *Hydra vulgaris* were used for searching against the gene models and genome using BLASTP and TBLASTN, respectively. Putatively identified orthologues with a threshold of E-value equals to 10E-3 were tested by reciprocal searches in the NCBI nr database using BLASTP. For neuropeptide preprohormones, amino acid sequences were translated manually and aligned with MEGA 7.0 (Kumar et al., 2016), while the signaling sequences were analysed with SignalP 3.0 (Dyrløv Bendtsen et al., 2004). The cleavage sites were predicted by software ProP 1.0 (Duckert et al.,

2004) and checked manually accordingly to the criteria suggested by Veenstra (2000). The potential mature neuropeptides were aligned using MEGA 7.0 (Kumar et al., 2016).

Results and discussion

High quality genome

Here, we presented a high-quality chromosome-level genome assembly of *C. jardinei* (2n = 28) (Heyward, 1985; Kenyon, 1997; Flot et al., 2006), the assembled genome size was 651 Mb, which is compatible with the kmer 21 estimate of a genome size of 685.5 Mb (Figure 1, Supplementary Information S3). 69.64% of the genomic sequences were contained on 14 pseudomolecules (Supplementary Information S1.3). The BUSCO score for complete genes is 88.05% (BUSCO version 5.1.3, metazoa_odb10), with complete and single-copy BUSCOs (S) being 84.28%, complete and duplicated BUSCOs (D) being 3.77%, fragmented BUSCOs (F) being 6.60% and Missing BUSCOs (M) being 5.35% (Figure 1C). Its scaffold N50 size (28.9Mb) represents the highest physical contiguity among the published coral genomes (Table 1). Using the transcriptomes, we predicted a total of 44,407 gene models including 37,003 protein coding genes and 7,404 tRNA genes, in the *C. jardinei* genome, which is within the range of 21,369 to 39,160 for other published coral genomes (Table 1).

Synteny analysis

To clarify the syntenic relationship and gene linkage blocks between *C. jardinei* and other cnidarians, we generated the Oxford synteny plots of species pairs using the orthologues anchored by mutual best BLAST hit (e-value 1e-3) (Figure 2, Supplementary Information S4). Global gene orthogroup inference identified 26,260 orthogroups. The phylogenetic tree was constructed using 1,029 single-copy orthogroups presented in 31 out of 34 species, where single-copy indicated only one gene was assigned to specific orthogroup for each species. The chromosomal organisations are conserved in most soft corals, and each pseudo-chromosome in *C. jardinei* was associated with a different chromosome in another soft coral *Acropora millipora*. Further comparisons of *C. jardinei* against the more distant species, such as the sea anemone (*Nematostella vectensis*) and the true jellyfish (*Rhopilema esculentum*), displayed the one-to-one relationship on most synteny blocks, and a few one-to-many blocks (Supplementary Figures 1–3). Evidence on breakage, fusion or large-scale duplication was rarely found in these investigated cnidarians, suggesting that the genomes of these cnidarians have not undergone massive evolutionary changes.

Homeobox genes

Homeobox genes are important developmental genes in animals and have been used as markers to understand genomic changes in animal evolution (e.g. Nong et al., 2020, Nong et al., 2021, Nong et al., 2022; Li et al., 2020; So et al., 2022; Qu et al., 2020; Shum et al., 2022). A total of 93 ANTP-class homeobox genes have been identified in the *C. jardinei* genome, including clusters of Hox-like and NK-like genes, and a ParaHox gene cluster (Figure 3; Supplementary Information S5). The data here further strengthens the idea that if distinct Hox and NK genes clusters are associated with ectodermal and mesodermal patterning, it could be a bilaterian-lineage specific event (Simakov et al., 2013; Nong et al., 2020), and the three gene ParaHox gene cluster could only be retained in the medusozoans than anthozoans among the extant cnidarians.

Heat shock protein family genes

Corals experiences abiotic stresses such as temperature, salinity, and oxygen concentration, and heat shock proteins (HSP) can assist and reconstruct the structure of damaged proteins under stresses (Collier and Benesch, 2020; Matambo et al., 2004; Whitley et al., 1999; Supplementary Figure 4). In general, HSP can be divided into six subfamilies, including HSPE (GroEL, cpn10), small heat shock proteins, HSP40, HSP70, HSP90, and HSP110, and HSP70 has been shown as chaperone proteins participated in response to heat stress in reef-building scleractinian corals (Franzellitti et al., 2018), (Haslbeck et al., 2016). In *C. jardinei*, we identified members of six HSP subfamilies, and their numbers were similar to those identified in the stony coral *Acropora millepora* chromosomal-level genome (Supplementary Figure 5, Supplementary Information S6). The identified heat shock protein gene families will be useful for future investigation of their roles in *C. jardinei* under different environmental conditions.

Neuropeptide genes

Neuropeptides play essential roles as endocrine factors and neurotransmitters, and are involved in the cellular differentiation and development of cnidarians (Takahashi, 2020). Here, Scleractinia conserved neuropeptides GLWamide, GRFamide, PRGamide, HIRamide, RWamide, RPamide and pQITRFamide were identified in *C. jardinei* (Figures 4A, B, Supplementary Information S7). A total of 6 mature peptides were identified from the preprohormone sequences of GLWamide in *C. jardinei*, and sequence alignment showed a conserved C-terminal GXW motif contained in these sequences (Figures 4C). Two of the GLWamides had "-GIW" replacement and such mutations were

TABLE 1 Statistics of published coral genomes.

Species	Assembled genome size (bp)	N50	Number of Proteins	Sum of Amino Acids	Sum of Exons (bp)	Sum of Introns (bp)	Sum of gene region (bp)	References
Acropora acuminata	397,781,777	1,004,888	22,306	11,844,585	66,338,114	234,162,220	234,529,491	Shinzato et al., 2021
Acropora awi	430,482,902	1,088,407	22,653	11,755,030	65,880,915	249,482,354	241,506,016	Shinzato et al., 2021
Acropora cytherea	430,309,169	1,083,946	23,363	12,256,657	67,552,835	247,246,641	245,571,636	Shinzato et al., 2021
Acropora digitifera	415,842,489	1,856,312	22,326	10,509,359	62,321,781	215,573,311	233,203,300	Shinzato et al., 2021
Acropora echinata	409,669,900	1,812,701	21,943	11,333,551	65,943,777	246,278,370	236,046,259	Shinzato et al., 2021
Acropora florida	442,860,187	751,376	23,857	12,087,368	64,685,340	240,937,980	244,285,300	Shinzato et al., 2021
Acropora gemmifera	405,217,165	1,134,581	22,247	11,698,576	65,230,873	237,013,391	233,312,317	Shinzato et al., 2021
Acropora hyacinthus	452,727,592	1,562,592	23,147	12,513,951	69,389,302	254,370,978	250,891,995	Shinzato et al., 2021
Acropora intermedia	416,883,045	577,312	23,343	11,998,377	64,476,112	232,793,965	237,988,598	Shinzato et al., 2021
Acropora microphthalma	387,940,075	1,050,196	22,618	11,614,443	65,390,591	234,712,549	235,057,382	Shinzato et al., 2021
Acropora millepora	475,381,253	19,840,543	28,188	12,836,117	49,237,008	158,255,732	207,492,740	Fuller et al., 2020
Acropora muricata	420,750,014	574,627	23,646	12,079,124		237,931,003	242,349,835	Shinzato et al., 2021
Acropora nasuta	419,444,168	1,045,289	23,319	12,115,884	67,461,458	248,696,816	245,388,094	Shinzato et al., 2021
Acropora selago	393,159,869	657,172	23,115	11,696,416	65,591,025	233,912,084	234,017,974	Shinzato et al., 2021
Acropora tenuis	406,871,833	1,160,220	23,118	11,917,129	68,612,749	192,068,808	237,497,938	Shinzato et al., 2021
Acropora yongei	443,890,770	3,019,482	23,500	12,103,783	67,790,062	248,352,452	249,216,954	Shinzato et al., 2021
Astreopora myriophthalma	381,883,822	1,590,751	28,711	13,287,976	42,124,462	116,058,587	155,181,959	Shinzato et al., 2021
Catalaphyllia jardinei	**651,363,123**	**28,947,999**	**37,003**	**13,815,766**	**59,489,494**	**221,415,763**	**282,642,405**	**This study**
Dendronephthya gigantea	286,150,628	1,445,523	28,741	17,717,918	74,944,700	345,593,618	147,908,393	Jeon et al., 2019
Fungia sp.	606,319,501	323,149	38,209	15,470,321	56,333,027	194,127,360	250,460,387	Ying et al., 2018
Galaxea fascicularis	334,165,880	87,933	22,418	9,704,883	42,730,289	132,589,881	175,320,170	Ying et al., 2018
Goniastrea aspera	764,857,003	518,949	35,901	15,491,306	51,803,637	238,014,146	289,817,783	Ying et al., 2018
Montipora cactus	652,728,006	898,511	21,982	13,478,399	50,412,387	311,983,610	337,284,991	Shinzato et al., 2021
Montipora capitata	614,509,607	185,537	36,691	13,448,127	40,454,043	222,885,069	148,531,395	Helmkampf et al., 2019
Montipora efflorescens	643,312,941	1,132,316	21,369	13,130,866	49,077,197	308,033,328	331,889,023	Shinzato et al., 2021
Orbicella faveolata	485,548,939	1,162,446	32,587	16,554,995	95,196,829	556,036,559	266,375,485	Prada et al., 2016
Pachyseris speciosa	984,430,632	766,649	39,160	17,175,307	72,350,345	264,758,179	337,108,524	Bongaerts et al., 2021

(Continued)

TABLE 1 Continued

Species	Assembled genome size (bp)	N50	Number of Proteins	Sum of Amino Acids	Sum of Exons (bp)	Sum of Introns (bp)	Sum of gene region (bp)	References
Pocillopora damicornis	234,350,878	326,133	25,183	13,735,379	63,957,019	274,910,693	151,175,419	Cunning et al., 2018
Pocillopora verrucosa	380,505,698	333,696	27,439	17,115,890	66,501,999	140,069,492	208,011,644	Buitrago-López et al., 2020
Porites lutea	552,020,673	660,708	31,126	14,351,123	56,249,572	199,362,641	255,612,213	Robbins et al., 2019
Stylophora pistillata	400,120,318	457,453	33,252	18,275,238	86,199,075	513,138,303	223,994,894	Voolstra et al., 2017

Underline, the statistics of *C. jardinei* genome

also identified in hard coral *Euphyllia ancora* (Shikina et al., 2020) (Figure 4C, Supplementary Information S8). For GRFamide preprohormones, 16 mature peptides were predicted. Among the identified PRGamide genes in *C. jardinei*, a single preprohormone gene was found to yield 46 different mature peptides (Figure 4B, Supplementary Information S8). For HIRamides, it was found that there was no glutamine residue identified from the predicted HIRamides in *C. jardinei*, where this phenomenon is also observable in other cnidarian HIRamides (Koch and Grimmelikhuijzen, 2019; Supplementary Information S8). For RWamide and RPamide, only 1 and 2 mature peptide(s) are yielding from the precursor respectively. Meanwhile, the precursor of pQITRFamide could be identified from the genome, but there was no expression shown in the sequenced transcriptomes, thus the number and form of mature peptides could not be identified (Figures 4B, C). The identified neuropeptides will be useful for future investigation of their developmental roles in *C. jardinei*.

Sesquiterpenoid biosynthetic pathway genes

Sesquiterpenoid hormones, such as juvenile hormone, regulate the development, metamorphosis, and reproduction in insects, and have long been thought to be confined to the arthropods (e.g. Qu et al., 2018; Tsang et al., 2020). A recent study has unexpectedly identified the sesquiterpenoid hormonal system in jellyfishes, suggesting that the sesquiterpenoid hormone system is established at the bilaterian-cnidarian ancestor (Nong et al., 2020). To test whether coral species contain a sesquiterpenoid hormone system, we searched the

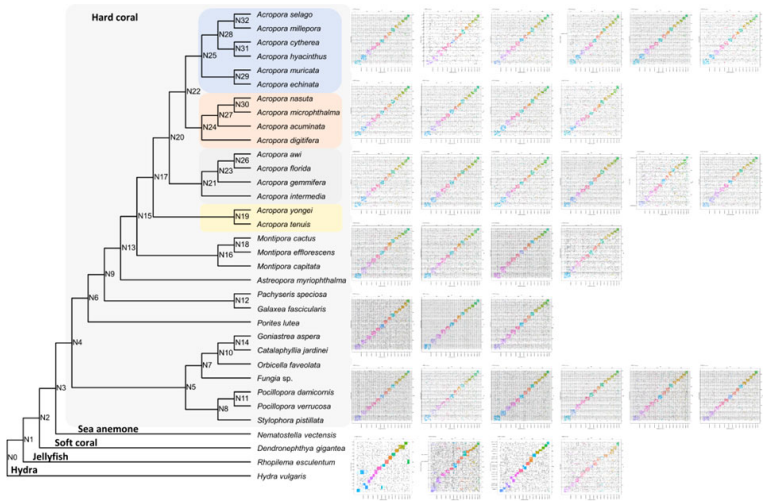


FIGURE 2
Oxford synteny plot of orthologous genes between *Catalaphyllia jardinei* and other 33 cnidarians. The divergence tree was constructed based on the concatenated alignment of single-copy orthogroups. Supporting values were inferred from STAG algorithm, and all were equal to 1 except that N26 = 0.583 and N28 = 0.713. Subplots were listed from left to right according to the top to bottom order of the phylogenetic tree subclades.

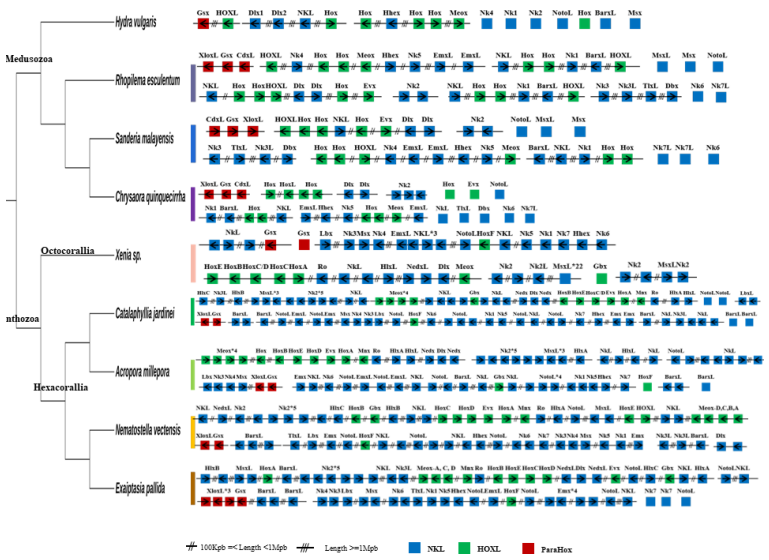


FIGURE 3
ANTP-class homeobox genes arrangement in high-quality cnidarian genomes. Double slash denotes genomic distance >100 kb and <1 Mb; triple slash denotes genomic distance over 1 Mb.

A

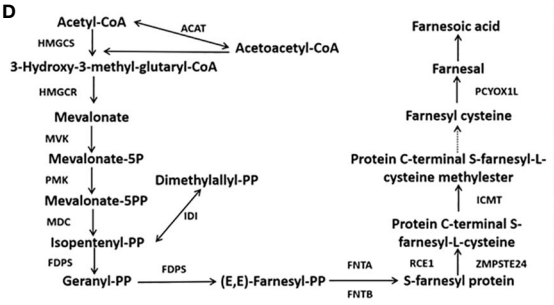
Neuropeptide	✔ / ✘
GLWamide	✔
GRFamide	✔
PRGamide	✔
HIRamide	✔
RWamide	✔
RPamide	✔
pQITRFamide	✔
RNamide	✘
RIamide	✘
KAamide	✘

B

Neuropeptide	Gene copy	Mature peptide paracopy	Different Structural paracopy
GLWamide	1	11	6
GRFamide	1	17	16
PRGamide	2	49	46
HIRamide	1	5	5
RWamide	1	1	1
RPamide	1	2	2
pQITRFamide	1	★	★

C

D



Gene_symbol	KEGG_KO	*C.jardinei*	Jellyfish
ACAT	K00626	+	+
HMGCS	K01641	+	+
HMGCR	K00021	+	+
MVK	K00869	+	+
PMK	K13273	+	+
MDC	K01597	+	+
IDI	K01823	+	+
FDPS	K00787	+	+
FNTA	K05955	+	+
FNTB	K05954	+	+
ZMPSTE24	K06013	+	+
RCE1	K08658	+	+
ICMT	K00587,K09276	+	+
PCYOX1L	K05906	+	+
ALDH	K00128,K00129	+	+

FIGURE 4
(A) The presence of anthozoan neuropeptides identified in *C jardinei*; **(B)** The numbers of mature peptides identified in each Scleratinian neuropeptides. Black star indicates unknown number due to its absence in the transcriptome. **(C)** The sequence logos of the Scleratinian conserved mature neuropeptides identified in *C jardinei*. **(D)** Schematic diagram showing the sesquiterpenoid hormone biosynthetic pathway in cnidarians. "+" sign denotes the presence of particular gene in respective class. The green background refers to genes in the mevalonate pathway, while the blue and yellow backgrounds refer to genes in the different downstream pathways. ACAT, Acetyl-CoA acetyltransferase, HMGCS, 3-hydroxy-3-methylglutaryl-CoA synthase, HMGCR, 3-hydroxy-3-methylglutaryl-CoA reductase, MVK, Mevalonate kinase, PMK, Phosphomevalonate kinase, MDC, Mevalonate (Diphospho) decarboxylase, IDI, Isopentenyl-diphosphate delta isomerase, FDPS, Farnesyl diphosphate synthase, FNTA, Farnesyltransferase, CAAX box, alpha, FNTB, Farnesyltransferase, CAAX box, beta, ZMPSTE24, STE24 endopeptidase, RCE, prenyl protein protease, ICMT, isoprenylcysteine carboxyl methyltransferase, PCYOX1L, Prenylcysteine oxidase 1, ALDH, Aldehyde dehydrogenase.

sesquiterpenoid biosynthetic pathway genes in *C. jardinei* genome (Figure 4D) and identified the mevalonate pathway, aldehyde dehydrogenase (ALDH), farnesyl transferase (FNT), Ste 24 endopeptidase (ZMPSTE24), prenyl protein peptidase (RCE1), isoprenylcysteine carboxymethyl transferase (ICMT) and prenylcysteine oxidase (PCYOXIL) in a similar manner as the jellyfishes (Figure 4D, Supplementary Information S9). This result suggests that coral also has the sesquiterpenoid hormone system, and the functional roles of these hormones remain to be seriously tested in different cnidarians.

microRNA gain and loss in corals

Unlike the situation in bilaterians which contain lots of conserved microRNAs across different lineages, the cnidarians and bilaterians are well known to share only one conserved microRNA miR-100 (Griffiths-Jones et al., 2011). Information of small RNA sequences among different cnidarians reveals limited number of conserved microRNAs among different cnidarian lineages (Nong et al., 2020; Praher et al., 2021). Here, we sequenced the small RNA from *C. jardinei*, and annotated a total of 35 microRNAs in this species (Figure 5, Supplementary Information S10). In comparison with other published cnidarian microRNAs, in congruent to previous studies (e.g. Nong et al., 2020), there were more lineage-specific microRNAs than conserved microRNAs among different cnidarian lineages. We also identified conserved microRNAs at different key nodes in the cnidarian phylogeny, including miR-2022 and miR-2030 that are conserved across all cnidarians, six other microRNAs (miR-2023, miR-2025, miR-2036, miR-2037, miR-2050, miR-9425) that are conserved across all anthozoans, and 4 and 1 other microRNAs that are conserved in the Actiniaria and Scleractinia, respectively (Figure 5). Our findings established the foundation for further investigation of the different roles of these conserved microRNAs in cnidarians.

Conclusion

In the present study, we provided a high-quality genome assembly and transcriptome resources of the elegance coral *Catalaphyllia jardinei* (Euphylliidae). Abiotic stress regulator, hormonal gene families, and microRNAs were annotated, which

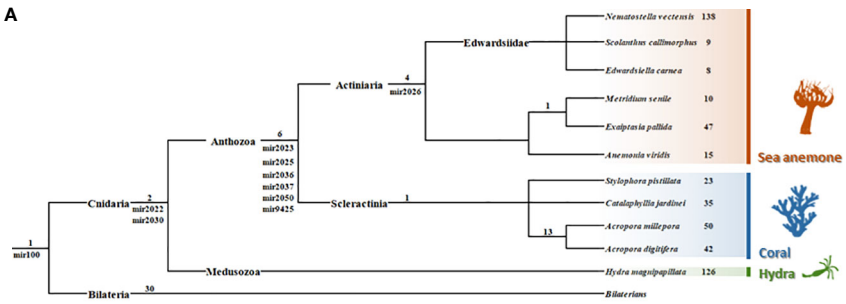


FIGURE 5
(A) Evolutionary gains of microRNAs in the Cnidaria. Numbers shown at nodes of the phylogenetic tree represent the gains of shared microRNAs, while numbers at the end of the branches describe the total numbers of identified microRNAs in each species. **(B)** Cnidarian microRNAs that are shared between at least four species. "+" and "-" signs denote the presence and absence of microRNAs in respective species. *Nve, Nematostella vectensis; Eca, Edwardsiella carnea; Epa, Exaiptasia pallida, Sca, Scolanthus callimorphus; Mse, Metridium senile; Avi, Anemonia viridis; Spi, Stylophora pistillata; Ami, Acropora millepora; Adi, Acropora digitifera; Hma, Hydra magnipapillata; Cja, Catalaphyllia jardinei.*

will serve as a foundation for further investigation into their roles in development and responses to climate change. Due to the easiness to culture *C. jardinei* in reef tanks and the established resources in this study, we propose this species to be adopted as a new laboratory model.

Data availability statement

The final chromosome assembly was submitted to NCBI Assembly under accessionnumber JAEMPF000000000 in NCBI. The raw reads generated in this study havebeen deposited to the NCBI database under the BioProject accessions:PRJNA687327, the genome annotation files were deposited in the Figshare (https:// Emms, D. M., & Kelly, S. (2018). STAG:species tree inference from all genes. BioRxiv, 267914.doi.org/10.6084/m9.figshare.19619700).

Author contributions

JHLH conceived and supervised the study. YY performed the extraction of DNA and RNA, and analyses of homeobox gene, heat shock protein, and microRNA. WN, JH, and TS performed genome assembly. WN performed gene model prediction, and transcriptomic analyses of mRNA and sRNA. WLS performed the neuropeptide analyses. YY and WLS performed the sesquiterpenoid analyses. YX performed synteny analyses. HYY and YY maintained the animal culture. DMB, WGB, TFC, APYC, KFL, PYQ, JWQ, BT, FX, JHLH obtained the funding. YY, WN, WLS, YX, JHLH wrote the first draft of the manuscript. All authors approve the final version of the manuscript.

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Conflict of interest

JHa and TS are employees of Dovetail Genomics, but have no roles in experimental design.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.991391/full#supplementary-material

SUPPLEMENTARY INFORMATION 1
Genome and transcriptome sequencing data statistics.

SUPPLEMENTARY INFORMATION 2
Symbiodinium genomes.

SUPPLEMENTARY INFORMATION 3
Reports of GenomeScope2.

SUPPLEMENTARY INFORMATION 4
Species used in orthologues searches.

SUPPLEMENTARY INFORMATION 5
ANTP-class homeobox genes.

SUPPLEMENTARY INFORMATION 6
Heat shock proteins.

SUPPLEMENTARY INFORMATION 7
Anthozoan conserved neuropeptides

SUPPLEMENTARY INFORMATION 8
Mature neuropeptides.

SUPPLEMENTARY INFORMATION 9
Sesquiterpenoid biosynthetic pathway genes.

SUPPLEMENTARY INFORMATION 10
MicroRNAs.

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