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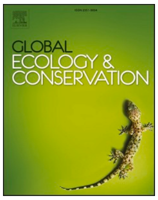

Original research article

Uncovering cryptic coral species in Japan's precious coral fishery: Conservation and sustainable management implications

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ABSTRACT

Accurate estimates of catch and trade volumes for target species are essential for effective resource management. In the precious coral fishery, lesser-known species may be unintentionally harvested in addition to major targets, due to identification based solely on color, ignoring biological species boundaries that are critical for sustainable use. In this study, we identified an unknown coral species, *Pleurocorallium* sp. 1, that was collected together with three major species commonly harvested in Japan (*Corallium japonicum*, *P. konojoi*, and *P. elatius*). Phylogenetic analysis based on three mitochondrial regions showed that *P.* sp. 1 forms a monophyletic group with *P. secundum*, which is primarily distributed in Hawaii. In contrast, a phylogenetic tree based on 4,077 SNPs from Multiplexed ISSR Genotyping by sequencing revealed that *P.* sp. 1 forms a clade distinct from *P. secundum*, suggesting that it may represent an undescribed species. To our knowledge, this is the first study to reveal that genetically distinct species beyond the three major ones are being harvested in Japan's precious coral fishery. Surprisingly, our analysis also uncovered a novel cryptic lineage among samples identified using gross morphology, as *P. konojoi* called *Pleurocorallium* sp. 2. These findings highlight the need for genomic identification of harvested precious corals to ensure sustainable use and proper resource management. Future work should clarify the taxonomic status of *P.* sp. 1 and *P.* sp. 2 through detailed morphological

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assessments. It should also investigate their geographic distributions and abundance, and assess the extent to which these undescribed species have been harvested in commercial fisheries.

1. Introduction

Precious corals, renowned for their beautiful axial skeletons, have been harvested for ornaments and jewelry since ancient times (Chen, 2012). In Japan, three major species of the family Coralliidae, *Corallium japonicum* Kishinouye, 1903, *Pleurocorallium konojoi* (Kishinouye, 1903), and *P. elatius* (Ridley, 1882), are commonly targeted by commercial fisheries (Uda et al., 2013). These are mainly collected using ROVs and coral nets on the deep shelf in Kochi, Okinawa, and Kagoshima Prefectures, and in the Ogasawara Islands (Iwasaki et al., 2012; Luan et al., 2013). These species are characterized by low fecundity (Nonaka et al., 2015), slow growth rates (Yamada et al., 2023), and low population densities (Iwasaki, 2019). Due to overfishing and poaching driven by their high commercial value, discussions have been underway at the CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora, CITES, 2020) to prevent their extinction.

Many species in the family Coralliidae, especially those in the genera *Corallium*, *Pleurocorallium*, and *Hemicorallium*, are characterized by hard and attractive axial skeletons, as seen in the three main species harvested in Japan. Consequently, it is possible that species other than Japanese red coral (*C. japonicum*), white coral (*P. konojoi*), and pink coral (*P. elatius*) may inadvertently be included in coral harvests. However, no study in Japan has attempted to precisely identify harvested precious coral species, particularly using genomic information, to ensure the conservation of each biologically meaningful unit.

We collected seven colonies of *Pleurocorallium*, exhibiting two distinct gross morphological features, during a survey conducted by the Fisheries Agency at depths of 100–300 m in Kagoshima, Japan. The first morphotype (henceforth, *Pleurocorallium* sp. 1) exhibited the following characteristics: thin and peach-colored at the base, gradually turning whitish at each branch tip. The axis was consistently white. Hemispherical autozooid mounds appear on only one side of the branch, with branch tips swelling to form mounds with autozooid clusters (Fig. 1A, B). These gross morphological features distinguish it from both *P. konojoi* and *P. elatius*. In addition, we purchased three specimens of *P.* sp. 1 that had been labeled as white coral (*P. konojoi*). These specimens were acquired directly from a coral-fishing company before being auctioned at the precious coral market in Kochi. These findings suggest that *P.* sp. 1 has been harvested without proper taxonomic recognition, likely being mixed with the white coral *P. konojoi.* Consequently, resource estimates for *P. konojoi* may be inflated, and stocks of *P.* sp. 1 may have declined unnoticed, mirroring other precious corals that are similarly harvested without species-level identification. Furthermore, the other *Pleurocorallium* morphotype (hereafter, *Pleurocorallium* sp. 2) is characterized by cortical mounds clustered in groups, a smooth surface, a cortex ranging from yellowish white to orange, and a white axis (Fig. 1C), features that closely resemble *P. konojoi*. If this morphotype is distinct from *P. konojoi*, it is highly likely that it has also been covertly harvested. To prevent these precious corals from continuing to be harvested and accidentally driven to local extinction, it is imperative to clarify their taxonomic status.

A molecular phylogenetic analysis of three genera in the family Coralliidae, including 13 species of the genus *Pleurocorallium*, was conducted by Tu et al. (2015) using eight mitochondrial regions. Subsequently, Lendvay et al. (2025a) added sequences data of three mitochondrial regions for *P. gotoense* (Nonaka et al., 2012) and *P. uchidai* (Nonaka et al., 2012). Currently, for all known species of the genus *Pleurocorallium*, except *P. pusillum* (Kishinouye, 1903) and *P. johnsoni* (Gray, 1860), sequence data are available on NCBI and can be used for species identification. However, as some species in the genus *Pleurocorallium* are challenging to distinguish using mitochondrial genes, e.g., *P. elatius* and *P. konojoi* (Tu et al., 2015), a genome-wide analysis with higher resolution is required for closely

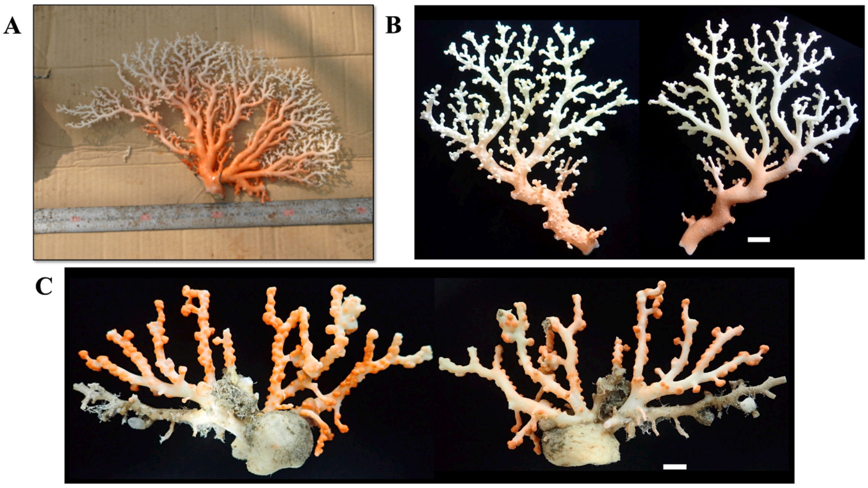

Fig. 1. A: *Pleurocorallium* sp. 1 (specimen P. sp.1–02) purchased from a fishing company. B: Gross morphology of *P.* sp.1 (specimen P. sp.1-S01) found during the survey by the Fisheries Agency. C: *P.* sp. 2 (specimen P. sp. 2-S01) found during the survey by the Fisheries Agency.

related species.

The objective of this study was to determine the taxonomic status of *P.* sp. 1 and *P.* sp. 2 by reconstructing phylogenetic relationships among members of the genus *Pleurocorallium* that were collected from the precious coral market in Japan. To achieve this, we performed two complementary analyses: one based on mitochondrial markers (IGS–MutS–LR) using a comprehensive reference dataset in Lendvay et al. (2025a), and another based on genome-wide SNPs obtained through Multiplexed Inter-Simple Sequence Repeat (ISSR) Genotyping by sequencing (MIG-seq), which offers higher resolution in the family Coralliidae (Takata et al., 2019). Genome-wide SNPs analysis was conducted using samples collected mainly in and around Japan.

2. Material & methods

2.1. Sample collection and DNA extraction

In total, 57 samples from the family Coralliidae were newly sequenced in this study, including six samples of *P.* sp. 1 and four samples of *P.* sp. 2 collected using remotely operated vehicles (ROV) from a depth of 187 – 343 m from Okinawa to Kagoshima (Fig. 2; Table 1). Four samples of *P.* sp.1 were collected in a survey conducted by the Fisheries Agency in Japan, and two were purchased from a fishing company. In addition, five *Pleurocorallium* species inhabiting Japan and Hawaii [*P. konojoi*, *P. elatius*, *P. inutile* Kishinouye, 1902, *P. secundum* (Dana, 1846), and *P. niveum* (Bayer, 1956)] were examined and two *Corallium* species [*C. japonicum* and *C. rubrum* (Linnaeus, 1758)] were included as outgroups (Table 1).

DNA extraction was carried out at the University of Tokyo for specimens from Japan, Oahu Island in Hawaii, and the Emperor Seamounts. DNA from Taiwanese specimens was extracted at National Sun Yat-sen University, and that from four colonies of *P. secundum* and eight colonies of *C. rubrum* was extracted at the University of Zurich. QIAGEN DNeasy Blood & Tissue Kits (QIAGEN, Hilden, Germany) were employed at the University of Tokyo and National Sun Yat-sen University, and QIAmp DNA Mini Kits (QIAGEN, Hilden, Germany) were used at the University of Zurich.

2.2. Mitochondrial genome sequences and analyses

To clarify overall phylogenetic relationships in the genus *Pleurocorallium* by comparing sequences of *P.* sp. 1 and *P.* sp. 2 with those of described *Pleurocorallium* species, we constructed mitochondrial genomes for both species. Since genetic differences within species are better resolved using genome-wide SNPs, we used two colonies of each species (P. sp. 1-S01, P. sp. 1-S02, P. sp. 2-S01, and P. sp. 2-S03) to construct mitochondrial genomes, following the protocol of Takata et al. (2025). Sequence reads were obtained using an Illumina MiSeq platform with MiSeq Reagent kit v3 (2 × 300 bp) after DNA extraction. Genomic DNA libraries were prepared using the Nextera Prep Kit (Illumina) according to the Illumina Sample Preparation Guide. After trimming adapters using Fastp (Chen et al., 2018), bacterial and human-derived reads were subsequently removed using Kraken2 (Lu and Salzberg, 2020) and the minikraken2_v1 database. The ‘extract_kraken_reads.py’ script was used with –exclude -t 9606, 2’ options. The remaining reads were assembled using NOVOPlasty (Dierckxsens et al., 2017) with complete mitochondrial genome data of *P. elatius* (accession number: AB700134) as the reference genome.

From the constructed mitochondrial genomes, three regions, the mtND6-COI intergenic spacer (IGS), a fragment of the DNA mismatch repair protein (MutS) and gene a fragment of the large ribosomal RNA gene subunit (LR), used in Lendvay et al. (2025b) were aligned using Geneious Prime v.2024.0.7 along with sequences of 15 described and four undescribed *Pleurocorallium* species from

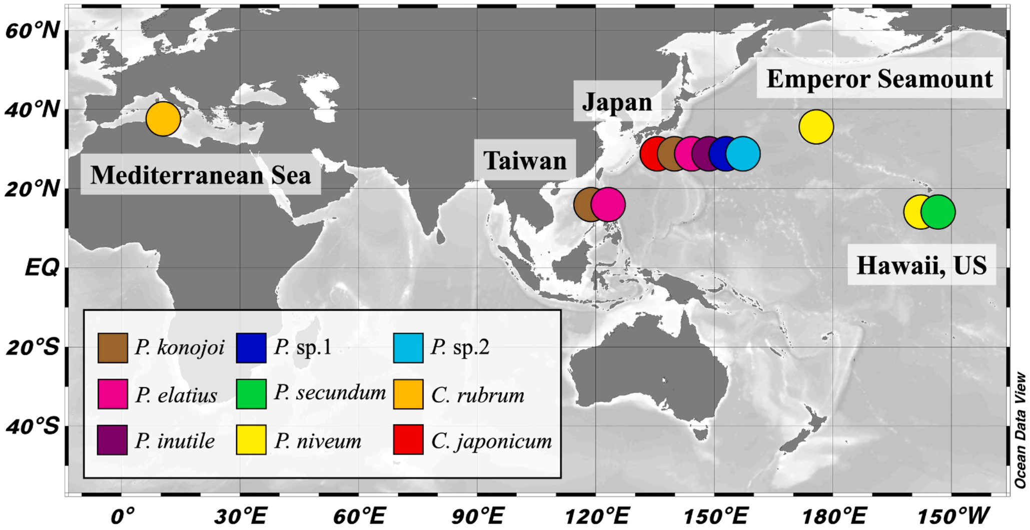

Fig. 2. Sampling locations of the specimens collected in this study. The map was created using Ocean Data View.

Table 1
Sequenced samples in this study.

Species	Sample name	Polymerase kit used for PCR (Takara/ Qiagen)	DRA Accession No.	Location	Depth (m)	Sampling year	Samples used for mtDNA analysis (Fig. 2)	Remark
Corallium japonicum	Cj-G1342	T & Q	DRR911913, DRR911914	off the coast of Ashizuri, Kochi, Japan	100–140	Aug. 2014		Consistent with sample used in Takata et al. (2021)
C. japonicum	Cj-G1344	T	DRR911915	off the coast of Ashizuri, Kochi, Japan	100–140	Aug. 2014		Consistent with sample used in Takata et al. (2021)
C. japonicum	Cj-G1345	T & Q	DRR911916, DRR911917	off the coast of Ashizuri, Kochi, Japan	100–140	Aug. 2014		Consistent with sample used in Takata et al. (2021)
C. japonicum	Cj-S01	Q	DRR911918	off the Yaku Is., Kagoshima, Japan	155	Sep. 2022		Survey by Fisheries Agency
C. rubrum	Cr-PLA1	T & Q	DRR911919, DRR911920	Plane ile, France	25	1999		
C. rubrum	Cr-KOR1	T	DRR911921	Vela Luka, Croatia	45	2004		
C. rubrum	Cr-MED1	T	DRR911922	Medes, Spain	25–30	1999		
C. rubrum	Cr-SANF1	T	DRR911923	San Fruttuoso, Liguria, Italy	25	2005		
C. rubrum	Cr-GIA1	T	DRR911924	Giannutri, Toscana, Italy	45	2004		
C. rubrum	Cr-PUG1	T	DRR911925	Santa Caterina, Puglia, Italy	55	2011		
C. rubrum	Cr-POR1	T	DRR911926	Portofino, Liguria, Italy	25	2012		
C. rubrum	Cr-CAL1	T	DRR911927	Calafuria, Toscana, Italy	25	2005		
Pleurocorallium elatius	Pe-IOU05	T	DRR911928	off the Iou Is., Kagoshima, Japan	130	May 2010		Consistent with sample used in Takata et al. (2019)
P. elatius	Pe-IOU09–2	T & Q	DRR911929, DRR911930	off the Iou Is., Kagoshima, Japan	253	Apr. 2009		Consistent with sample used in Takata et al. (2019)
P. elatius	Pe-TNG02	T	DRR911931	off the Tanega Is., Kagoshima, Japan	200	Feb. 2006		Consistent with sample used in Takata et al. (2019)
P. elatius	Pe-TNG05	T	DRR911932	off the Tanega Is., Kagoshima, Japan	175	Dec. 2007		Consistent with sample used in Takata et al. (2019)
P. elatius	Pe-TNG06	T	DRR911933	off the Tanega Is., Kagoshima, Japan	220	Feb. 2006		Consistent with sample used in Takata et al. (2019)
P. elatius	Pe-S01	T	DRR911934	off the Amami Ohshima Is., Kagoshima, Japan	219	Sep. 2022		Survey by Fisheries Agency
P. elatius	Pe-NSYSU12	Q	DRR911935	Northern Taiwan	120	Feb. 2009		National Sun Yat-sen University ID:ASIZ-80176
P. elatius	Pe-NSYSU13	Q	DRR911936	Southwestern Taiwan	140	Nov. 2009		National Sun Yat-sen University ID:ASIZ-80272
P. elatius	Pe-NSYSU15	Q	DRR911937	Northern Taiwan	-	May 2010		National Sun Yat-sen University ID:NSYSU-OCT-536
P. elatius	Pe-NSYSU16	Q	DRR911938	Northern Taiwan	149	May 2010		National Sun Yat-sen University ID:ASIZ-80344
P. inutile	Pinu	T	DRR911939	off the Tanega Is., Kagoshima, Japan	245	Nov. 2007		Consistent with sample used in Nonaka M, Muzik K (2016) and Takata et al. (2025)
P. konojoi	Pk-IOU02	T	DRR911940	off the Iou Is., Kagoshima, Japan	115	Dec. 2007		Consistent with sample used in Takata et al. (2019)

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Table 1 (*continued*)

Species	Sample name	Polymerase kit used for PCR (Takara/ Qiagen)	DRA Accession No.	Location	Depth (m)	Sampling year	Samples used for mtDNA analysis (Fig. 2)	Remark
P. konojoi	Pk-IOU03	T	DRR911941	off the Iou Is., Kagoshima, Japan	150	May 2008		Consistent with sample used in Takata et al. (2019)
P. konojoi	Pk-IOU04	T	DRR911942	off the Iou Is., Kagoshima, Japan	120	May 2009		Consistent with sample used in Takata et al. (2019)
P. konojoi	Pk-IOU07	T	DRR911943	off the Iou Is., Kagoshima, Japan	120	Aug. 2009		Consistent with sample used in Takata et al. (2019)
P. konojoi	Pk-TAK01	T	DRR911944	off the Take Is., Kagoshima, Japan	150	Sep. 2008		Consistent with sample used in Takata et al. (2019)
P. konojoi	Pk-TAK03	T	DRR911945	off the Take Is., Kagoshima, Japan	115	Apr. 2009		Consistent with sample used in Takata et al. (2019)
P. konojoi	Pk-TAK05	T	DRR911946	off the Take Is., Kagoshima, Japan	115	May 2009		Consistent with sample used in Takata et al. (2019)
P. konojoi	Pk-TAK06	T & Q	DRR911947, DRR911948	off the Take Is., Kagoshima, Japan	120	Feb. 2008		Consistent with sample used in Takata et al. (2019)
P. konojoi	Pk-NSYSU17	Q	DRR911949	Northern Taiwan	150	Mar. 1998		National Sun Yat-sen University ID:ASIZ-80156
P. konojoi	Pk-NSYSU18	Q	DRR911950	Northern Taiwan	220	Feb. 1998		National Sun Yat-sen University ID:ASIZ-80157
P. konojoi	Pk-NSYSU20	Q	DRR911951	Northern Taiwan	160	Feb. 1998		National Sun Yat-sen University ID:ASIZ-80170
P. konojoi	Pk-NSYSU21	Q	DRR911952	Northern Taiwan	145	Mar. 2009		National Sun Yat-sen University ID:ASIZ-80180
P. konojoi	Pk-NSYSU23	Q	DRR911953	Northern Taiwan	170	Mar. 2009		National Sun Yat-sen University ID:ASIZ-80215
P. konojoi	Pk-NSYSU26	Q	DRR911954	Southwestern Taiwan	145	Dec. 2009		National Sun Yat-sen University ID:ASIZ-80279
P. konojoi	Pk-NSYSU29	Q	DRR911955	Northern Taiwan	149	May 2010		National Sun Yat-sen University ID:ASIZ-80318
P. konojoi	Pk-NSYSU30	Q	DRR911956	Northern Taiwan	-	May 2010		National Sun Yat-sen University ID:NSYSU-OCT-80338
P. niveum	Pn-NSMT1861	T	DRR911957	Oahu Is., Hawaii, US	396	Mar. 1983		Bishop Museum ID: BPBM-D984, National Museum of Nature and Science ID: NSMT1861
P. niveum	Pn-NSMT1863	T	DRR911958	Oahu Is., Hawaii, US	396	Jan. 1984		Bishop Museum ID: BPBM-D1025, National Museum of Nature and Science ID: NSMT1863
P. niveum	Ppu-157	T	DRR911959	Koko Seamount, Pacific Ocean	336–410	Jun. 2011		Consistent with 'NSMT-Co1727' in Nonaka and Hayashibara (2021)
P. niveum	Ppu-282	T	DRR911960	Koko Seamount, Pacific Ocean	372	May 2010		Consistent with 'NSMT-Co1725' in Nonaka and Hayashibara (2021)
P. secundum	Ps-CB275	Q	DRR911961	Hawaii Is., Hawaii, US	273	Sep. 2016		Collected by Hawaii Undersea Research Laboratory. Samples consistent with '106' in Lendvay et al. (2022), (2025a), (2025b); Connor et al. 2023
P. secundum	Ps-CB276	Q	DRR911962	Hawaii Is., Hawaii, US	238	Sep. 2016		Collected by Hawaii Undersea Research Laboratory. Samples consistent with '107' in Lendvay et al. (2022),

(*continued on next page*)

Table 1 (*continued*)

Species	Sample name	Polymerase kit used for PCR (Takara/ Qiagen)	DRA Accession No.	Location	Depth (m)	Sampling year	Samples used for mtDNA analysis (Fig. 2)	Remark
								(2025a), (2025b); Connor et al. 2023
P. secundum	Ps-CB277	Q	DRR911963	Hawaii Is., Hawaii, US	221	Sep. 2016		Collected by Hawaii Undersea Research Laboratory. Samples consistent with '108' in Lendvay et al. (2022), (2025a), (2025b); Connor et al. 2023
P. secundum	Ps-CB278	Q	DRR911964	Hawaii Is., Hawaii, US	269	Sep. 2016		Collected by Hawaii Undersea Research Laboratory. Samples consistent with '204' in Lendvay et al. (2022), (2025a), (2025b); Connor et al. 2023
P. sp.1	P.sp.1–01	T	DRR911965	off the Aguni Is., Okinawa, Japan	343	Jun. 2011		Collected for commercial purposes by a contracted fishing company
P. sp.1	P.sp.1–02	T	DRR911966	off the Tanega Is., Kagoshima, Japan	235	Nov. 2007		Collected for commercial purposes by a contracted fishing company
P. sp.1	P.sp.1–03	T	DRR911967	off the Satsuma Peninsula, Kagoshima, Japan	203	Aug. 2017		Survey by Fisheries Agency
P. sp.1	P.sp.1-S01	T	DRR911968	off the Satsuma Peninsula, Kagoshima, Japan	225	Sep. 2022	○	Survey by Fisheries Agency
P. sp.1	P.sp.1-S02	T	DRR911969	off the Satsuma Peninsula, Kagoshima, Japan	225	Sep. 2022	○	Survey by Fisheries Agency
P. sp.1	P.sp.1-S03	T	DRR911970	off the Satsuma Peninsula, Kagoshima, Japan	205	Sep. 2022		Survey by Fisheries Agency
P. sp.2	P.sp.2-S01	T	DRR911971	off the Satsuma Peninsula, Kagoshima, Japan	216	Sep. 2022	○	Survey by Fisheries Agency
P. sp.2	P.sp.2-S02	T	DRR911972	off the Satsuma Peninsula, Kagoshima, Japan	201	Sep. 2022		Survey by Fisheries Agency
P. sp.2	P.sp.2-S03	T	DRR911973	off the Satsuma Peninsula, Kagoshima, Japan	201	Sep. 2022	○	Survey by Fisheries Agency
P. sp.2	P.sp.2-S04	T	DRR911974	off the Danjo Gunto Is., Kagoshima, Japan	187	Sep. 2022		Survey by Fisheries Agency

Tu et al. (2015) and Lendvay et al. (2025a). A list of samples used in the analysis is provided in Table S1.

2.3. *MIG-seq and analysis*

Multiplexed inter simple sequence repeat (ISSR) genotyping by sequencing (MIG-seq) is a high-throughput sequencing method that amplifies genomic regions flanked by simple sequence repeat regions (SSRs) and identifies genome-wide SNPs without the necessity of prior genome information. It offers a cost-effective solution for detecting Single Nucleotide Polymorphisms (SNPs) in non-model organisms. Previous studies demonstrate its effectiveness for population genetics (Richards et al., 2018; Takata et al., 2021) and phylogenetic studies (Taninaka et al., 2021) on marine invertebrates, especially in coral species. In short, we performed two-step PCR to build an ISSR library following Suyama et al. (2022), which was modified from the original protocol (Suyama and Matsuki, 2015). In this study, either the Multiplex PCR Assay Kit Ver.2 (Takara Bio Inc.) or the QIAGEN Multiplex PCR Kit (QIAGEN) was used for the first PCR.

The first PCR was conducted at the institution where DNA extraction was performed. To assess whether the choice of enzyme affects the analysis, PCR was performed on five samples (Table 1) using both kits, and resulting phylogenetic relationships were compared. For each sample, the first PCR was performed in three replicates, and the resulting PCR products were ultimately pooled into a single combined sample. Sequencing was performed using MiSeq (sequencing control software v2.0.12, Illumina) using MiSeq Regent v3 150 cycle kit (Illumina). Image analysis and base calling were performed using real-time analysis software v1.17.21 (Ilumina). The DarkCycle option was changed from “Amplicon-dark 17–3” to “Amplicon-dark 17–17” on the “Chemistry” line.

Primer sequences and low-quality reads were removed from raw data. The ‘fastx_trimmer’ (FASTX-toolkit version 0.0.13) was used with a setting of -f 22, and ‘fastaq_quality_filter’ with a setting of –q 30 and -p 40. Adapter sequences for the Illumina platform were trimmed with Cutadapt v4.6 (Martin, 2011). After quality control, the Stacks 2.64 pipeline (Catchen et al., 2013; Rochette et al., 2019) was used for de novo SNP discovery. We used the wrapper script denovo_map.pl in Stacks to execute a pipeline of commands. The wrapper executed ustacks (de novo loci construction), cstacks (loci cataloging and matching across samples), sstacks (matches samples against the catalog), tsv2bam (transposes data such that it is organized by locus), gstacks (calls SNPs for each locus), and the populations command (which calculates the percentage of missing SNPs among individuals) (Catchen et al., 2013). “ustacks” was used with optional settings of “minimum depth of coverage required to create a stack (m)” = 3, and population employed, the options “the minimum minor allele frequency required to process a nucleotide site at a locus (min_maf)” = 0.01, “the maximum observed heterozygosity required to process a nucleotide site at a locus (max_obs_het)” = 0.09, and “the minimum proportion of individuals required to process a locus across all data (R)” = 0.1, 0.2 and 0.5. We calculated within-species Nei’s genetic distance from data for *Pleurocorallium* individuals (R - 0.5) with GenAlEx 6.502 (Peakall and Smouse, 2012).

2.4. Phylogenetic Analysis using mitochondrial gene data and MIG-seq genome-wide data

We estimated phylogenetic trees based on the Maximum likelihood (ML) method. The program IQ-TREE2 version 2.0.6 (Minh et al., 2020), using the HKY+F+G4 model (mitochondrial genes data) selected based on the Bayesian Information Criterion (BIC) and GTR+F+ASC (MIG-seq genome-wide data) model, were used to reconstruct a phylogenetic tree for *Pleurocorallium*. *Corallium japonicum* and *C. rubrum* were used as outgroups. The bootstrap analysis was performed with 1000 replicates using UFBoot, Ultrafast Bootstrap Approximation (Minh et al., 2013). Single-branch tests were also performed with 1,000 replicates using SH-aLRT, an SH-like approximate likelihood ratio test (Guindon et al., 2010). The final tree was drawn using FigTree version 1.4.4 (Rambaut, 2012).

3. Results

3.1. Mitochondrial Genome analysis

As a result of the mitochondrial genome assemblies of *P.* sp. 1 and *P.* sp. 2, genome sizes were found to be 19,027 bp and 19,043 bp, respectively. Consistent with other species in the same genus (Takata et al., 2025), each genome consisted of 14 protein-coding genes, two rRNA genes (rnL and rnS), and one tRNA gene (trnM). Mitochondrial genome sequence data supporting this study’s findings are openly available in DDBJ under the accession no. LC921273-LC921276. A total of 1,091 bp (comprising 400 bp from Muts, 152 bp from LR, and 537 bp from IGS sequences after trimming unreliable regions) were obtained from 61 individuals including *P.* sp. 1 and *P.* sp. 2, and concatenated to reconstruct the phylogenetic tree (Fig. 3). *P.* sp. 1 showed 100% sequence identity with *P. secundum* and was nested within the same clade in the phylogenetic tree. In contrast, *P.* sp. 2 formed an independent clade distinct from all known species, including the white coral (*P. konojoi*), which shares similar external morphology (Fig. 3).

3.2. MIG-seq analysis

In total, 19,104,500 raw reads with an average of 308,137 reads per sample were obtained for the 62 individuals. We obtained 13,552,464 reads with an average of 218,588 reads per individual after filtering out adapter and low-quality reads. First, to examine the effect of using two different enzymes on phylogenetic relationships, a phylogenetic analysis was conducted including data from ten samples derived from five individuals, each amplified with both enzymes (Table 1). These results showed that regardless of the enzyme used, samples from the same individuals formed monophyletic groups (Fig. S1). Therefore, in this study, we assumed that differences in enzymes had minimal effect on phylogenetic inference and proceeded with 57 individuals for the main analysis, excluding the lower-read sample from each enzyme pair. The ML phylogenetic analysis using 4,077 SNPs (R - 0.1; Figs. 4) and 1560 SNPs (R - 0.2; Fig. S2) showed that, whereas *P.* sp. 2 appeared more derived than *P. niveum* and *P. secundum* in the mitochondrial phylogeny, it occupied the most basal position among *Pleurocorallium* species included in the MIGseq-based phylogenetic analysis. Phylogenetic relationships differed slightly between two datasets (R - 0.1; Fig. 4 and R - 0.2; Fig. S2), but this species consistently formed a monophyletic group, indicating that it is genetically distinct from *P. konojoi* and other species. Additionally, while *P.* sp. 1 showed the closest phylogenetic relationship to *P. secundum*, it formed an independent monophyletic clade distinct from *P. secundum*, in contrast to the mitochondrial results. The results of within-species genetic distance calculations for *Pleurocorallium*, including the combined group of *P.* sp. 1 and *P. secundum*, showed that taxa with relatively larger intraspecific sample sizes (*P. elatius, P. konojoi*, and *P.* sp. 1 & *P. secundum*) exhibited higher values (mean > 1000), whereas other species had lower values (mean < 1000) (Fig. 5).

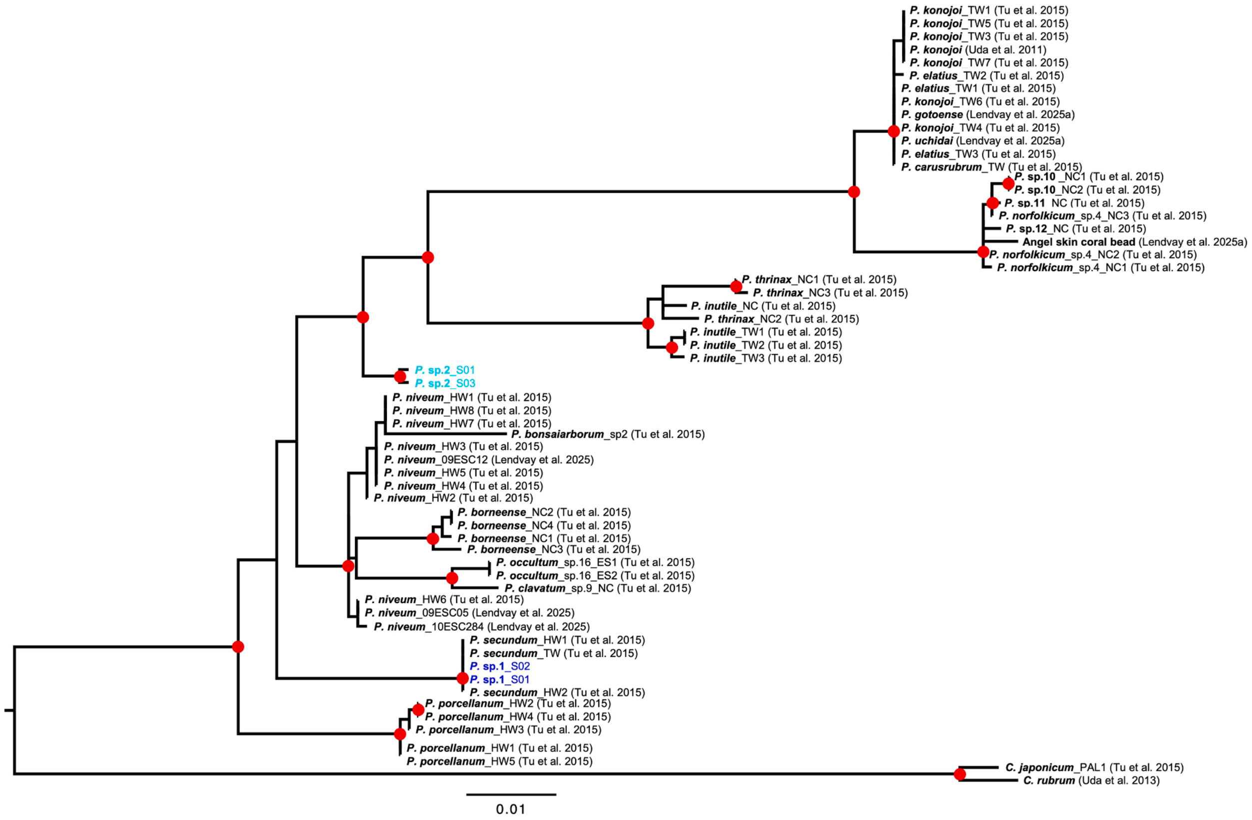

Fig. 3. Maximum likelihood phylogenetic tree of the genus *Pleurocorallium* using mitochondrial IGS-MutS-LR data. Red circle symbols indicate internal nodes with SH-aLRT support (%) ≥ 80% and ultrafast bootstrap support (%) ≥ 95%. Blue and light blue indicate samples of *P.* sp. 1 and *P.* sp. 2, respectively. *Corallium japonicum* and *C. rubrum* from the genus *Corallium* were used as outgroups.

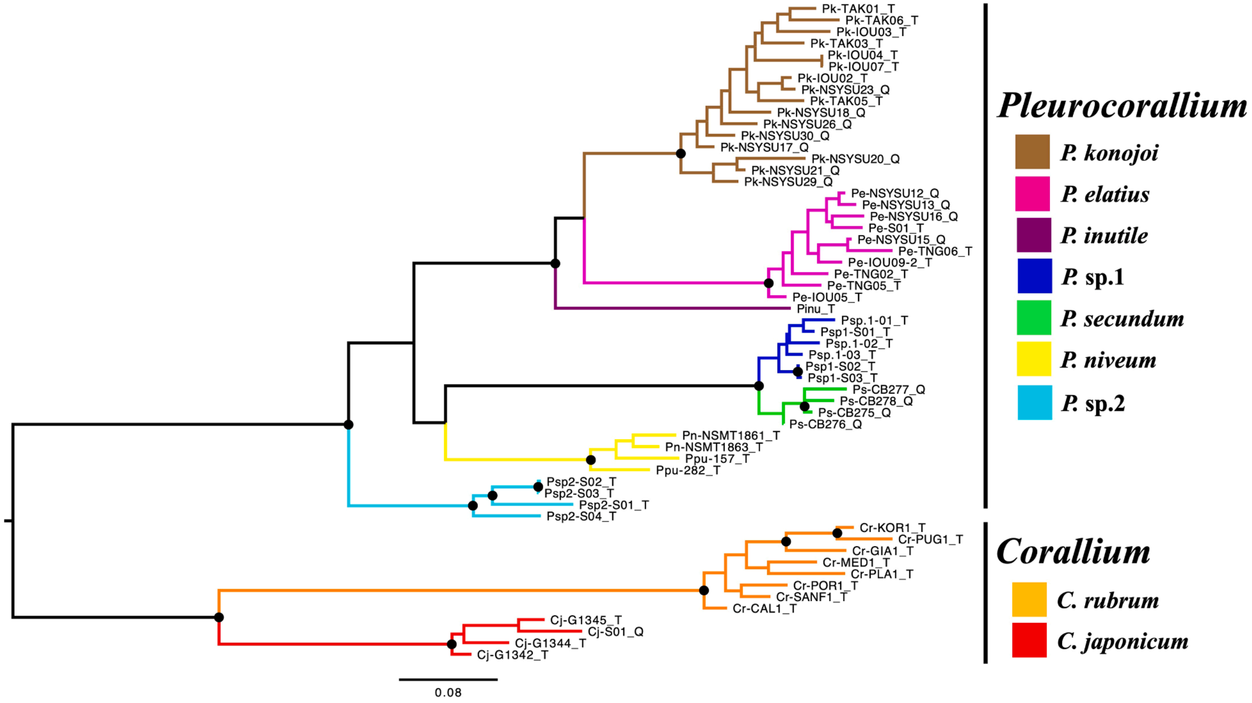

Fig. 4. Maximum likelihood phylogenetic tree of the genus *Pleurocorallium* using MIGseq data (R-0.1). Circle symbols indicate internal nodes with SH-aLRT support (%) ≥ 80% and ultrafast bootstrap support (%) ≥ 95%.

4. Discussion

Historically, Japan's precious coral harvests have been identified and tracked under the assumption of three distinct species (*Corallium japonicum, Pleurocorallium konojoi,* and *P. elatius*; Sakita, 2016). This classification has also been utilized to assess abundance of each precious coral species, guiding discussions for CITES regulation (Iwasaki, 2018). However, recent studies suggest the presence of cryptic species among recognized precious coral species (Cannas et al., 2019). In the future, the challenge will be to clarify actual species boundaries using scientific methods and to implement appropriate conservation and management measures. In this study, we provide the first evidence that genetically distinct species beyond the three major recognized species are being harvested by the Japanese precious coral fishery.

Based on the phylogenetic tree constructed from three mitochondrial regions, *P.* sp. 1 could not be genetically distinguished from *P. secundum*. In contrast, the phylogenetic tree based on MIG-seq analysis revealed that *P.* sp. 1 forms a distinct genetic lineage with high bootstrap support, indicating that it is genetically differentiated not only from the three major Japanese precious coral species but also from all other known *Pleurocorallium* species for which genetic data are available. On the other hand, intraspecific genetic distances calculated from the combined dataset of *P.* sp. 1 and *P. secundum* did not show marked differences from those of other *Pleurocorallium* species, yielding values that fit both an intraspecific or interspecific interpretation (Fig. 5). Because the genetic distance results in this study are likely to depend heavily on intraspecific sample sizes, caution is required in interpreting these indices. To determine whether these two represent the same or distinct species, it is necessary to assess whether the genetic differentiation between *P.* sp. 1 and *P. secundum* revealed by MIG-seq reflects intraspecific geographic structuring or true interspecific divergence. Preliminary morphological observations of sclerites showed that *P. secundum* is dominated by double-club forms with few multi-radiates (Bayer, 1956; Lendvay et al., 2025b), whereas *P.* sp. 1 is dominated not by double-clubs but by 6-radiates and also exhibits multi-radiates (Fig. S3). Especially, sclerites sizes of the two species are clearly different (Fig. S3; Lendvay et al., 2025b; Takata et al. in prep). Given the genetic results of this study, the presence of morphological differences would make it highly likely that these two taxa represent distinct species. *Pleurocorallium secundum* is a species primarily recorded from the Hawaiian Islands and has not yet been reported from waters near Japan, where *P.* sp. 1 was discovered. Despite this, their depth ranges are highly similar. *Pleurocorallium secundum* inhabits depths of 230–380 m (Lendvay et al., 2025b), whereas *P.* sp. 1 occurs at 203–343 m. Lendvay et al. (2025b) successfully extracted DNA from the type specimen of *P. secundum*, a species of previously uncertain taxonomic status, and conducted phylogenetic analysis using three mitochondrial regions (IGS–MutS–LR). As a result, they confirmed that "P. secundum_TW, " reported from Taiwan by Tu et al. (2015), indeed belongs to *P. secundum*, thereby extending the known distribution of this species into the South China Sea. If *P.* sp. 1 is ultimately recognized as a distinct species, it raises a new question: should "*P. secundum*_TW" reported by Tu et al. (2015) be reassigned to *P.* sp. 1 or retained as *P. secundum*? This would also necessitate a revision of their respective geographic distributions. In addition, we were unable to compare *P.* sp. 1 with *P. pusillum* and *P. johnsoni*, for which mitochondrial sequence data are lacking. To resolve these taxonomic uncertainties, detailed morphological comparisons of sclerites and polyps between *P.* sp. 1 and related species are needed.

In this study, we also identified *P.* sp. 2, a genetically highly divergent lineage that is morphologically very similar to *P. konojoi*. The occurrence of such genetically distinct but morphologically cryptic species has been reported in other octocoral taxa as well (Taninaka et al., 2021). All *P.* sp. 2 specimens were collected from the waters off the Satsuma Peninsula in Kagoshima. These colonies not only resemble *P. konojoi* in gross morphology but also share overlapping habitat and depth ranges. These findings suggest that *P.* sp. 2 may have been mistakenly harvested as *P. konojoi*, potentially leading to an overestimation of *P. konojoi*'s population size based on harvest records. *P. konojoi* is dominated by 6-radiates (Kishinouye, 1903; Nonaka et al., 2012), whereas *P.* sp. 2 is dominated by 8-radiates (Fig. S4; Takata et al. in prep), indicating morphological differences; nevertheless, a formal species description is warranted using detailed morphological characters, such as the relative proportions of sclerite types and polyp size. As with *P.* sp. 1, comparative morphological assessments of sclerites and polyps are also needed for *P.* sp. 2. In any case, the distributions of *P.* sp. 1 and *P.* sp. 2 overlap with those of the three major Japanese precious coral species, and these undescribed species may have been misidentified as white coral (*P. konojoi*), particularly due to the shared characteristic of a white axial skeleton. Although no direct evidence is available, it is also possible that *P. inutile*, a species with low commercial value (Takata et al., 2025), was misidentified and harvested as white coral due to its similar white axial skeleton. Given that these species are reproductively isolated from other precious coral species, it is essential to monitor and manage their harvest and export quantities independently from those of the other three Japanese precious coral species.

This study also highlights the importance of incorporating genetic methods into sustainable use and management of precious corals. In general, the commercially valuable portion of a precious coral colony is the thick basal part, whereas the thinner branch tips are often discarded during auctions or processing (based on interviews with local fishers, personal communication). In this study, only a few millimeters of tissue were used for DNA extraction, indicating that sufficient genetic material can be obtained from these discarded fragments without compromising the commercial value of the specimens. In the future, preserving branch tip tissues from harvested precious corals and linking each sample to its genetic information could contribute to more accurate species-specific catch estimates and detection of cryptically harvested species. While proper species identification at the time of harvest is another key element, *P.* sp. 2, like *P. konojoi*, may be difficult to distinguish based on gross morphology, especially when relying on ROV footage. Notably, both *P.* sp. 1 and *P.* sp. 2 were discovered in Kagoshima and Okinawa Prefectures, where coral harvesting is only permitted using specific gear such as manned submersibles or ROVs (Chang et al., 2013). Selective fishing is generally considered effective for precious corals, given the extensive overlap in species distributions within Japanese waters. However, when visual identification becomes unreliable, it may be necessary to incorporate more precise methods. At least, it is crucial to raise awareness among local fishery authorities and fishers that cryptically harvested species may be present in current catch practices.

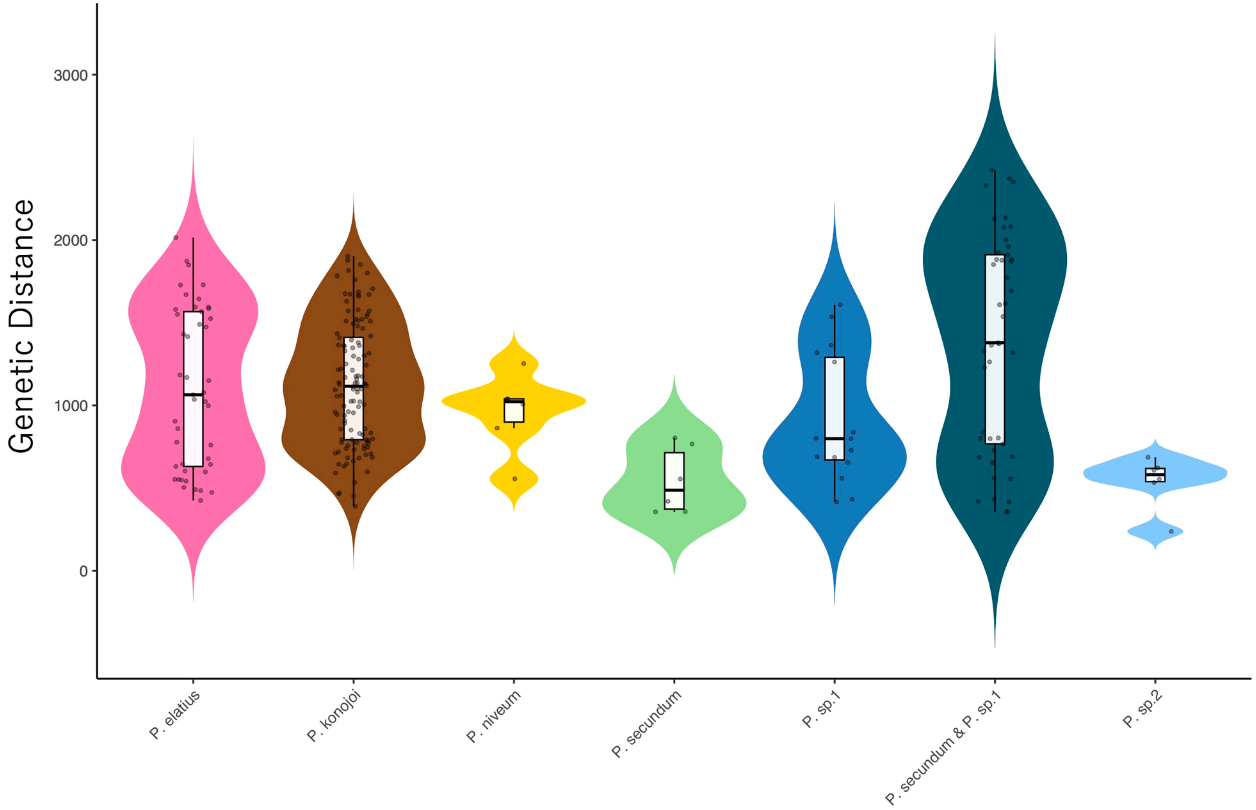

Fig. 5. Violin plot and Boxplot showing the genetic distances within species using MIGseq data (R-0.5).

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04125.

Data availability

Mitochondrial genome data is available at DDBJ: LC921273-LC921276. MIG-seq data is available at DRA: DRR911921-DRR911974.

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