Journal of Applied Phycology
https://doi.org/10.1007/s10811-026-03784-1

RESEARCH

Mitochondrial phylogenomics of eucheumatoids (Solieriaceae, Rhodophyta) from the Indo-Pacific

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Received: 3 October 2025 / Revised: 2 January 2026 / Accepted: 6 January 2026

Abstract

Eucheumatoid seaweeds are highly valued globally for their carrageenan. Members of this group are widely distributed and cultivated throughout the Indo-Pacific. Despite various molecular studies on this group, mitogenome research in eucheumatoids has only recently explored a limited number of species, leaving overall diversity largely unexplored. In this study, 26 complete mitogenomes of eucheumatoids from the Indo-Pacific were sequenced, including the first complete sequences for wild genotypes of *Eucheuma platycladum*, *Kappaphycus striatus*, *Kappaphycopsis cottonii,* and an unidentified species of *Kappaphycus* from Africa. The eucheumatoid mitogenomes range from 25.1 to 25.5 kb in size, containing 50 genes (24 protein-coding genes, 24 tRNA genes, two rRNA genes, and a single intron) bearing extensive gene synteny across species. Phylogenetic analyses using concatenated mitochondrial genes recovered strong clades for each group, with the exception of the genus *Eucheuma*. Apart from *atp*9, gene marker evaluations showed that all genes could be used for species identification. The utility of four genes, *atp*4, *nad*3, *nad*4, and *nad*6, was found to be effective for resolving intergeneric relationships. These findings provide a foundation for comparative analysis useful for resolving phylogenetic relationships and outstanding taxonomic issues, cultivar development, and conservation efforts. Expanding species coverage and incorporating plastome analyses would contribute to a more complete understanding of the genomic diversity and evolutionary history of this economically important group of seaweeds.

Keywords *Kappaphycus* · *Eucheuma* · Molecular · Mitogenome · Phylogeny · Phylogenomic

Introduction

Eucheumatoids are tropical red seaweeds belonging primarily to the genera *Betaphycus*, *Eucheuma*, *Mimica*, *Kappaphycopsis*, and *Kappaphycus*. These seaweeds contain carrageenan, a commercially valuable polysaccharide widely used in the food and cosmetic industries. By far, only *Kappaphycus* and *Eucheuma* are cultivated commercially. The global carrageenan market reached US$ 967.6 million in 2024 and is projected to increase to US$ 1, 607.12 million by 2033 (Straits Research 2025). Indonesia and the Philippines dominate global carrageenan production, primarily supplying China, which has recently emerged as a major carrageenan processor and exporter through expanded facilities and value-chain integration (Zhang et al. 2024). Eucheumatoid farming plays an important role in coastal communities of developing countries, providing a source of livelihood and contributing to poverty alleviation (Hurtado et al. 2013; Tan et al. 2013; Msuya et al. 2022).

Although genetic markers have proven useful for addressing key challenges in eucheumatoids, their taxonomy remains unresolved due to missing critical information from type specimens that originally defined the generic and species concepts (Tan et al. 2024). The morphologically plastic nature of eucheumatoids also makes them difficult to identify based on morphology alone, and this is compounded by the confusing use of commercial and vernacular names (Zuccarello et al. 2006; Lim et al. 2014; Dumilag et al. 2022; Tan et al. 2024). The use of genetic markers facilitated the identification of seaweed cultivars which improved efficiency in farm management and carrageenan processing, while the identification of wild specimens provided valuable insights into eucheumatoid genetic diversity and conservation, as well as the

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description of new species (Dumilag et al. 2016a, 2016b; Brakel et al. 2021; Roleda et al. 2021; Dumilag and Zuccarello 2022; Tan et al. 2022a, 2022b, 2024). While DNA barcodes were able to resolve the interspecific phylogenetic relationships of most commercial eucheumatoids, they still fail to confidently resolve intergeneric relationships (Tan et al. 2012, 2024; Lim et al. 2014).

The characterization of circular, maternally-inherited, and rapidly evolving mitochondrial genomes (mitogenomes) has yielded valuable insights into the phylogeny and evolution of red algae (Boo et al. 2016a, 2016b, 2020). The extensive gene synteny found across phylogenetically diverse red algae lineages underscores its significant utility in species delimitation, novel species discovery, and resolving complex phylogenetic relationships. While complete mitochondrial genomes have been sequenced for several eucheumatoid species (Tablizo and Lluisma 2014; Li et al. 2018; Crisostomo et al. 2023), many remain largely unknown. Recently, advancements in genome-skimming technology have enabled the rapid acquisition of mitogenomes from large specimen collections, facilitating mitogenomic research (Trevisan et al. 2019; Nagano et al. 2021). Genome skimming employs a shallow sequencing coverage relative to deep whole-genome sequencing methods. It is an efficient method to recover high-copy genomic regions, including repetitive elements, typically of organellar genomes. This technique lowers sample costs, avoids PCR-related bias associated with primer mismatch, and is also considered effective for degraded or low-quantity DNA from herbarium or ethanol-preserved samples (Trevisan et al. 2019; Li et al. 2021; Wu et al. 2021). Although complete organellar genome data have only recently become available for a limited number of eucheumatoids using next-generation sequencing approaches (Li et al. 2018; Zhang et al. 2020), similar datasets generated in other red algae have reportedly provided sufficient resolution for strain-level discrimination and organellar phylogenomic inference (Hughey et al. 2014; Boo et al. 2016a; Patil et al. 2025; Song et al. 2025).

A clearer resolution of eucheumatoid phylogeny is essential in guiding selective breeding and biotechnology in developing superior cultivars. This need has become increasingly urgent amid increasing industry reports of lower growth rates, reduced production yields, poorer carrageenan quality, and higher occurrences of pests and diseases (Brakel et al. 2021; Cottier-Cook et al. 2022). As such, the objectives of the present study are: (i) to sequence the mitochondria of commercially and taxonomically important eucheumatoid species from Indo-Pacific using genome-skimming, (ii) to better resolve the phylogeny of these eucheumatoids, and (iii) to identify potentially useful loci for molecular species identification and for the investigation of intraspecific variation.

Materials and methods

Sample collection and DNA extraction

Eucheumatoid specimens were gathered using haphazard sampling from farms and wild seabed locations in Madagascar, Tanzania, Indonesia, the Philippines, and Malaysia. Most specimens from Malaysia and Indonesia utilized in this study were originally reported from Tan et al. (2022a, 2022b, 2024) and Lim et al. (2014). Farmed specimens were collected directly from the cultivation lines of seaweed farms, while wild specimens were gathered through snorkelling or diving. The identification of these specimens was initially based on their gross morphology and was subsequently confirmed using DNA analysis.

The following genotypes previously reported to be genetically distinct from widely cultivated commercial strains were also included in the analysis, namely *Kappaphycus* sp. (Africa) relative to the commercial *K. alvarezii* cultivar, wild-type *K. striatus* from Southeast Asia compared with the commercial *K. striatus* "cottonii" cultivar (Tan et al. 2022a), and the less common *Eucheuma denticulatum* "cacing" from Malaysia relative to the commercial *E. denticulatum* "spinosum" cultivar (Lim et al. 2014).

For each specimen, a small section (~ 2 cm) was excised from the thallus and preserved in silica gel or 95% ethanol for future molecular analysis. The remaining part of the specimen was dried, pressed, and preserved as an herbarium voucher. Genomic DNA isolation was carried out at three different laboratories by using the i-genomic Plant DNA Extraction Mini Kit (iNtRON Biotechnology; Korea) for samples from Malaysia and Indonesia, and CTAB extraction for samples from Madagascar, Philippines and Tanzania. The latter uses CTAB and Proteinase K for lysis, chloroform, and isoamyl alcohol for separation, and the NucleoMag (Macherey–Nagel; Germany) kit for the final DNA purification, typically yielding 30–60 ng of high-quality DNA.

Herbarium specimens were deposited at the University of Malaya Seaweeds and Seagrasses Herbarium (KLU), Pusat Unggulan Biosains dan Bioteknologi (PUBB) Mataram University, Sorsogon State University Herbarium Sorsogonense (HS), and University of the Philippines, The Marine Science Institute (UP-MSI). Details of the species used in the study are summarized in Table S1.

Genome skimming, mitogenome assembly and annotation

The extracted DNA was submitted for whole genome amplification using the Repli-g Mini-kit (Qiagen, UK) according to the manufacturer's instructions. Thirty μL of each sample (with a DNA concentration ranging from 500 to 880 ng μL^{-1}) were then submitted to Novogene for library preparation using the NEBNext Ultra II DNA Library Prep Kit, followed by shotgun sequencing on an Illumina NovaSeq platform in order to generate an average of 10 Gb of 150 bp-long paired-end reads for each sample, corresponding to an estimated 50 × coverage of a 200 Mb genome.

After standard quality-control, deduplication and trimming steps using MultiQC and Trimmomatic with default parameters, the genome skimming data was first analyzed using Phyloflash (Gruber-Vodicka et al. 2020) using default parameters, which reconstructed 18S rRNA sequences to investigate the phylogenetic composition of the sequenced specimen. The genome skimming data of red algal specimens devoid of any contaminating DNA sequences were then subjected to Getorganelle (Jin et al. 2020a, 2020b) to assemble the mitochondrial genome. This was performed using default parameters (1 thread, 10 rounds) with the Embryophyta plant mitochondria genome (i.e., embplant_mito) as reference, while the mitogenome of related species, i.e., *Kappaphycus alvarezii* (NC_031814), *K. striatus* (NC_024265), *K. malesianus* (NC_068226), *Eucheuma denticulatum* (NC_036432) and *Betaphycus gelatinus* (NC_036431) were used as the seed (Tablizo and Lluisma 2014; Li et al. 2018; Crisostomo et al. 2023).

The results were accessed using Geneious Prime 2024.0.7 (https://www.geneious.com), which was also employed for genome circularization, annotation, and editing using the aforementioned reference genome sequences. Secondary structure prediction was performed using default parameters in RNAstructure (Reuter and Mathews 2010). Translation frames for protein-coding sequences (CDS) annotations were verified by visual inspection of amino acid sequences to detect frameshifts and premature stop codons. The final genome map was generated using OGDRAW (Greiner et al. 2019) and edited using Adobe Photoshop 2025 (https://www.adobe.com/products/photoshop.html). Gene synteny was visualized by aligning the mitogenomes of selected taxa representing nine different eucheumatoid species utilized in this study. Default alignment parameters, including automatic seed weight calculation and minimum Locally Collinear Block (LCB) scores, were set using the MAUVE alignment plugin v1.1.3 (Darling et al. 2004) in Geneious Prime.

Phylogenetic analysis

Specimens with complete genomes consisting of 24 mitochondrial protein-coding sequences (CDS; i.e., *atp*4, *atp*6, *atp*8, *atp*9, *cob*, *cox*1, *cox*2, *cox*3, *nad*1, *nad*2, *nad*3, *nad*4, *nad*4L, *nad*5, *nad*6, *rpl*16, *rpl*20, *rps*3, *rps*11, *rps*12, *sdh*2, *sdh*3, *sdh*4, and *tat*C) and two ribosomal RNA genes (*rns* and *rnl*), herein defined as the concatenated dataset, were selected for phylogenetic analysis. A separate, more inclusive analysis was performed by incorporating incompletely sequenced specimens that contained at least 15 mitochondrial CDS, with any gaps in the DNA sequences substituted with ambiguous N nucleotides. Multiple sequence alignment was performed for all individual, protein-coding (i.e., 24 CDS) and concatenated dataset (i.e., 24 CDS + 2 rRNA) sequences using MUSCLE (Edgar 2004). An additional *cox*2–3 spacer dataset was also analyzed considering its vast use in eucheumatoid phylogeny. The outgroup taxa *Chondrus crispus* (Gigartinales) and *Gracilaria vermiculophylla* (Gracilariales) of the subclass Rhodymeniophycidae were chosen based on their genetic relatedness to eucheumatoids (Tan et al. 2024).

Optimal partitioning schemes and substitution models of each dataset were generated using the default "greedy" algorithm in Partition Finder v2.1.1 (Lanfear et al. 2018). Each rRNA gene was treated as a single block without defining code positions. IQTREE web server (Trifinopoulos et al. 2016) at http://iqtree.cibiv.univie.ac.at/ was used to construct ML trees over 2,000 ultrafast bootstrap replicates using the best-fit models of substitution suggested for each partition.

Bayesian Inference (BI) analysis was conducted using MrBayes v3.2.6 (Ronquist et al. 2012), applying the recommended partitions and substitution models identified by Partition Finder. The analysis employed the Markov chain Monte Carlo (MCMC) method, comprising two independent runs of 20,000,000 generations, with each run utilizing four Markov chains and sampling trees at every 100th generation. Convergence of log-likelihood values was assessed using Tracer v1.7 (Rambaut et al. 2018), with the first 25% of samples discarded as burn-in. All phylogenetic trees were subsequently visualized and annotated using Figtree v1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/).

Marker assessment for molecular identification and phylogeny

The MSA genetic information of the 24 mitochondrial protein-coding sequences and 2 rRNA sequences was retrieved from Geneious Prime. Individual marker trees were compared to that of the concatenated tree to evaluate similarities in topology and resolution. The ability of individual trees in accurately identifying species was assessed using the tree-based assessment approach from Tan et al. (2024).

Species delimitation was conducted using Assemble Species by Automatic Partitioning (ASAP) and Automatic Barcode Gap Discovery (ABGD) on concatenated mitochondrial coding sequences (CDS) to rapidly generate initial exploratory groupings based on distance-based methods. Both analyses were performed using the ASAP and ABGD extensions implemented in iTaxoTools (https://itaxotools.org/) (Puillandre et al. 2012, 2021; Vences et al. 2021).

Genetic distance

Uncorrected pairwise genetic distances (GD) were estimated for the concatenated dataset using PAUP 4.0b10 (Swofford 2003).

Results

A total of 26 complete mitochondrial genomes (Fig. 1; Fig. S1–S6) were successfully recovered from the 46 specimens subjected to genome-skimming, with 8 specimens achieving 90% sequencing coverage (Table S1). The mitogenomes of *E. platycladum*, *Kappaphycus* sp. (Africa), *K. striatus* (wild genotype) and *K. cottonii* were fully sequenced for the first time (Fig. 1). A summary of the mitogenome

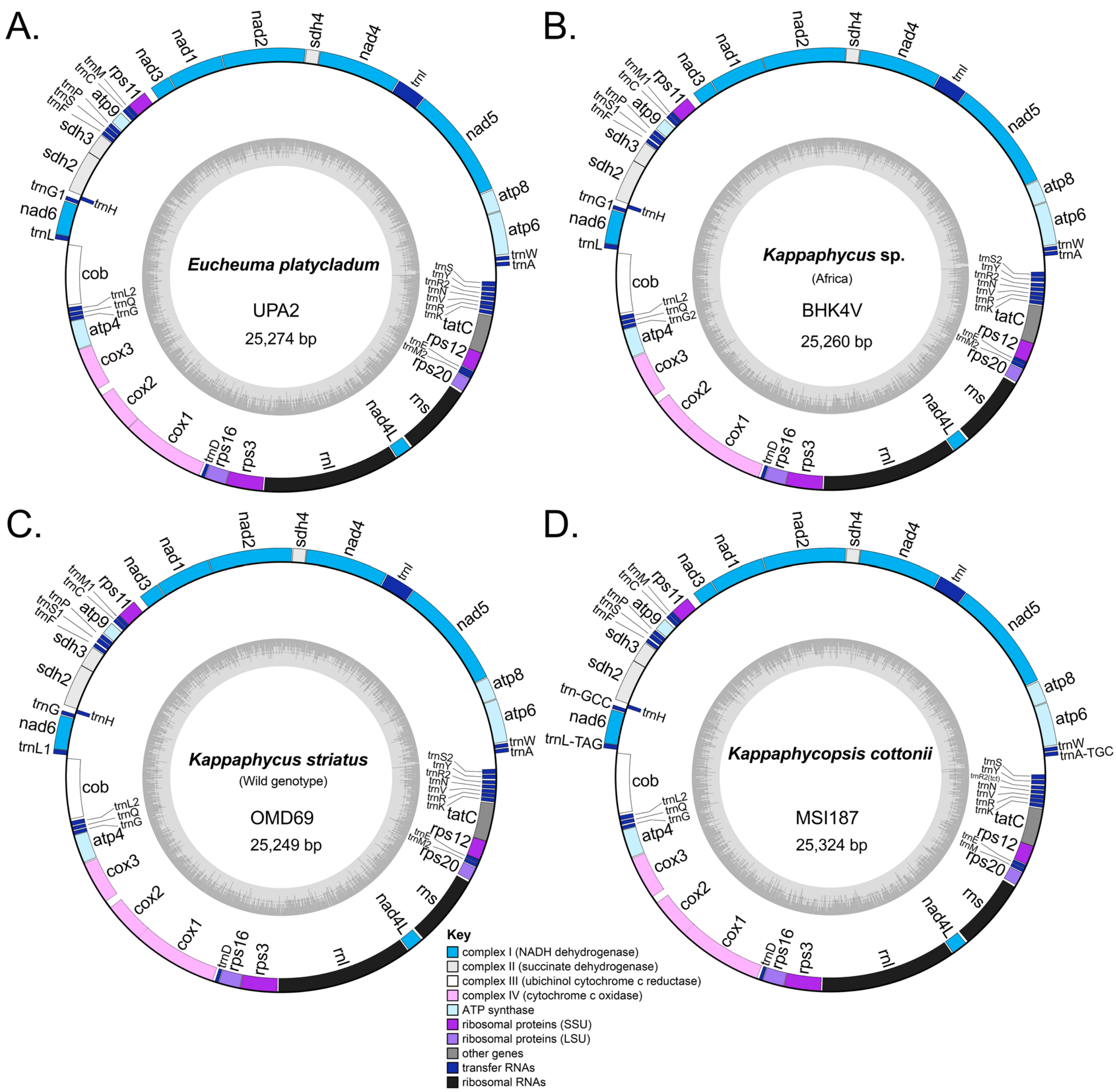

Fig. 1 Maps of novel mitochondrial genomes sequenced in this study **A**. *Eucheuma platycladum* (UPA2); **B**. *Kappaphycus* sp. Africa (BHK4V); **C**. *Kappaphycus striatus* (Wild genotype; OMD69); **D**. *Kappaphycopsis cottonii* (MSI187)

characteristics of sequenced species from this study is presented in Table 1. Complete representation was achieved for all eucheumatoid genera defined in this study (*Betaphycus*, *Eucheuma*, *Mimica*, *Kappaphycopsis*, and *Kappaphycus*). The sequenced taxa represent approximately 60% of the currently accepted species of *Kappaphycus*, ~ 0.1% of *Eucheuma*, 50% of *Mimica*, 50% of *Betaphycus*, and 100% of the monotypic *Kappaphycopsis* (Guiry and Guiry 2025).

All examined taxa contained identical genomic features: two transcriptional units oriented in opposite transcriptional directions, 50 total genes comprising 24 protein-coding genes, 24 tRNA genes, two rRNA genes, and one intron (inserted in the tRNA-Ile gene), with extensive gene synteny across species (Fig. S7). GC content ranged from 29.7% to 31.4%, while spacer content varied between 4.03% and 7.78%. A stem-loop was identified at the *trn*A–*trn*S or *trn*A–*trn*S2 region and a short hairpin structure (*cob*–*trn*L) in the opposite stem-loop.

In coding sequences (CDS), all species except *B. gelatinus* and *E. denticulatum* had 23 ATG and one TTG start codons. TAA and TAG were the exclusive stop codons. The sizes of most genes were identical across all tested eucheumatoid species, except for *atp*6, *atp*8, *cob*, *cox*1, *cox*2, *nad*5, *nad*6, *sdh*2, *rpl*20, *rps*3, *rps*12, and both rRNA (Table S1). No overlapping genes were identified except for three distinctive cases: (i) *tat*C–*rps*12 overlaps were exclusively observed in *M. arnoldii* (35 bp), *B. gelatinus* (35 bp), and *E. denticulatum* (50 bp); (ii) *cox*1–*cox*2 overlaps of 8 bp observed in all tested eucheumatoids except *E. denticulatum*; and (iii) *nad*4L–*rnl* overlaps of 3 bp exclusive to *B. gelatinus*, *E. denticulatum* and *E. platycladum*.

Despite having 24 tRNA genes and a conserved gene order, all samples exhibited increased variability in tRNA sequences, particularly at the junction of the two transcriptional units. Specific amino acid tRNAs are missing in various species. For example, glycine (Gly), methionine (Met), and threonine (Thr) are absent in *K. alvarezii*, while only Gly and Thr are missing in *K. striatus*. Threonine alone is absent in *K. malesianus*, *Kappaphycus* sp. Indonesia, *K. cottonii*, *Mimica arnoldii*, *B. gelatinus*, and *E. platycladum*. Finally, arginine (Arg) and Thr are missing in both *E. denticulatum* and *E. platycladum*.

The genetic details of incompletely sequenced mitogenome specimens are also summarized in Table S1.

Table 1 Complete mitogenome features of nine eucheumatoid species sequenced in this study

	Betaphycus gelatinus	*Eucheuma denticulatum*	*Eucheuma platycladum*	*Kappaphycopsis cottonii*	*Kappaphycus alvarezii*	*Kappaphycus malesianus*	*Kappaphycus* sp. (Africa)	*Kappaphycus striatus*	*Mimica arnoldii*
No. of sequenced sample	2	4	1	3	2	7	2	4	1
Genome size (bp)	25,330–25,370	25,102–25,520	25,274	25,221–25,340	25,198–25,314	25,213–25,434	25,231–25,260	25,225–25,296	25,200
GC content (%)	29.7–29.8	30.3–30.4	30.4	31.4	29.8	30.2–30.3	29.8–30.0	30.1	30.5
Spacer content (%)	4.04–7.80	4.03	4.17	4.19–4.21	4.10–4.21	4.11–5.58	4.09–5.44	4.10–5.16	5.35
Total no. of genes	50	50	50	50	50	50	50	50	50
Protein-coding genes	24	24	24	24	24	24	24	24	24
tRNA genes	24	24	24	24	24	24	24	24	24
rRNA genes	2	2	2	2	2	2	2	2	2
Intron	1	1	1	1	1	1	1	1	1
Start Codons*									
ATG	22	24	23	23	23	23	23	23	23
GTG	-	-	-	-	-	-	-	-	-
TTG	1	0	1	1	1	1	1	1	1
ATA	1	-	-	-	-	-	-	-	-
Stop Codons*									
TAA	22	21	19	21	22	22	22	22	20
TAG	2	3	5	3	2	2	2	2	4
TGA	-	-	-	-	-	-	-	-	-

Asterisks indicate start and stop codons for protein-coding sequences (CDS) only

Although incomplete, 21 out of the 24 protein-coding genes (*atp*6, *atp*8, and *nad*5 genes not sequenced) from an undescribed species of *Kappaphycus* (ARW8) from Indonesia were characterized. The genetic distinction of ARW8 was supported by both ASAP and ABGD species delimitation models (Fig. S8).

Phylogeny and species delimitation

The concatenated phylogenetic tree was constructed using 24 CDS and 2 rRNA sequences (Fig. 2). The topology of this concatenated tree is largely consistent with those derived from only the 24 CDS (Fig. S9) and the tree featuring only the 26 specimens with complete genome sequences (Fig. S10). All three trees supported the monophyly of the eucheumatoids characterized by generally strong nodal support.

Although the monophyly of every genus was well supported (Figs. 2, S9 and S10), *Eucheuma* was paraphyletic, albeit based on a notably small sample size of specimens involving two *Eucheuma* species. Two subclades were identified in *K. alvarezii*, corresponding to the global cultivar and African genotypes. *Kappaphycus striatus* was also divided into two clades: one consisting of wild specimens collected from Malaysia, and the other comprising cultivars. An exception was a wild specimen from Malaysia (SBK71) which grouped with the latter. Although *K. malesianus* appears to be closely related to the clade comprising *K.*

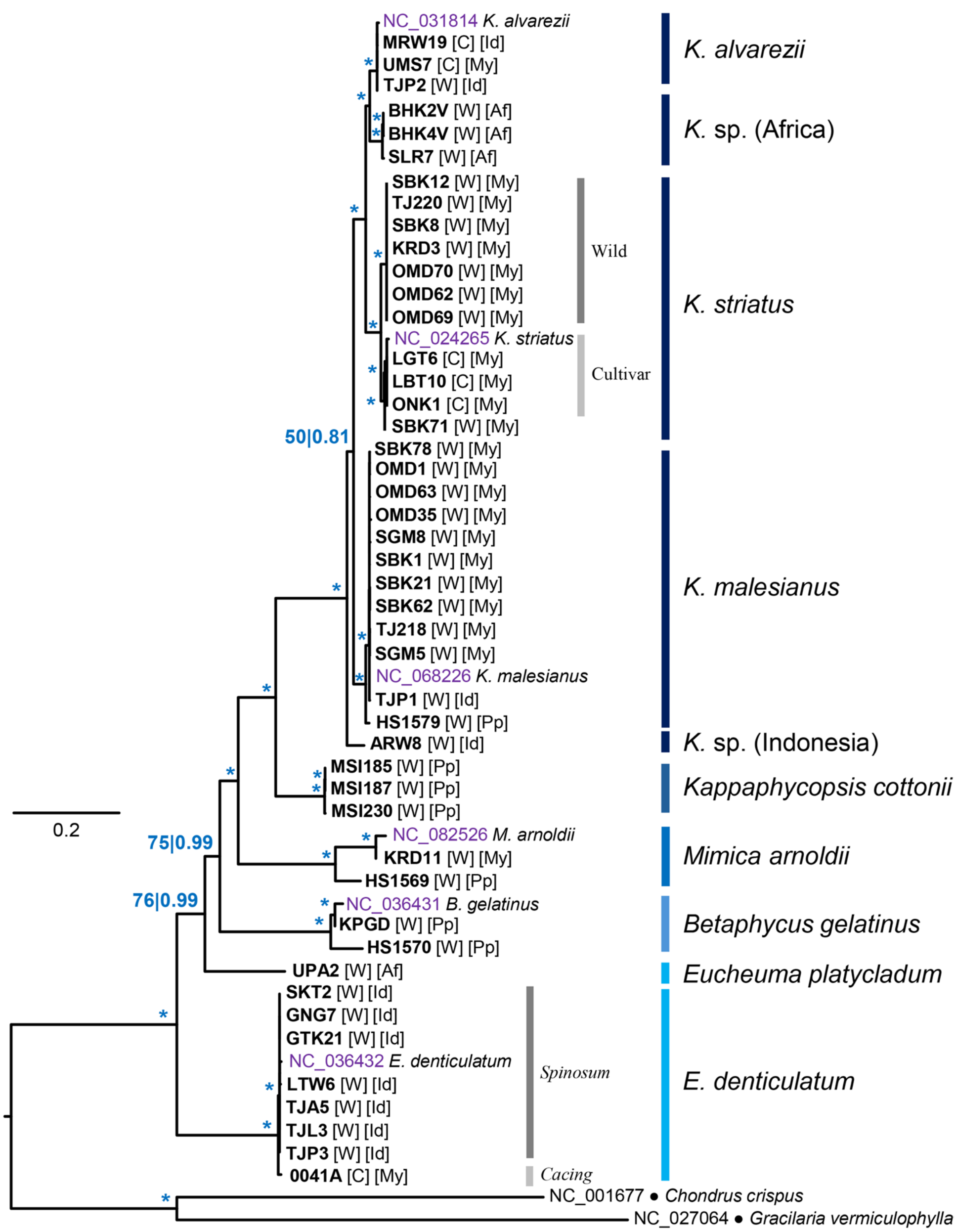

Fig. 2 Bayesian tree of eucheumatoids reconstructed from the concatenated data of 24 mitochondrial protein-coding sequences (CDS) and two ribosomal RNA. Numbers at nodes indicate ultrafast UFML bootstrap support and Bayesian posterior probabilities. Asterisks indicate ML = 100%; PP = 1.00. Letters in parentheses indicate cultivar (C) or wild specimen (W). Letters in square brackets indicate locality of origin: ID, Indonesia; Mg, Madagascar; My, Malaysia; Pp, Philippines; Tz, Tanzania. Scale bar represents number of substitutions per site

alvarezii, *Kappaphycus* sp. (Africa), and *K. striatus*, this relationship is weakly supported (50/0.81) and therefore remains unresolved.

The genetic distinctiveness of the Indonesian specimen ARW8 was strongly supported. *K. cottonii*, *B. gelatinus* and *M. arnoldii* were each inferred to be monophyletic, with the latter two clades containing haplotypes which were genetically distinct from each other.

Species delimitation using ASAP and ABGD (Fig. S8), based on mitochondrial genes excluding *atp*6, *atp*8, and *nad*5, delimited 12–13 putative species, with ASAP being able to differentiate the wild and cultivar genotypes of *K. striatus*. Both species-delimitation models also consistently identified two putative species within *M. arnoldii* and *B. gelatinus*, respectively.

Marker performance

The phylogenetic trees reconstructed from every individual marker and *cox*2–3 spacer is provided as Figs. S11–S37. Results of individual marker performance in tree-based identification and phylogenetic resolution are summarized in Table S2. Out of the 26 markers tested, *nad*5, *rnl* and *nad*2 recorded the highest number of parsimony-informative sites, at 810, 647 and 615, respectively. All markers except for *atp*9 could be used to delineate species into monophyletic clades. However, only *atp*4*, nad*3*, nad*4 *and nad*6 resulted in phylogenetic tree topology similar to that of the concatenated tree (Fig. 2) albeit with relatively lower resolution. Most individual markers were unable to resolve the placements of *B. gelatinus*, *M. arnoldii*, *E. denticulatum* and *E. platycladum*.

Genetic distance

Genetic distance data of eucheumatoid species (except *Kappaphycus* sp. from Indonesia) based on the 24 CDS and 2 rRNA mitochondrial genes is summarized in Table 2 (and Table S3). Intergeneric distance was ranged from 14.05–19.43%. Interspecific distance within *Kappaphycus* and *Eucheuma* were recorded as 2.51–6.66% and 17.58–17.60%, respectively. Notably, a genetic difference of 1.41–1.45% was observed between the "wild" and "cultivar" genotypes of *K. striatus* (see Fig. 2). Meanwhile, *K. malesianus* HS1579 showed a genetic difference of 1.23–1.29% compared to other *K. malesianus* specimens from Malaysia and the Philippines. Additionally, *E. denticulatum* "cacing" (specimen 0041 A) exhibited a genetic difference of 0.71–0.86% from the rest of the *E. denticulatum* specimens. Relatively large intraspecific genetic distances were also observed within both *B. gelatinus* (0.13–3.61%) and *M. arnoldii* (7.96%).

Table 2 Summary of p–distance (%) among selected eucheumatoid species based on 24 CDS and 2 rRNA mitochondrial genes

No	Species	1	2	3	4	5	6	7	8	9	10
1	*K. alvarezii*	0.01–0.04									
2	*Kappaphycus* sp. (Africa)	2.51–2.62	0.44								
3	*K. striatus* (wild)	4.58–4.60	4.63–4.70	0.06–0.18							
4	*K. striatus* (cultivar)	4.62	4.66–4.72	1.41–1.45	0						
5	*K. malesianus*	5.56–5.76	5.71–5.85	6.36–6.63	6.46–6.66	0.03–1.29					
6	*Kappaphycopsis cottonii*	14.23–14.30	14.32–14.57	14.53–14.64	14.63–14.68	14.05–14.44	0.22				
7	*Mimica arnoldii*	17.56–17.85	17.57–18.00	17.72–18.22	17.78–18.23	17.38–17.89	17.61–17.71	7.96			
8	*Betaphycus gelatinus*	17.88–17.95	17.76–18.11	17.92–18.12	17.99–18.19	17.53–18.18	17.35–17.60	17.84–18.49	0.13–3.61		
9	*Eucheuma platycladum*	17.30–17.31	17.09–17.27	17.22–17.23	17.33	16.93–17.40	16.78–16.82	17.23–17.77	16.86–16.97	0	
10	*Eucheuma denticulatum*	19.01–19.12	18.73–19.05	19.09–19.26	19.18–19.29	18.27–18.95	18.73–18.82	19.01–19.43	18.16–18.46	17.58–17.60	0.04–0.86

Dataset includes sequences with complete mitogenomes from this study ($n = 26$) in addition to *Kappaphycus alvarezii* (NC_031814), *K. striatus* (NC_024265), *K. malesianus* (NC_068226), *Eucheuma denticulatum* (NC_036432) and *Betaphycus gelatinus* (NC_036431)

Diagonal values represent within-species genetic divergence

Discussion

Mitogenome data

The results of this study represent the largest dataset to resolve the phylogeny of eucheumatoids, involving the sequencing of complete mitochondrial genomes from common eucheumatoid species from the Indo-Pacific, *B. gelatinus, E. denticulatum, E. platycladum, K. cottonii, K. alvarezii, K. malesianus, Kappaphycus.* sp. (Africa), *K. striatus*, and *M. arnoldii.* The gene composition and arrangement of these mitogenomes were consistent with each other, as well as reports from earlier mitogenome studies (Tablizo and Lluisma 2014; Li et al. 2018; Crisostomo et al. 2023). The mitogenome sizes range from approximately 25,100 to 25,500 bp, with size differences mostly caused by indels in intergenic regions. The stem-loop (*trn*A–*trn*S or *trn*A–*trn*S2) is similar to the displacement-loop (D-loop) in other higher organisms and could potentially be a promoter region or origin of transcription (Boore 1999; Li et al. 2018). The observed gene overlaps in *tat*C–*rps*12, *cox*1–*cox*2, and *nad*4L–*rnl* regions could reflect an evolutionary strategy to maximize essential protein encoding while maintaining genomic compactness and efficiency. Similar overlapping gene arrangements have been documented in other red algae (e.g., *Fushitsunagia* and *Porphyra* species), although these involve different gene combinations (Cai and Scofield 2020; Patil et al. 2024). The generally higher tRNA sequence variability observed at the junction of the two transcriptional units of the mitogenome corroborated Li et al. (2018) who reported that region to be variable region comparing between several species of the order Gigartinales.

The complete mitogenome dataset excludes the Indonesian *Kappaphycus* sp. (ARW8) as only 88% of genes sequenced. *Kappaphycus* sp. Hawaii (ARS 02860, ARS 03513 and ARS 08101), a genetically distinct species identified using five DNA regions (UPA, *rbc*L, ITS, *cox*3, and *cox*2–3 spacer) (Tan et al. 2024) was also excluded because genetic data could not be retrieved. This result suggested that sequencing success may vary among herbarium specimens, influenced by factors such as specimen age, preservation quality and DNA degradation. The species is inferred to be related to *K. alvarezii*, *Kappaphycus* sp. (Africa), and *K. striatus*, although its exact phylogenetic position remained poorly resolved. The current dataset is notably deficient in eucheumatoids like *K. inermis*, *E. perplexum* and *E. serra*, and lacks many species known only from their original descriptions. As such, the inclusion of these overlooked species in future genomic studies is recommended.

Eucheumatoid phylogeny

The concatenated mitogenome CDS-based phylogeny of eucheumatoids (Figs. 2, S9 and S10) corroborated previous phylogenetic frameworks (Zuccarello et al. 2006; Dumilag et al. 2014; Lim et al. 2014) and demonstrated significantly stronger nodal support across all examined taxa. Despite the limited sampling of *Eucheuma* in this study, the basal placement of *E. denticulatum* is congruent with its position in the plastid phylogeny of Zhang et al. (2020). The inclusion of further *Eucheuma* species mitogenomes would be valuable in confirming this finding. Additionally, the substantial genetic divergence between *E. denticulatum* and *E. platycladum* (17.58–17.60%), in combination with the designation of *E. denticulatum* as the type species of *Eucheuma*, suggests that *E. platycladum* may represent a distinct genus. The observed paraphyly of the genus *Eucheuma* indicates the need for more data, including the inclusion of a wider range of species identified as *Eucheuma* and additional plastid data. Efforts are currently underway to obtain sequence data from the Linnaean type of *E. denticulatum* to resolve the placement of the genus.

The finding that *K. striatus* consisted of two distinct subclades, one comprising the commercial cultivar and the other primarily consisting of wild specimens from Southeast Asia, agreed with earlier studies (Lim et al. 2014; Tan et al. 2024). The genetic analysis also showed that the wild specimen SBK71 from Sebangkat, East Malaysia, was closely related to the commercial *K. striatus* cultivar. The absence of *K. striatus* specimens from its purported type locality in Tanzania, Africa (Doty 1988), combined with this finding, raises questions about the cultivar's origin and emphasizes the need for rigorous species surveys in the region to clarify its biogeographic history and distribution.

The molecular results also indicated the necessity for taxonomic updates of several taxa, including unidentified *Kappaphycus* species from Africa and Indonesia, while supporting recent genus elevations of *M. arnoldii* and *K. cottonii* (Santiañez and Wynne 2020; Dumilag and Zuccarello 2022). Although the two genotypes of *K. striatus* were found to be genetically distinct, their genetic difference of 1.41–1.45% is significantly lower than the interspecific divergence of 2.51–6.66%. This suggests that they are not sufficiently genetically divergent to be considered distinct species. Similarly, *E. denticulatum* "cacing" and the common *E. denticulatum* "spinosum" exhibit a genetic difference of only 0.71–0.86%, supporting the conclusion by Tan et al. (2024) that they are conspecific. Additionally, the results also hint at unsuspected species diversity within both *Betaphycus* and *Mimica*, although this hypothesis would need being investigated with a better sampling of both clades. These findings were further supported by preliminary species delimitation using Assemble Species by Automatic Partitioning (ASAP), although Automatic Barcode Gap Discovery (ABGD) suggested that the wild and cultivar *K. striatus* are conspecific. Notably, these species delimitation methods are primarily exploratory tools relying on genetic distance thresholds, which are suitable for datasets with little or no gene tree discordance (as observed here) (Puillandre et al. 2012; Zhang et al. 2013).

Individual marker performance

The rapid and cost-effective identification of eucheumatoid species is crucial for cultivar selection and development, germplasm preservation, bioinvasion detection and conservation efforts (Halling et al. 2013; Dumilag et al. 2016a, 2016b, 2018; Brakel et al. 2021; Tan et al 2022a, 2022b). All 26 coding sequences, except *atp*9, accurately identified species using a tree-based approach. This finding was consistent with earlier reports, which also indicated that *atp*9 exhibits the lowest substitution rates across the family Solieriaceae and Geliadiales (Boo et al. 2016b; Li et al. 2018). These data offer a valuable and updated reference database for rapid and accurate tree-based species identification, particularly in industrial contexts, leveraging genetic markers like *cox*1, *cox*2, the *cox*2–3 spacer, and *rbc*L which were already in use (Tan et al. 2012, 2024; Lim et al. 2014; Dumilag et al. 2022). Primer information for these markers is provided in Table S4. These resources are important because GenBank entries may be misidentified or outdated due to limitations in sequence accuracy, barcode resolution, or database coverage (Sherwood et al. 2010; Jin et al. 2020a, b; Gabriel et al. 2024).

On the other hand, the *atp*4, *nad*3, *nad*4 and *nad*6 trees were similar to the concatenated tree (Fig. 2), suggesting their potential utility in inferring intergeneric relationships. This pattern was further supported by analyses combining these four markers (Fig. S38–S40); however, relationships among *Betaphycus*, *Eucheuma*, and *M. arnoldii* were recovered only under Bayesian inference and not under Maximum Likelihood. Nevertheless, the potential utility of these markers, whether applied individually or in combination, is noteworthy, as commonly used mitochondrial DNA barcodes or genetic markers (e.g., *cox*1 and the *cox*2–3 spacer) often exhibit limited resolution for such relationships (Zuccarello et al. 2006; Tan et al. 2013, 2024), a challenge also evident in the present results (Figs. S30 and S37). Genes encoding NADH dehydrogenase and cytochrome *c* oxidase have been reported to exhibit greater genetic variation (Boo et al. 2016a, 2020; Lee et al. 2018), making them suitable for future molecular phylogenetic analysis of eucheumatoids (Li et al. 2018; Tan et al. 2024).

Conclusion

This study provides the most comprehensive phylogenetic analysis of eucheumatoids to date by sequencing and analysing complete mitochondrial genomes from key species across the Indo-Pacific. The results revealed consistent gene arrangements and strong support for monophyletic clades, although the paraphyly of *Eucheuma* underscores the need for further taxonomic investigation. Genetic divergences between wild and cultivated specimens, as well as among geographically distinct populations, emphasize the importance of conserving genetic diversity for long-term population viability, as well as supporting cultivar development.

The phylogenetic framework generated in this study offers a valuable reference for future taxonomic studies, cultivar development programs, and conservation efforts. Individual marker assessments highlight the effectiveness of most mitochondrial genes for species identification, with implications for industrial use and conservation efforts. Future studies should expand sampling efforts, increase species coverage, and conduct plastome analyses to fully capture the genetic diversity and elucidate the evolutionary pathways of these economically important seaweeds.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10811-026-03784-1.

Acknowledgements The authors thank the PCIA Intensive Computing and Algorithmic Platform, National Museum of Natural History, National Center for Scientific Research, UAR 2047 DoHNÉE, CP 26, 57 rue Cuvier, F-75231 Paris Cedex 05, France for server support. The authors would like to dedicate this paper in memory of the late Dr. Flower E. Msuya.

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Funding Open access funding provided by The Ministry of Higher Education Malaysia and Universiti Malaya. This work is part of the GlobalSeaweedSTAR project supported by the UK Research and Innovation – Global Challenges Research Fund (GCRF), Biotechnology and Biological Sciences Research Council Grant 2017 No. (BB/PO27806/1). Part of the study was funded by the Safe Seaweed Coalition SSC 2021 – Project Gateway (LS248520; IF054-2022). The authors acknowledge infrastructure and resources support from the Higher Institution Centre of Excellence (HiCOE) Programme (HICoE IOES-2023F) by Ministry of Higher Education Malaysia. Specimen collection in the Philippines was further supported by research grants awarded to RVD from the Nagao Natural Environment Foundation (NEF) and the Department of Science and Technology–Philippine Council for Agriculture, Aquatic and Natural Resources Research and Development (DOST–PCAARRD). The DOST–PCAARRD grant also supported MYR.

Data availability Sequence data that support the findings of this study are currently being submitted to Genbank and the accession numbers will be provided in due course.

Declarations

Competing interests . PE Lim and MY Roleda are editorial board members of Journal of Applied Phycology and co-authors of this article. They were excluded from editorial decision-making related to the acceptance of this article for publication in the journal.

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