

Review

Diversity and Geographical Distribution of Coralline algae in China: A Comprehensive Literature-Based Assessment

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Abstract

Coralline algae are important calcifying red algae that contribute substantially to marine ecosystem structure and biogenic reef formation. However, their species diversity and geographic distribution in China remain poorly documented due to their extensive calcification, morphological convergence, and ongoing revisions of taxonomic frameworks. In this study, we reviewed published Chinese and English literature from 1980 to 2026 using Web of Science and the China National Knowledge Infrastructure (CNKI), with the literature search completed on 2 July 2026. By integrating species records, taxonomic revisions, and regional distribution data, we assessed the diversity and spatial distribution patterns of coralline algae in China. Historical records were revised by incorporating updated taxonomic information, including corrections of synonyms and taxonomic changes, resulting in an updated and verifiable checklist of accepted species. Our results showed that 109 coralline algal species, belonging to 30 genera, 8 families, and 3 orders, are currently recorded in China. Among these taxa, Corallinales contains the highest species diversity, Corallinaceae represents the most species-rich family, and *Jania* is the most species-rich genus. Taiwan, Hainan, and Sansha exhibit relatively high species richness, whereas differences among regions may be associated with variations in survey intensity. Spearman correlation analysis revealed a positive relationship between regional publication numbers and recorded species richness, suggesting that current understanding of coralline algal diversity in China remains influenced by sampling effort. This study provides an updated assessment of coralline algal diversity and spatial distribution patterns in China, establishing baseline information for future taxonomic research, biodiversity assessments, and conservation efforts.

Keywords: species checklist; taxonomic revision; literature synthesis; Corallinophycidae; cryptic diversity

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1. Introduction

Coralline algae constitute a diverse lineage of marine red algae within Rhodophyta, Florideophyceae, and Corallinophycidae. A defining feature of this group is the deposition of magnesium-rich calcite within cell walls and thallus structures [1], which confers high mechanical strength and enhances resistance to physical disturbance [2]. Nearly all coralline algae are exclusively marine and are distributed across shallow photic and mesophotic coastal habitats [3]. As globally important marine calcifying organisms, coralline algae play essential roles in ecosystem functioning and habitat formation. Their thalli and coralline algal nodule beds create structurally complex benthic habitats that support diverse marine organisms by providing shelter, refuge, and recruitment substrates, thereby promoting biodiversity through habitat heterogeneity and species interactions [4–6]. In coral reef ecosystems, crustose coralline algae (CCA), a major ecological form of non-geniculate coralline algae, contribute to carbonate framework development, with carbonate production rates that can equal or exceed those of reef-building corals under certain environmental conditions [7]. Furthermore, CCA serve as critical settlement substrates for coral larvae, thereby contributing to coral reef formation, persistence, and regeneration [8]. Through their coupled photosynthetic and calcification processes, coralline algae participate in marine carbon and carbonate cycling. Globally, coralline algal beds exhibit high productivity and carbon sequestration potential [5]. However, these ecological functions are closely linked to growth and calcification processes, rendering coralline algae vulnerable to global environmental changes, particularly ocean acidification and warming. Such disturbances may consequently alter habitat structure, biodiversity, and ecosystem functioning [7,9]. Therefore, coralline algae represent key ecosystem engineers and carbonate producers that link biodiversity maintenance, coral reef development, and marine carbon cycling.

The taxonomic history of coralline algae has been long and complex [10]. Prior to 2003, their classification was primarily based on thallus morphology, anatomical characteristics, and reproductive features [11–14]. However, species identification and systematic classification based solely on traditional morphological and anatomical characters remain challenging, particularly for non-geniculate coralline algae. This difficulty is largely attributed to their highly calcified thalli, simple anatomical structures, considerable phenotypic plasticity, and widespread morphological convergence [10]. Since 2003, molecular phylogenetic approaches have been increasingly applied to coralline algal studies. The integration of molecular data with morphological and anatomical evidence has substantially advanced revisions of coralline algal systematics and taxonomy [15–18]. In recent years, multilocus phylogenetic analyses and DNA barcoding studies have further revealed cryptic diversity and phylogenetic heterogeneity within traditionally recognized morphological groups, driving continuous revisions at both generic and species levels [10,19,20]. As of 22 June 2026, our compilation of the World Register of Marine Species (WoRMS) database indicates that Corallinophycidae comprises 5 orders, 14 families, and 82 genera [21] (Table 1).

Table 1. Global classification of coralline algae as recorded in WoRMS.

Subclass	Order	Family	Genus	Species
Corallinophycidae	Corallinales	Corallinaceae	23	184
		Lithophyllaceae	7	236
		Lithothamniaceae	/	/
		Spongitaceae	/	/
		Spongitiaceae	3	56
		Hydrolithaceae	3	29

	Mastophoraceae	4	14
	Porolithaceae	5	32
	Corallinales incertae sedis	1	1
Corallinapetrales	Corallinapetraceae	1	2
	Hapalidiaceae	15	137
Hapalidiales	Mesophyllumaceae	14	89
	Rhodogorgonaceae	3	3
Rhodogorgonales			
Sporolithales	Sporolithaceae	3	34

Note: Global data in this table were derived from the WoRMS database [21], with species counts updated as of 22 June 2026.

China possesses an extensive coastline spanning temperate, subtropical, and tropical climatic zones, with diverse marine environments including the Yellow Sea, East China Sea, and South China Sea. These environmental gradients provide potential conditions for the development of complex geographic distribution patterns of coralline algae. However, compared with the recognized ecological importance of coralline algae in global marine ecosystems, nationwide assessments of their taxonomy, diversity, and geographic distribution in China remain relatively limited [22–27]. Existing information is either scattered among regional surveys of marine algae [25,28–31] or restricted to diversity assessments of specific taxonomic groups [32–34]. Moreover, discrepancies exist among studies in the taxonomic frameworks applied and the criteria used for species identification. In recent years, rapid advances in molecular phylogenetics have resulted in the redefinition of several traditional taxonomic groups [18–20,35,36], accompanied by the publication of additional regional surveys and species records [29–34]. These developments have led to inconsistencies between historical checklists and current taxonomic concepts. Consequently, previously reported species numbers and geographic distribution patterns of coralline algae in China may no longer fully represent current taxonomic knowledge.

Based on these considerations, we systematically searched and compiled published Chinese and English literature from 1980 to 2026, integrating information from authoritative databases, including WoRMS and AlgaeBase, to standardize and validate species names, taxonomic status, geographic records, and growth forms of coralline algae in China. Accordingly, this study aimed to (1) establish a validated checklist of accepted coralline algal species currently recorded in China; (2) assess the effects of recent taxonomic revisions on species composition and taxonomic hierarchy; (3) characterize regional patterns of coralline algal diversity and geographic distribution; and (4) evaluate the potential influence of literature accumulation and sampling effort on regional differences in species records. Furthermore, we identify key knowledge gaps in current assessments of coralline algal diversity in China and provide baseline information for future standardized surveys, molecular systematic studies, and biodiversity conservation and monitoring.

2. Materials and Methods

2.1. Compilation of an Initial Checklist of Coralline Algal Diversity and Geographic Distribution in China

This study covered published Chinese and English literature from 1980 to 2026. Literature searches were conducted using Web of Science and the China National Knowledge Infrastructure (CNKI), with the search completed on 2 July 2026. The retrieved literature included research articles, proceedings papers, review articles, and book chapters. The English search terms mainly included “coralline algae”, “Corallinophycidae”, “calcified macroalgae”, “intertidal macroalgae”, and major coralline algal genera. These terms were combined with geographic keywords, including “China”, “Chinese”, “Taiwan”, “Hainan”, “Sansha”, “Hong Kong”, “South China Sea”, “East China Sea”, “Yellow Sea”, “Bohai Sea”, and the names of major coastal provinces. Corresponding Chinese terms and genus names were used for searches in CNKI (Figure 1).

The criteria for inclusion of species in the checklist were as follows: (1) peer-reviewed publications, monographs, dissertations, and formal survey reports addressing coralline algal taxonomy, distribution, ecological surveys, or molecular identification within Chinese waters; (2) records that could be traced to an accepted species name or a verifiable taxonomic unit; and (3) records with at least one confirmed geographic occurrence in China.

Records were excluded if they: (1) focused on calcified algae or macroalgae other than coralline algae; (2) were secondary records with unverifiable species identities or geographic origins; (3) were duplicate species records from the same survey area; or (4) discussed coralline algae only at a global scale without providing occurrence records from China.

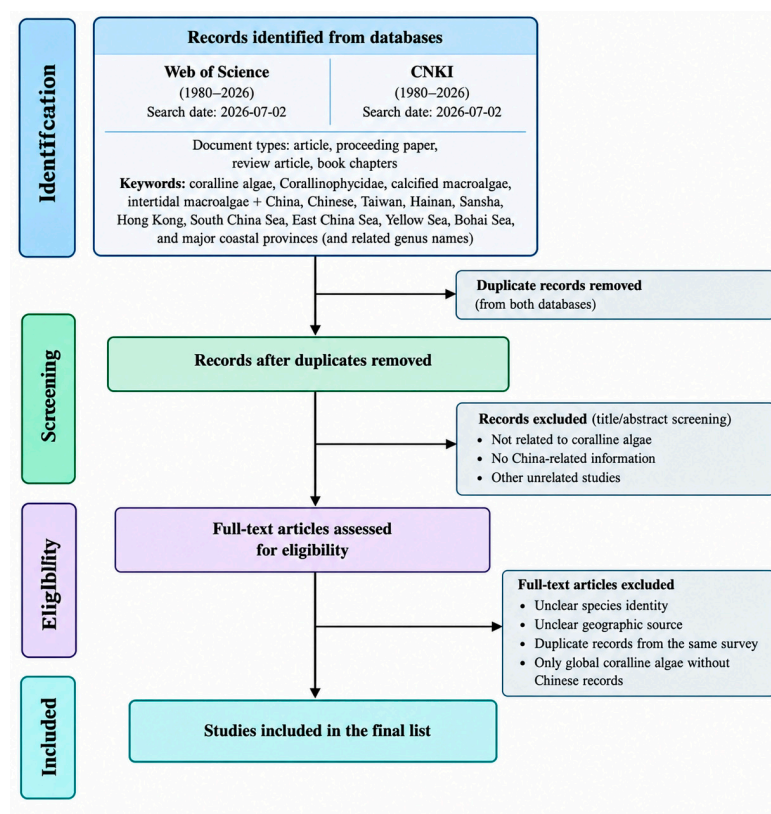


Figure 1. PRISMA-style flow diagram illustrating the literature screening and species inclusion process used to compile the checklist of coralline algae in China.

2.2. Taxonomic Standardization, Synonym Screening, and Validation of Species Records

(1) The preliminary checklist was first verified against AlgaeBase and WoRMS to obtain accepted species names, author citations, original names, taxonomic placement (order, family, and genus), type species, synonyms, WoRMS AphiaIDs, and AlgaeBase IDs.

(2) Based on the preliminary checklist, synonym screening and species record consolidation were conducted according to current taxonomic frameworks. Species records that were absent from databases or considered taxonomically uncertain were further examined using AlgaeBase, WoRMS, Flora Algae Marinarum Sinicarum: Rhodophyta: Corallinales (Chinese Seaweed Flora: Rhodophyta: Corallinales), and other relevant taxonomic literature [21,26,27] for final verification.

(3) For taxonomic units with controversial status or those differing from the checklist compiled by Lei et al. [27], the original taxonomic literature was reviewed to document the primary evidence supporting their classification. For taxa involving changes in family or genus-level placement, we distinguished between the current taxonomic status accepted by databases and the taxonomic treatment adopted in this study based on the original literature.

2.3. Classification of External Morphological Forms

External morphological forms of coralline algae have been categorized into several types, including articulated (geniculate) coralline algae, non-articulated (non-geniculate) coralline algae, encrusting non-geniculate coralline algae, articuliths, and rhodoliths [37–39]. Following recent studies [34,40,41], this study adopted the classification framework proposed by Adey and Johansen [42], in which coralline algae were broadly categorized into two major morphological groups: geniculate coralline algae and non-geniculate coralline algae. The latter group includes encrusting non-geniculate coralline algae and rhodoliths.

2.4. Geographic Regionalization and Quantitative Analysis

Geographic records were standardized according to the regional categories provided in Table S1. When a single species occurred in multiple regions, each region was treated as an independent occurrence record. The observed regional species diversity was defined as the number of accepted species recorded in each region, rather than the actual species diversity.

Spearman correlation analysis was performed to examine the monotonic relationship between the number of survey publications and observed species diversity among regions.

3. Results and Discussion

3.1. Taxonomic Revisions at the Family and Genus Levels of Coralline Algae in China

Compared with the checklist compiled by Lei [27], the present checklist revealed changes in the family and genus-level classification of Chinese coralline algae, including the merging of one family, the addition of five genera, and revisions of four genera.

In the checklist compiled by Lei [27], *Lithothamnion* Heydrich and *Phymatolithon* Foslíe were assigned to Lithothamniaceae. However, both AlgaeBase and WoRMS currently place *Lithothamnion* and *Phymatolithon* within Hapalidiaceae (Hapalidiales) [21,43]. Following the taxonomic framework proposed by Harvey et al. [15], we adopted this revised placement.

Manevelde et al. [44] demonstrated that *Phymatolithon* comprises two monophyletic lineages within Hapalidiales. By integrating DNA sequence data with comparisons of

type specimens and recently collected specimens, Jeong et al. [45] established a new genus, *Phymatolithopsis* S.Y. Jeong, Maneveldt, P.W. Gabrielson and T.O. Cho. The genus *Phymatolithopsis* differs from *Phymatolithon* in the origin of conceptacle primordia (surface origin in the former, directly derived from the subepidermal initial cell layer beneath epidermal cells) and the distribution pattern of sterile filaments within carposporangial conceptacles (located along the margins of fused cells in the former). Jeong et al. [45] further suggested that *Phymatolithon repandum* (Foslie) Wilks and Woelkerling, previously assigned to *Phymatolithon*, does not conform to the revised generic concept of *Phymatolithon* and should instead be transferred to *Phymatolithopsis*. We adopted this taxonomic treatment in the present study.

Several studies have suggested that *Lithothamnion*, another genus within Hapalidiales, represents a polyphyletic group [18,19,46]. Gabrielson et al. [20] found that several species historically assigned to *Lithothamnion* formed a monophyletic lineage with other Northern Hemisphere cold-water species but were phylogenetically distant from *Lithothamnion sensu stricto*. Based on these findings, they established the new genus *Boreolithothamnion* P.W. Gabrielson, Maneveldt, Hughey and V. Peña, and transferred seven sequenced species previously assigned to *Lithothamnion* to this genus [36]. We adopted this taxonomic treatment and transferred *Lithothamnion sonderi* Hauck and *Lithothamnion japonicum* Foslie from the previous checklist to *Boreolithothamnion sonderi* (Hauck) P.W. Gabrielson, Maneveldt, Hughey and V. Peña and *Boreolithothamnion japonicum* (Foslie) S.Y. Jeong, B.Y. Won, Fredericq, and T.O. Cho, respectively. Furthermore, Coutinho et al. [19] proposed the new genus *Roseolithon* L.M. Coutinho and Barros-Barreto based on molecular data and morphological characteristics. They suggested that the depressed surface of the conceptacle roof in tetra-/bisporangial conceptacles represents a diagnostic feature distinguishing *Roseolithon* from *Lithothamnion*. Based on RAxML phylogenetic analyses, Gabrielson et al. [20] assigned *Lithothamnion crispatum* Hauck; *L. indicum* Foslie; and *L. superpositum* Foslie to *Roseolithon*. We followed this treatment and transferred *L. crispatum* from the previous checklist to *R. crispatum*.

Athanasiadis and Ballantine [47] revised the classification of species previously assigned to *Mesophyllum* Me. Lemoine based on a phylogenetic framework combined with evidence from thallus morphology, vegetative anatomy, and reproductive structures. They established the new genus *Magnephycus* Athanasiadis and D.L. Ballantine and recombined *Mesophyllum engelhartii* (Foslie) W.H. Adey and *Mesophyllum simulans* (Foslie) Me. Lemoine as *Magnephycus engelhartii* (Foslie) Athanasiadis and D.L. Ballantine and *Magnephycus simulans* (Foslie) Athanasiadis and D.L. Ballantine, respectively. We adopted this taxonomic revision.

In the previous checklist, *Pneophyllum* Kützinger was assigned to Hydrolithaceae. However, Rösler et al. [48] suggested that the sequenced specimens showed a considerable geographic distance from the type locality of *P. conicum* (E.Y. Dawson) Keats, Y.M. Chamberlain and M. Baba, and therefore considered the generic placement of this species uncertain. Based on morphological and molecular evidence, Caragnano [35] assigned *Pneophyllum* to the newly established subfamily Chamberlainoideae (Corallinaceae, Corallinales). We adopted this taxonomic treatment in the present checklist.

Rösler et al. [48] revised the subfamily Metagoniolithoideae based on morphological and molecular evidence and established the new genus *Harveyolithon* A. Rösler, Perfectti, V. Peña and J.C. Braga. Several species previously assigned to *Lithophyllum* Philippi; *Neogoniolithon* Setchell and L.R. Mason; and *Pseudolithophyllum* Me. Lemoine were transferred to this genus. We followed this taxonomic treatment and synonymized *N. accretum* (Foslie and M. Howe) Setchell and L.R. Mason from the previous checklist with *H. munitum* (Foslie and M. Howe) A. Rösler, Perfectti, V. Peña and J.C. Braga.

Woelkerling et al. [49] revised the generic boundaries between *Titanoderma* Nägeli and *Lithophyllum* based on type specimen examinations and morphological–anatomical evidence. They recombined *L. tumidulum* Foslie, which was previously assigned to *Lithophyllum*, as *T. tumidulum* (Foslie) Woelkerling, Y.M. Chamberlain and P.C. Silva. We adopted this taxonomic treatment.

Kato et al. [50] resurrected *Porolithon* Foslie based on molecular phylogenetic evidence, including SSU rDNA and psbA sequences. Subsequently, Maneveldt and Keats [51] combined evidence from type specimens and morphological–anatomical characteristics to reinstate *Hydrolithon gardineri* (Foslie) Verheij and Prud'homme, previously assigned to *Hydrolithon* (Foslie) Foslie, as *P. gardineri* (Foslie) Foslie. We adopted this treatment.

These taxonomic revisions represent not only changes at the family and genus levels but also directly affect estimates of coralline algal diversity in China. Therefore, reassessment of historical records based on the current taxonomic framework is necessary.

3.2. Diversity of Coralline Algae in China

The number of recognized coralline algal species worldwide continues to be updated and revised as taxonomic concepts are refined. During the reconstruction of the red algal classification system in 2007, 564 coralline algal species were included [52]. In 2018, AlgaeBase recognized 744 accepted species [53]. As of 22 June 2026, WoRMS [21] recognizes 817 species of Corallinophycidae, representing 5 orders, 14 families, and 82 genera (Table 1).

From 1980 to 2026, the number of recorded coralline algal species in China showed an overall increasing trend (Figure 2) [22–27]. In 1983, only 38 species were recorded, which increased to 42 species by 2008. Subsequently, with increased survey efforts and advances in molecular techniques, the number of recorded species further increased to 60 and 88 species in 2013 and 2015, respectively, reaching a peak of 112 species in 2019. In the present study, 109 recorded species were compiled from the available literature, representing a slight decrease compared with the number reported in 2019 but remaining substantially higher than that documented in earlier surveys. Linear regression analysis showed that the number of recorded species exhibited an overall increasing trend over time ($R^2 = 0.651$), indicating that continued research efforts have contributed to the accumulation of coralline algal species records in China.

Based on the taxonomic revisions described in Section 3.1 and the verification of species names against AlgaeBase and WoRMS, a total of 109 accepted coralline algal species were compiled from Chinese records published between 1980 and 2026 (Table S1). These species belonged to 3 orders, 8 families, and 30 genera. Among the three orders, Corallinales was the most species-rich, with 83 species, followed by Hapalidiales with 21 species and Sporolithales with 5 species (Figure 3c). At the family level, Corallinaceae showed the highest species richness (34 species), followed by Lithophyllaceae (27 species) and Hapalidiaceae (21 species) (Figure 3b). At the genus level, *Jania* J.V. Lamouroux was the most species-rich genus, comprising 18 species, followed by *Amphiroa* J.V. Lamouroux (15 species); *Lithophyllum* (10 species); *Corallina* Linnaeus (8 species); and *Neogoniolithon* (7 species) (Table S1). Regarding external morphological forms, geniculate coralline algae comprised 45 species belonging to 6 genera, whereas non-geniculate coralline algae included 64 species belonging to 24 genera.

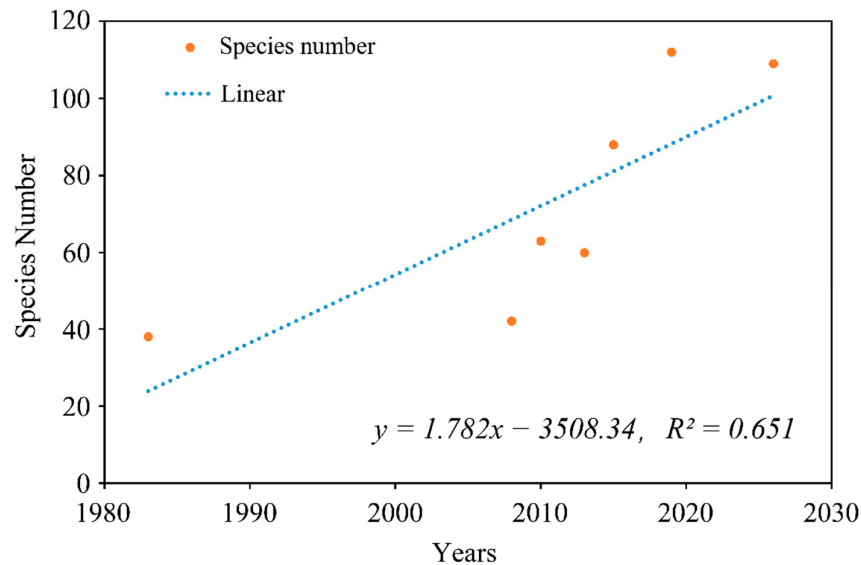


Figure 2. Temporal changes in recorded coralline algal species richness in China during 1980–2026.

China possesses an extensive coastline spanning temperate, subtropical, and tropical climatic zones. Based on our literature compilation, the recorded species richness of coralline algae in China is higher than that reported from countries or regions restricted to a single climatic zone. For example, the tropical Spermonde Archipelago harbors 63 recorded species belonging to 3 orders and 11 genera [54]. Similarly, the number of recorded non-geniculate coralline algal species in China exceeds that reported from tropical regions, including the Florida Keys and Roatán Island, where 34 species belonging to 2 orders and 11 genera have been documented [55], as well as the Great Barrier Reef in Australia, with 30 species from 12 genera [56]. The relatively high number of recorded species in China may reflect the combined effects of its broad latitudinal environmental gradients and intensified taxonomic and biodiversity surveys in recent years.

Jania and *Amphiroa* were the two genera with the highest number of recorded species in China. Together with *Corallina*, *Alatocladia* (Yendo) H.W. Johansen, *Metagoniolithon* Weber-van Bosse, and other related taxa, they are collectively referred to as geniculate coralline algae. Due to the taxonomic complexity and broad ecological adaptation of *Jania* and *Amphiroa*, these genera have received considerable research attention [38,57–60]. Species of *Jania* are distributed worldwide except in high-latitude regions [43], with up to 13 species recorded in Taiwan. *Amphiroa* is widely distributed across tropical, subtropical, and temperate regions [57] and has been recorded throughout coastal areas of China. Geniculate coralline algae possess erect and flexible axes, which provide high mechanical flexibility [61,62]. Previous studies have demonstrated that, compared with non-geniculate coralline algae, these characteristics allow geniculate species to reduce the risk of burial by sediments [63,64] and facilitate more efficient photosynthesis and calcification [1]. Their flexible joints also enhance resistance to wave-induced mechanical stress, enabling adaptation to highly variable environments [65]. *Amphiroa beauvoisii* J.V. Lamouroux and *Corallina pilulifera* Postels and Ruprecht are widely distributed species in China. *Amphiroa beauvoisii* generally occurs on rocky substrates in the lower intertidal zone or in subtidal rock pools. *C. pilulifera* is widely distributed on intertidal rocky shores and in rock pools and has been recognized as a sensitive species responding to ocean acidification. Previous studies on *C. pilulifera* have mainly focused on its chemical composition [66], allelopathic effects and inhibition of harmful algal blooms [67,68], as well as the impacts of ocean acidification on marine organisms [69].

Lithophyllum and *Neogoniolithon* were also among the frequently recorded genera in China. Together with *Pneophyllum*, *Hydrolithon*, and *Harveyolithon*, these taxa are classified as non-geniculate coralline algae. Non-geniculate coralline algae are distributed across a broad range of environments, from tropical regions to polar areas, and occur under highly variable light conditions, ranging from shallow tropical intertidal habitats to environments with extremely limited light availability. Previous studies have demonstrated that temperature, light availability, and grazing intensity are major factors influencing the growth rates of non-geniculate coralline algae [63,70,71]. For example, growth rates of non-geniculate coralline algae are generally lower in temperate environments than in warmer regions [72].

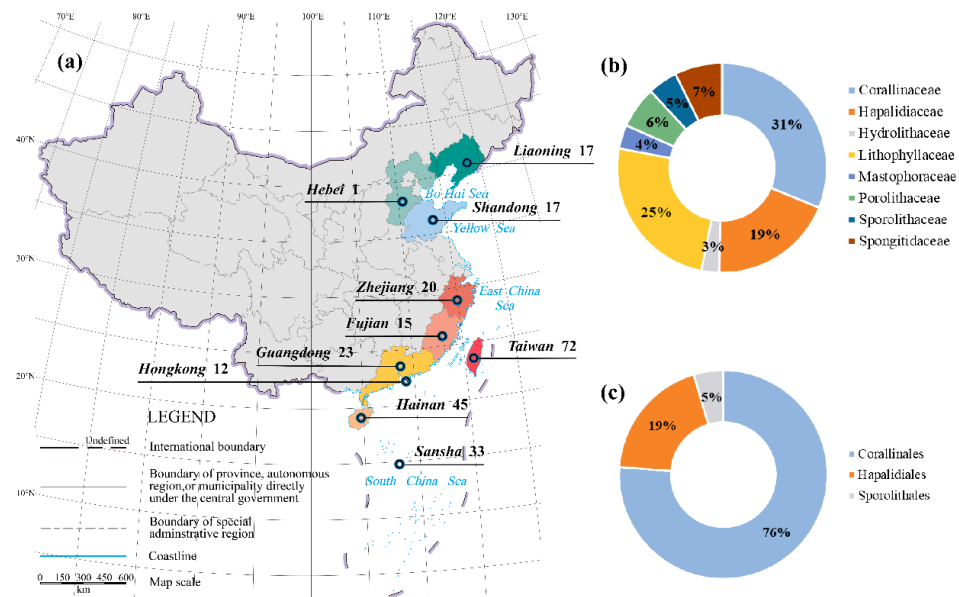


Figure 3. (a) Number of coralline algal species recorded in different sea areas of China; (b) order; (c) genus. This map is produced based on the standard map (GS(2019)1659) issued by the Ministry of Natural Resources of China.

3.3. Geographic Distribution of Coralline Algae in China

The recorded species richness of coralline algae in China exhibits a clear southward increasing pattern, with higher species numbers in southern regions and fewer records in northern regions. Taiwan harbors the highest number of recorded species (71 species), followed by Hainan (44 species) and Sansha (32 species). In contrast, regions north of Fujian generally contain fewer than 20 recorded species (Figure 3a). A Spearman correlation analysis was conducted between the number of publications available for each region and the recorded species richness of coralline algae (Figure 4). The results showed a moderate positive correlation between publication number and recorded species richness (Spearman's $\rho = 0.627$), although the relationship did not reach statistical significance ($p = 0.053$). This finding suggests that increased research efforts may facilitate species discovery; however, regional patterns of coralline algal diversity are likely influenced by multiple factors beyond survey intensity. For example, Taiwan exhibited relatively high species richness despite having a comparatively limited number of survey publications, suggesting that the high number of recorded species in this region cannot be fully explained by survey effort alone. The potential diversity of coralline algae in Taiwan therefore warrants further investigation.

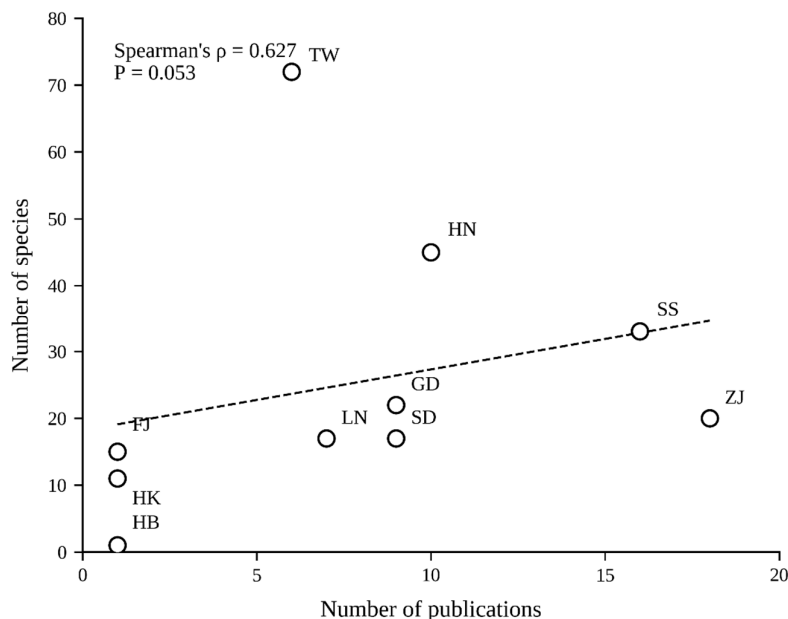


Figure 4. Spearman correlation between the number of publications and recorded coralline algal species richness among different regions. Regional abbreviations: LN, Liaoning; HB, Hebei; SD, Shandong; ZJ, Zhejiang; FJ, Fujian; GD, Guangdong; HK, Hong Kong; TW, Taiwan; HN, Hainan; SS, Sansha.

Therefore, environmental factors may also represent important drivers influencing the diversity and distribution patterns of coralline algae. Previous studies have demonstrated that temperature and light availability regulate calcification metabolism in coralline algae and are among the major factors determining their latitudinal distribution ranges [70,71,73–75]. Dongshan, Fujian Province, is located near the Tropic of Cancer in the subtropical region, with monthly mean sea surface temperatures ranging from 14 to 30 °C. This area approaches the upper and lower thermal thresholds for reef-building scleractinian corals and represents the northernmost limit of reef-building coral communities in China [76]. Although coralline algae occur in both coral reef and non-reef habitats, our results revealed a spatial correspondence between coralline algal species richness and coral reef community distribution patterns. In regions north of Fujian (including Liaoning, Hebei, Shandong, Zhejiang, Fujian, Guangdong, and Hong Kong), 51 species belonging to 18 genera and 2 orders were recorded, of which 50.98% were geniculate coralline algae, mainly represented by *Jania*, *Amphiroa*, and *Corallina*. In contrast, regions south of Fujian (including Taiwan, Hainan, and Sansha) exhibited substantially higher coralline algal diversity, with 96 species belonging to 29 genera and 3 orders, among which 57.29% were non-geniculate coralline algae (Figure 5). This pattern is consistent with global surveys showing that non-geniculate coralline algae are dominant components of coral reef margins [7,77]. This dominance may be associated with the ability of coralline algae, particularly non-geniculate coralline algae, to contribute to reef framework development through carbonate deposition, substrate stabilization, and the formation of suitable settlement surfaces [78].

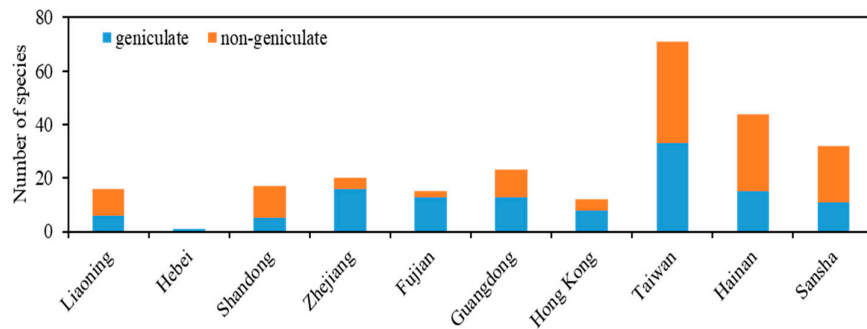


Figure 5. Proportional composition (%) of geniculate and non-geniculate coralline algal species richness across different regions of China.

Furthermore, this study revealed that Taiwan, Hainan, and Sansha exhibited substantially higher species richness than other regions, which may be associated with their unique geographic and environmental characteristics. Southern Taiwan is influenced by the combined effects of the Kuroshio Current intrusion, monsoon-driven South China Sea surface circulation, and tidal-induced upwelling [79,80]. This upwelling process reduces seawater temperature and generates fluctuating thermal conditions, which may facilitate the persistence of heat-tolerant species over long-term ecological timescales [81]. In addition, southern Taiwan is located adjacent to Luzon Island of the Philippines, which represents the northern boundary of the Coral Triangle. Previous studies have suggested that the relatively high diversity of coral reef-associated species in southern Taiwan is related to its biogeographic connection with the Coral Triangle [82,83]. These distinctive environmental conditions may contribute to the occurrence of unique taxonomic assemblages, with *Arthrocardia* Decaisne; *Titanoderma*; *Melobesia* J.V. Lamouroux; *Metagoniolithon*; *Rosolithon*; and *Heydrichia* R.A. Townsend, Y.M. Chamberlain and Keats representing genera uniquely recorded from this region. The South China Sea is characterized by its extensive geographic area, unique oceanographic setting, and widespread distribution of coral reef ecosystems [84,85]. Coralline algal diversity and endemic taxa in this region differ markedly from those in other regions. Several non-geniculate coralline algal genera, including *Lithoporella* (Foslie) Foslie, 1909, *Porolithon*, and *Phymatolithopsis*, have been recorded only from this region. These patterns are consistent with previous studies on coralline algal fossils and benthic macroalgal surveys in the South China Sea [86,87].

Notably, the observed geographic distribution patterns of coralline algae were consistent with the potential influences of environmental factors, including temperature, light availability, ocean circulation, and regional biogeographic connectivity. However, these relationships remain difficult to disentangle from differences in sampling effort among regions. Overall, higher observed species richness may reflect the combined effects of sampling intensity, historical research accumulation, and environmental heterogeneity.

3.4. Cryptic Diversity and Incompleteness of Morphology-Based Species Inventories

It should be noted that the diversity and distribution data compiled in the present checklist do not fully represent the overall diversity of coralline algae in China. Increasing evidence has revealed the widespread occurrence of cryptic species in coralline algae [29,34,54,88,89]. Traditionally, the classification of non-geniculate coralline algae has relied heavily on external morphological characteristics [10,90]. However, external morphology is often influenced by environmental factors, including grazing pressure and hydrodynamic conditions, resulting in considerable phenotypic plasticity [40]. In addition, the processing of calcified thalli is technically challenging, and detailed anatomical inves-

tigations are often difficult to perform. Therefore, the classification of non-geniculate coralline algae based solely on morphological and anatomical characteristics remains highly challenging [10,91]. For example, *Lithophyllum* is a highly diverse and widely distributed genus of non-geniculate coralline algae [18,19,46]. Currently, 10 species of this genus are recorded in China (Table S1). Due to its important role in habitat formation, *Lithophyllum* is considered an ecologically significant genus [92,93] and has attracted considerable research attention [94,95]. Several studies have suggested that the diversity of *Lithophyllum* has been substantially underestimated [10,33]. Therefore, we suggest that the species diversity represented in the present checklist may not fully capture the actual diversity of *Lithophyllum* in China.

In summary, the 109 accepted species included in the checklist should be regarded as a representation of the currently documented and verifiable diversity supported by available literature, rather than an unbiased estimate of the actual species richness of coralline algae in China. Future studies should prioritize standardized sampling in Hainan, Sansha, Taiwan, and other regions with limited historical records, combined with DNA barcoding markers (e.g., *rbcL*, *psbA*, and *COI-5P*) and multilocus phylogenetic analyses to further resolve coralline algal diversity.

3.5. Limitations of This Study

Although the present checklist was compiled based on published literature, several limitations should be acknowledged.

(1) Regions with higher recorded biodiversity may reflect a longer history of coralline algal research and more intensive field surveys, whereas regions with fewer recorded species may not necessarily represent intrinsically lower diversity. Instead, the lower number of recorded species may result from insufficient taxonomic investigations and sampling efforts compared with regions such as Hainan and Sansha.

(2) Historical records may contain misidentifications and redundant records resulting from taxonomic synonymy. For example, *Amphiroa beauvoisii* was identified as *Amphiroa zanata* by Chinese researchers for an extended period of time [24–26]. However, Norris and Johansen [96] considered *A. zanata* to be a taxonomic synonym of *A. beauvoisii*, and this treatment has subsequently been accepted by many researchers [57,97]. In addition, some historical records lack molecular evidence. Before 2003, coralline algal classification was entirely based on morphological and anatomical analyses [11–14]. Even after the introduction of molecular approaches, some studies continued to lack molecular evidence [30]. Therefore, these historical records may have a potential risk of misidentification.

(3) Coralline algae exhibit a high level of cryptic diversity. As mentioned above, numerous cryptic species have been reported in coralline algae [29,34,54,89]. Therefore, the 109 accepted species compiled in this checklist should be interpreted as the currently documented and verifiable diversity supported by available literature, rather than an unbiased estimate of the actual species richness.

(4) The compiled literature data were not derived from standardized surveys, and differences exist among studies in sampling area, depth, sampling period, and identification criteria. In addition, many historical records lack standardized information on species abundance and coverage.

(5) The taxonomic databases WoRMS and AlgaeBase are themselves continuously updated as taxonomic knowledge advances, and their accepted names and classification frameworks may change accordingly.

Based on these findings, future investigations should first focus on comprehensive surveys and systematic taxonomic studies of coralline algal resources. An auditable database integrating species, geographic locality, sampling year, voucher specimens, morphological and anatomical images, and molecular evidence should be established. In addition,

standardized sampling protocols should be developed at regional scales, accompanied by increased investment in coralline algal surveys, to improve our understanding of species diversity and resource status in China and provide a solid foundation for future research.

4. Conclusions

This study compiled a checklist of coralline algal diversity and geographic distribution in China based on published literature from 1980 to 2026 and incorporated the latest taxonomic frameworks from AlgaeBase and WoRMS. The results revealed that the currently validated checklist of coralline algae in China comprises 109 accepted species belonging to 3 orders, 8 families, and 30 genera. Among the orders, Corallinales contained the highest number of species, followed by Hapalidiales and Sporolithales. Corallinaceae was the most species-rich family, followed by Lithophyllaceae and Hapalidiaceae. *Jania* and *Amphiroa* represented the most species-rich genera, followed by *Lithophyllum*, *Coralina*, and *Neogoniolithon*. Regarding external morphological forms, geniculate coralline algae comprised 45 species from 6 genera, whereas non-geniculate coralline algae included 64 species from 24 genera. Based on the current checklist, Taiwan, Hainan, and Sansha exhibited relatively high recorded species richness; however, these patterns should not be interpreted as equivalent to actual species diversity.

The number of publications available for different regions showed a moderate positive relationship with observed species richness (Spearman $\rho = 0.63$, $p = 0.053$), indicating that sampling effort and research intensity should be considered when interpreting regional differences. Existing evidence supports the hypothesis that temperature, light availability, coral reef environments, and oceanic circulation may contribute to shaping coralline algal distributions. However, the literature-based dataset compiled in this study is insufficient to evaluate the independent causal effects of these environmental factors. Therefore, the relatively high species richness recorded in Taiwan, Hainan, and Sansha may reflect the combined influences of environmental suitability and accumulated research efforts.

In conclusion, the 109 species identified in this study should be regarded as the currently documented and verifiable number of accepted species supported by available literature, rather than the true species richness of coralline algae in China. Future studies integrating standardized regional surveys, DNA barcoding, voucher specimens, and harmonized data structures will further improve assessments of the actual diversity of coralline algae in China and help elucidate the biogeographic mechanisms underlying their distribution patterns.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d18100619/s1>, Table S1. Species and Distribution of Coralline Algae in China[24,26–28,30,98–102].

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