



Evolutionary History of *DMSP Lyase-Like* Genes in Animals and Their Possible Involvement in Evolution of the Scleractinian Coral Genus, *Acropora*

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Dimethylsulfoniopropionate (DMSP) lyase is an enzyme that mediates cleavage of DMSP into dimethyl sulfide (DMS) and acrylate. DMS is an aerosol substance that may affect cloud formation, solar radiation and ocean temperatures. DMSP lyases in marine organisms, such as marine bacteria, release DMS, which might contribute to atmosphere-ocean feedback. Although DMSP lyases were first identified in marine bacteria, eukaryotic DMSP lyases or genes similar to DMSP lyase, *DMSP lyase-like* (*DL-L*) genes have been found not only in coccolithophores (*Emiliana huxleyi*) and symbiotic algae of the Family Symbiodiniaceae, but also in animals, including scleractinian corals (Cnidaria: Anthozoa: Hexacorallia). Comparative genomic analysis showed that gene expansion events of *DL-L* genes have occurred specifically in the scleractinian genus, *Acropora*. In the present study, we performed molecular identification of *DL-L* genes in *Acropora digitifera*. Thirteen full-length Open Reading Frames were isolated, confirming that these duplicated *DL-L* genes are likely expressed. A comprehensive survey of available transcriptomic databases revealed that *DL-L* genes have been identified not only in scleractinians (Hexacorallia), but also Octocorallia (Anthozoa) and even in a jellyfish (Cnidaria: Hydrozoa). Molecular phylogenetic analyses showed that although some sequences from cnidarian transcriptomic databases apparently originated with their symbiotic algae, cnidarian sequences from Anthozoa and Hydrozoa clustered together, indicating that these evolved from a gene in the last common ancestor of Cnidaria, dating to the Precambrian. Interestingly, cnidarian species possessing *DL-L* genes apparently occur only in coral reefs or shallow, warmer environments, suggesting that these genes may be essential for animals to survive in such environments. *Acropora*-specific duplicated *DL-L* genes, which originated during the past warm geological periods, may enable them to adapt to environmental changes.

Keywords: DMPS lyase, DMS, Cnidaria, Scleractinia, *Acropora*, evolution, gene duplication

INTRODUCTION

Coral reefs in tropical and subtropical waters harbor about 30% of all marine life, making them the most biodiverse habitats in marine ecosystems (Knowlton et al., 2010). In addition, coral reefs provide many fishery resources, protect coastlines, and fix carbon and nitrogen. Scleractinian or stony corals (Anthozoa, Cnidaria) are the main builders of coral reefs, forming massive calcium carbonate skeletons. Corals are metaorganisms or “holobionts” associated with a variety of microorganisms, such as dinoflagellates of the family Symbiodiniaceae and diverse communities of bacteria, archaea, fungi, viruses, and protists (Rohwer et al., 2002; Ainsworth et al., 2010). They rely mainly on symbiotic algae (Symbiodiniaceae) to trap solar energy for survival, growth, and calcification (Goreau and Goreau, 1959; Muscatine, 1990; Davy et al., 2012). In stony corals, dinoflagellate symbionts use the substrates (nitrogen and phosphorus) produced by their hosts for photosynthesis (Muscatine and Porter, 1977). Prokaryotic microorganisms provide sources of nitrogen, sulfur, and other elements to corals or release them into the water column (Ainsworth et al., 2010; Rädercker et al., 2015). These allow coral reefs to remain highly productive in oligotrophic waters, while also facilitating global biogeochemical cycles.

The sulfur cycle is one of the most important of these cycles, providing biosynthetic proteins and cofactors. Dimethylsulfoniopropionate (DMSP) is an organic sulfur compound that is abundant in marine surface waters. The majority of it is produced by phytoplankton and algae, but it has also been reported in some angiosperms and bacteria (Keller et al., 1989; Hanson et al., 1994; Paquet et al., 1994; Gage et al., 1997; Kocsis et al., 1998; Lyon et al., 2011; Kettles et al., 2014; Curson et al., 2017). Although functions of DMSP are not entirely understood, several physiological functions, such as osmoregulation, oxidative stress protection, and cryoprotection, have been demonstrated in phytoplankton and green algae (Kirst et al., 1991; Karsten et al., 1996; Sunda et al., 2002; Lesser, 2006; Husband et al., 2012; Curson et al., 2018). Biological functions such as chemoattraction, predator deterrence, and mediation of bacterial virulence have been identified (Wolfe and Steinke, 1996; Miller and Belas, 2004; Barak-Gavish et al., 2018). The most notable and important aspect of DMSP is that it is a precursor of dimethyl sulfide (DMS) (van Boeckel and Stefels, 1993), which is a major source of sulfur in the atmosphere, promoting cloud formation and combating greenhouse gasses. DMSP is cleaved by an enzyme called DMSP lyase (EC 4.4.1.3), which converts DMSP to DMS. Recently, studies reported that DMSP lyase products, DMS and acrylate, may have ecological roles such as chemical defenses against predation (Strom et al., 2003; Teng et al., 2021) and enhancing predation by grazers (Shemi et al., 2021). When DMS enters the atmosphere, it is oxidized into aerosol particles that can induce cloud formation and increase reflectivity. This may reduce light levels and water temperatures in marine environments, thus contributing to local climate regulation (Figure 1) (Ayers and Gras, 1991; Vallina and Simo, 2007), although some studies suggest that sea-air DMS flux is low, and

that the role of DMS in climate regulation is likely insignificant (Woodhouse et al., 2010; Quinn and Bates, 2011).

Marine phytoplankton and macroalgae are considered the primary producers of DMSP, while marine bacteria are the primary degraders (Stefels et al., 2007; Reisch et al., 2011). DMSP is released from marine phytoplankton and macroalgae upon cellular lysis caused by zooplankton grazing, viral infection, and senescence (Figure 1) (van Boeckel and Stefels, 1993; Wolfe et al., 1997; Hill et al., 1998). Bacteria acquire DMSP mainly from the ocean and demethylate it into methanethiol and acetaldehyde, turning DMSP into DMS via the lysis pathway (Figure 1). DMSP lyase was first identified in bacteria, and at least eight prokaryotic DMSP lyase genes have been identified to date (Li et al., 2021).

Some studies have reported that eukaryotic phytoplankton, including dinoflagellates and algae, possess DMSP lyase activity (Stefels et al., 1995; Steinke and Kirst, 1996; Steinke et al., 1998; Niki et al., 2000; Yoch, 2002), but the responsible gene was difficult to isolate. In 2015, a gene, *Alma I*, was identified from the eukaryotic coccolithophore, *Emiliania huxleyi*, and was shown to have high DMSP lyase activity (Alcolombri et al., 2015). It has been suggested that *Alma I* can directly lyse algal DMSP, releasing acrylate and DMS (Figure 1). Interestingly, sequences similar to *Alma I*, *DMSP lyase-like (DL-L)* genes were also found in scleractinian corals and Symbiodiniaceae (Alcolombri et al., 2015). Furthermore, recent comparative genomic analysis of scleractinian and cnidarian genomes showed that numbers of *DL-L* genes in genomes of the scleractinian coral genus, *Acropora*, are significantly larger than in other cnidarian genomes and that gene expansion events specifically occurred in *Acropora* (Shinzato et al., 2021a).

Acropora is currently the most studied coral genus in the world (Maor-Landaw and Levy, 2016), as it includes the most widespread, abundant, and diverse scleractinian corals on Earth (Wallace and Rosen, 2006). Approximately 180 species have been recorded from the Red Sea to the Indo-Pacific Ocean and the Caribbean Ocean (Wallace, 1999; Veron, 2000; van Oppen et al., 2001). With the increase of research data, more genetic databases (genome and transcriptome databases) and molecular techniques (CRISPR/Cas9 and gene knockdown) have been developed (Yasuoka et al., 2016; Cleves et al., 2018; Ying et al., 2019; Shinzato et al., 2021a). Genetic analyses suggest that *Acropora* has been evolutionarily very successful and may have become a dominant genus through acquisition and expansion of gene families (Shinzato et al., 2011; Shinzato et al., 2021a). Examples of *Acropora*-specific gene duplication and expansion events have been reported (Hislop et al., 2005; Shinzato et al., 2021a). Symbiotic relationship with Symbiodiniaceae may also have contributed to rapid adaptation to changing environments (Qin et al., 2019). Interestingly, Shinzato et al. (2021a) showed that *DL-L* genes are the most diversified gene family in *Acropora* genomes and that possible coral- or cnidarian-specific stress response genes, including Caspase-X and SCRiPs, have also been tandemly duplicated in *Acropora* genomes. In this study, to better understand evolution of *DL-L* genes in animals and their possible involvement in *Acropora* evolution, we first confirmed

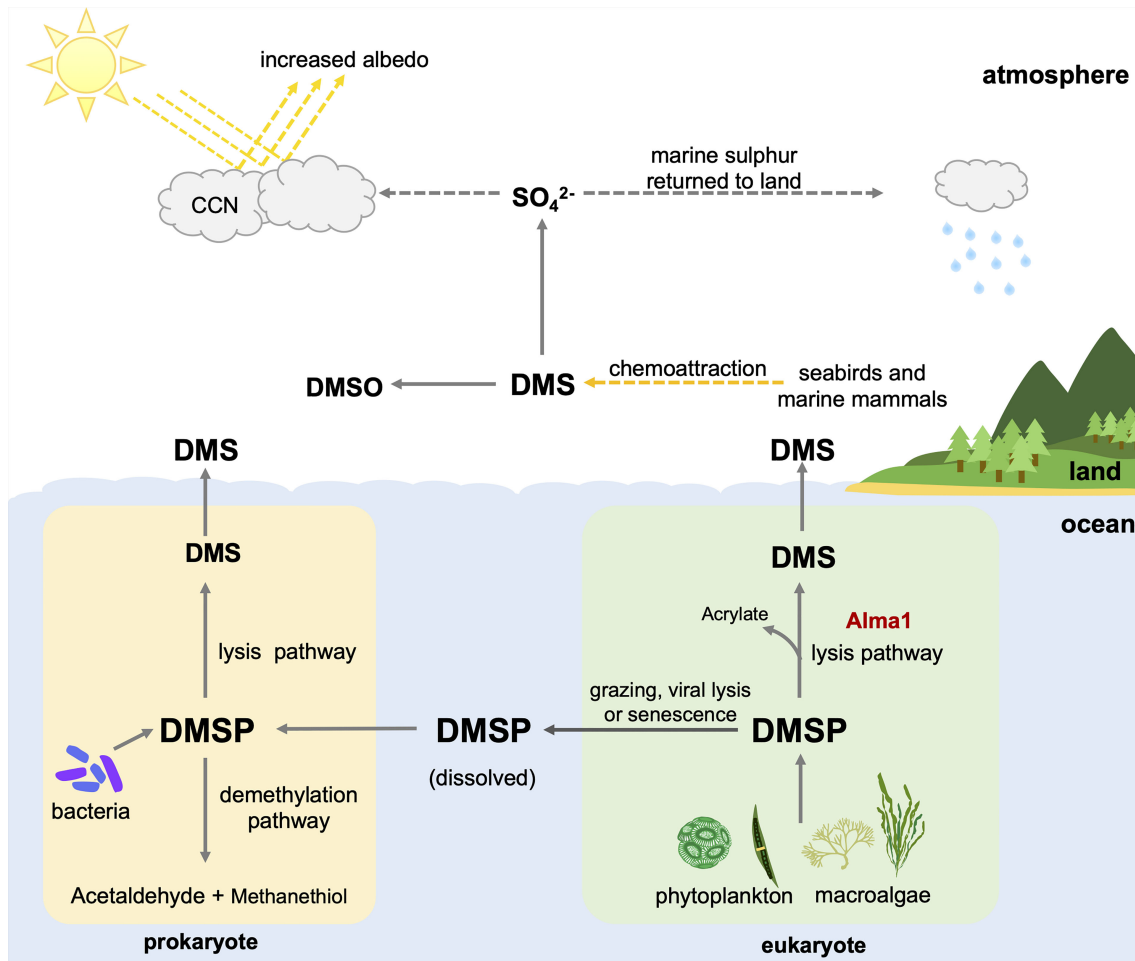


FIGURE 1 | Contributions of prokaryotes and eukaryotes to the biogeochemical cycle and possible functions of dimethylsulfoniopropionic acid (DMSP) and dimethyl sulfide (DMS). CCN, Cloud condensation nuclei; DMSO, dimethyl sulfoxide.

that *DL-L* genes are indeed expressed in *A. digitifera* as possible functional mRNAs without in-frame stop codons. Then, we performed a comprehensive database survey and molecular phylogenetic analyses to investigate the existence of *DL-L* genes in various eukaryotes, including scleractinian corals, cnidarians, and other animals, to gain insight into the evolutionary origin of *DL-L* genes in the animal kingdom.

MATERIALS AND METHODS

Cloning of *DL-L* Genes From *Acropora digitifera*

The same RNA samples used in previous studies including different developmental stages of *A. digitifera* (eggs, blastulae, gastrulae, planula larvae, early polyps, and adult branches) were used for cDNA synthesis (Shinzato et al., 2011; Shinzato et al., 2021a; Yoshioka et al., 2021). Samples were homogenized in TRIzol reagent (Invitrogen) on ice, and total RNA was extracted following

the manufacturer's instruction and Chiu et al. (2020). Extracted total RNA was treated with recombinant DNase I (Roche) to remove contaminating genomic DNA. First-strand cDNA was synthesized from 5 µg of DNase-treated RNA using SuperScript™ III reverse transcriptase (Thermo Fisher Scientific). Possible *DL-L* genes of *A. digitifera* were derived from predicted genes of *A. digitifera* (Shinzato et al., 2021a), and primers amplifying full length open reading frames (ORFs) were designed for each gene (**Supplementary Table 1**). PCR products were cloned into the pGEM-T Easy cloning vector (Promega), transformed into competent cells (*Escherichia coli*, DH5α strain), and plasmids were sequenced at a commercial laboratory (Eurofin Genomics, Tokyo, Japan).

Gene Expression Patterns of *Acropora digitifera DL-L* Genes Under Different Developmental Stages and Increased Sea Water Temperature

To investigate gene expression patterns of 18 *DL-L* genes predicted from the *A. digitifera* genome assembly (Shinzato et al., 2021a), we

used previously reported RNA-Seq transcriptome data of *A. digitifera* from different developmental stages (egg, blastula, gastrula, planula, polyp, Shinzato et al., 2021a), adult stages (Yoshioka et al., 2021), and increased seawater temperature treatments (25°C to 30°C, Shinzato et al., 2021b). Briefly, Illumina adaptor sequences and low-quality reads (Quality score < 20, length < 25 bp) in the RNA-Seq data were trimmed with CUTADAPT v1.16 (Martin, 2011), and cleaned reads were mapped to *A. digitifera* gene models (Shinzato et al., 2021a) using KALLISTO v0.44.0 (Bray et al., 2016) or MiniMap v2.9 (Li, 2018) with default settings. Mapping counts were normalized using the trimmed mean of M values (TMM) method, and then converted to counts per million (CPM) using EdgeR v3.28.1 (Robinson et al., 2010; McCarthy et al., 2012) in R v3.6.3 (team 2015).

Identification of DL-L Genes From Publicly Available Eukaryote and Cnidarian Transcriptomic Databases

Amino acid sequences were deduced from cloned cDNA sequences using the ExPASy translate tool (<https://web.expasy.org/translate/>; Gasteiger et al., 2003). To search for genes similar to DMSP lyase gene from transcriptomic databases, the deduced amino acid sequences of cloned *A. digitifera* *DL-L* genes, *Emiliania huxleyi* Alma1 (KR703620.1), and *Symbiodinium* A1 DMSP lyase (P0DN22) were used as query sequences in homology searches against the Transcriptome Shotgun Assembly (TSA) database at the National Center for Biotechnology Information (NCBI) using tBlastn (*A. digitifera* *DL-L* genes: e-value cutoff $1e^{-50}$, query coverage >80%, *Emiliania huxleyi* Alma1 and *Symbiodinium* A1 DMSP lyase: e-value cutoff $1e^{-5}$, query coverage >70%). Sequences satisfying these criteria were retrieved, and amino acid sequences were prepared using the ExPASy translate tool.

Sequence Alignment and Molecular Phylogenetic Analyses

Sequences downloaded from NCBI TSA databases, including cnidarians, animals, phytoplankton and macroalgae were used for phylogenetic analyses, with bacterial *DMSP lyase* genes (WP028324949.1, WP012448288.1, WP034745099.1, WP020674609.1, and WP006965703.1) as an outgroup. First, all amino acid sequences were aligned using MAFFT v7.310 (Katoh et al., 2002; Katoh and Standley, 2013), and poorly aligned sequences were removed manually. Gaps in alignments were removed using trimAl v1.2 (Capella-Gutiérrez et al., 2009) with the “gappyout” option. After removing gaps, maximum likelihood analyses were performed using RAXML v8.2.10 (Stamatakis, 2014) with the “bootstrap 100” and “progammaauto” options.

RESULTS

DL-L Genes Isolated From *Acropora digitifera* RNAs and Their Gene Expression Patterns

Among 18 *DL-L* genes predicted from the *A. digitifera* genome (Shinzato et al., 2021a), we successfully obtained 13 *DL-L* gene

sequences with full-length mRNA coding regions from cDNA (**Figure 2; Supplementary Figure 1**), demonstrating that multiple *DL-L* genes exist in the *A. digitifera* genome and that these are actually expressed as possible functional mRNAs without in-frame stop codons. The resultant 13 amino acid sequences had the same Asp/Glu/hydantoin racemase superfamily conserved domain as in Alma1 of *E. huxleyi* (**Figure 2; Supplementary Figure 1**) (Alcolombri et al., 2015). These 18 genes showed different levels and patterns of gene expression in different developmental stages (**Supplementary Table 2**) as shown by previous studies (Shinzato et al., 2021a; Shinzato et al., 2021b; Yoshioka et al., 2021). Gene expression of five genes was significantly changed (one upregulated and four downregulated) by increased sea water temperature (25°C to 30°C, $q < 0.05$, **Supplementary Table 2**).

DL-L Genes in Eukaryotes

Among the 6,258 eukaryotic TSA databases deposited in NCBI, we identified 123 gene sequences from 72 species that showed similarity to *A. digitifera* *DL-L* genes and satisfied the above criteria (tBlastn e-value cutoff $1e^{-50}$, query coverage >80%). Most sequences were identified from the Cnidaria (stony corals, sea anemones, jellyfish and hydra), phytoplankton (Phyla Haptophyta, Myzozoa, Ochrophyta) and macroalgae (Phyla Chlorophyta and Rhodophyta) (**Table 1**). Unexpectedly, four sequences were also identified from other animals, including a ctenophore (*Beroe forskalii*), a mollusk (*Limacina retroversa*) and arthropods (*Dendroctonus frontalis* and *Pleuromamma xiphias*) (**Table 1**). We further investigated the amino acid sequence similarity of these sequences with the only known DMSP lyases from eukaryotes to date (Alcolombri et al., 2015), *Emiliania huxleyi* Alma1 and *Symbiodinium* A1 DMSP lyase (**Supplementary Table 3**). Most eukaryote sequences similar to *A. digitifera* *DL-L* genes (**Table 1**) also showed sequence similarities to both DMSP lyases, but percent identities were lower than those to *A. digitifera* *DL-L* genes (**Supplementary Table 3**).

In order to infer evolutionary relationships of the identified sequences from eukaryotes and the four sequences from non-cnidarian animals, we performed molecular phylogenetic analyses with amino acid sequences of the 13 *A. digitifera* *DL-L* genes as representatives of Cnidaria and bacterial DMSP lyase genes from prokaryotes as an outgroup. Sequences from prokaryotes and eukaryotes separated into two distinct clusters, indicating that all of the sequences obtained from eukaryote TSA databases originated from eukaryotes, and were not contaminants from symbiotic bacteria (**Figure 3; Supplementary Figure 2**). All sequences from *A. digitifera* clustered, demonstrating that they originated from the host coral (**Figure 3; Supplementary Figure 2**). None of the sequences from non-cnidarian animals clustered with those from *A. digitifera*. Clustering of the *D. frontalis* sequence with dinoflagellate sequences displayed 100% bootstrap support, indicating that this sequence was derived from symbiotic or adhesive algae, not from the animal itself. However, the other three sequences from *B. forskalii*, *P. xiphias* and *L. retroversa* did not cluster with those of *A. digitifera* and other eukaryotes (**Figure 3; Supplementary Figure 2**); thus, the evolutionary origin (animals or other eukaryotes) are unclear.

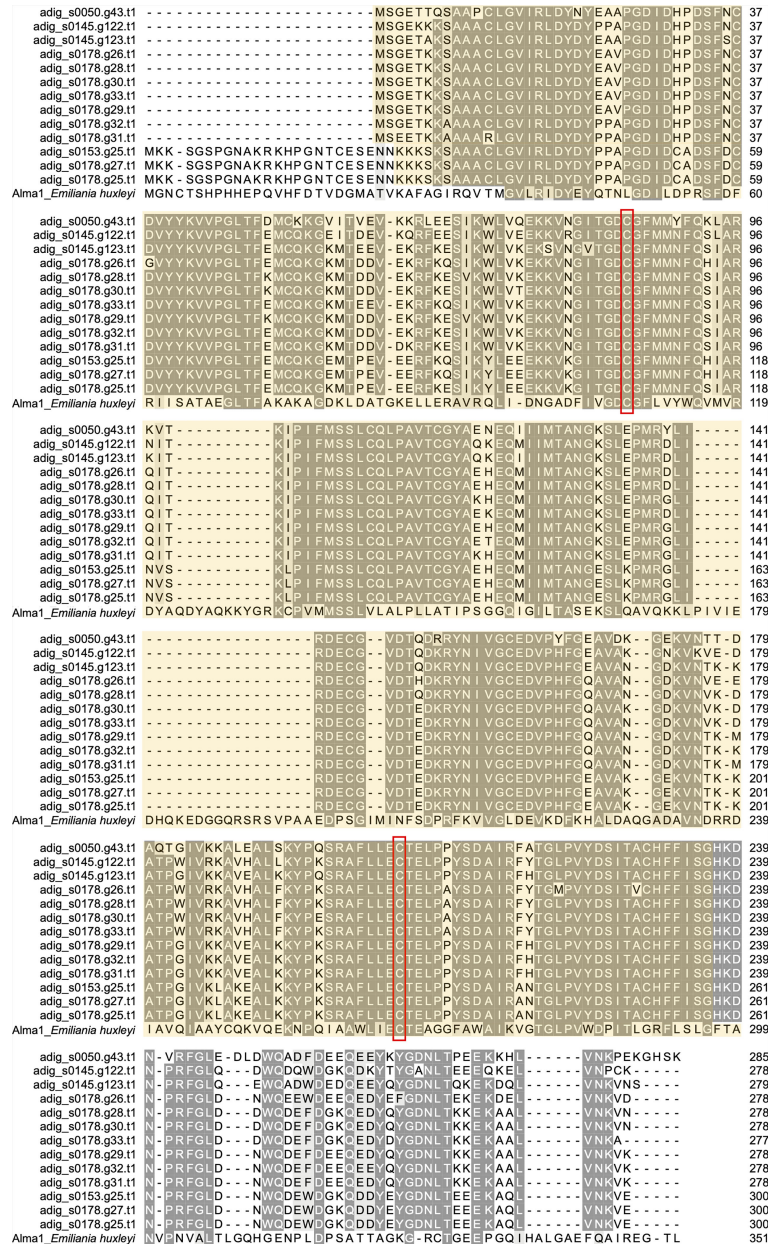


FIGURE 2 | Molecular characterization of *DL-L* genes in *Acropora digitifera*. Multiple sequence alignment of deduced amino acid sequences from 13 *DL-L* genes of *A. digitifera* and *Emiliana huxleyi*, Alma1 (KR703620.1). Identical residues are indicated in the same color. Lengths of amino acid sequences are shown at the right and positions of the Asp/Glu/hydantoin racemase superfamily conserved domain are shown in light yellow and the two putative active site residues are shown in red boxes.

DL-L Genes in Cnidaria

Among 137 Cnidarian TSA databases in NCBI, we found sequences similar to *DL-L* genes from 35 species (Table 2). Most of these sequences were from *Acropora millepora* and *A. tenuis* and had been previously identified (Alcolombri et al., 2015; Shinzato et al., 2021a). Interestingly, possible *DL-L* genes were found not only in the subclass Hexacorallia, including stony corals, sea anemones, and zoanths, but also in the Octocorallia, including soft corals and blue corals, and even from

Hydroidolina, including jellyfishes and fire corals (Table 2). We also investigated amino acid sequence similarity of these cnidarian sequences with known eukaryote DMS lyases from *E. huxleyi* and *Symbiodinium* A1 (see above), and all sequences except one from *Seriatopora caliendrum* had significant similarities with these eukaryote DMS lyases (Supplementary Table 4).

Coral and/or cnidarian transcriptomic databases often contain sequences originating with symbiotic algae, as well as associated microorganisms. In order to identify which sequences

TABLE 1 | *DL-L* genes in Eukaryotes, excluding those from cnidarians.

Kingdom	Phylum	Class	Species	Accession
Animalia	Ctenophora	Nuda	<i>Beroe forskalii</i> *	GHXY01272785.1
Animalia	Mollusca	Gastropoda	<i>Limacina retroversa</i> *	GBXC01047479.1
Animalia	Arthropoda	Insecta	<i>Dendroctonus frontalis</i> *	GAFI01013939.1
Animalia	Arthropoda	Hexanauplia	<i>Pleuromamma xiphias</i> *	GFCI01194001.1
Chromista	Foraminifera	Globobulimina	<i>Globobulimina</i> sp.	GGCD01090783.1
Chromista	Haptophyta	Prymnesiophyceae	<i>Emiliana huxleyi</i>	HBTT01010599.1
Chromista	Haptophyta	Prymnesiophyceae	<i>Gephyrocapsa muelleriae</i>	HBRT01085803.1
Chromista	Haptophyta	Prymnesiophyceae	<i>Haptolina ericina</i>	HBHX01042533.1
Chromista	Haptophyta	Prymnesiophyceae	<i>Pelagophyceae</i> sp.	HBPV01017070.1
Chromista	Haptophyta	Prymnesiophyceae	<i>Phaeocystis antarctica</i>	HBQY01084461.1
Chromista	Haptophyta	Prymnesiophyceae	<i>Phaeocystis globosa</i>	HBRY01017421.1
Chromista	Haptophyta	Prymnesiophyceae	<i>Phaeocystis rex</i>	HBRF01010364.1
Chromista	Haptophyta	Prymnesiophyceae	<i>Phaeocystis</i> sp.	HBRH01022669.1
Chromista	Haptophyta	Prymnesiophyceae	<i>Prymnesium parvum</i>	HBJC01021087.1
Chromista	Myzozoa	Dinophyceae	<i>Apocalathium aciculiferum</i>	HBPP01113651.1
Chromista	Myzozoa	Dinophyceae	<i>Breviolum minutum</i>	GICE01003031.1
Chromista	Myzozoa	Dinophyceae	<i>Cryptocodinium cohnii</i>	HBOA01074003.1
Chromista	Myzozoa	Dinophyceae	<i>Dinophysis acuminata</i>	HBJU01034009.1
Chromista	Myzozoa	Dinophyceae	<i>Alexandrium andersonii</i>	HBGQ01027533.1
Chromista	Myzozoa	Dinophyceae	<i>Alexandrium catenella</i>	HBGE01066426.1
Chromista	Myzozoa	Dinophyceae	<i>Alexandrium monilatum</i>	HBNR01038033.1
Chromista	Myzozoa	Dinophyceae	<i>Alexandrium tamarense</i>	GAIU01003918.1
Chromista	Myzozoa	Dinophyceae	<i>Amphidinium carterae</i>	HBNO01025899.1
Chromista	Myzozoa	Dinophyceae	<i>Amphidinium massartii</i>	HBLR01031444.1
Chromista	Myzozoa	Dinophyceae	<i>Ansanella granifera</i>	GFBE01033504.1
Chromista	Myzozoa	Dinophyceae	<i>Brandtodinium nutricula</i>	HBGW01061089.1
Chromista	Myzozoa	Dinophyceae	<i>Durinskia baltica</i>	GAAT01001280.1
Chromista	Myzozoa	Dinophyceae	<i>Gambierdiscus australes</i>	HBLT01061594.1
Chromista	Myzozoa	Dinophyceae	<i>Gambierdiscus excentricus</i>	GETL01004569.1
Chromista	Myzozoa	Dinophyceae	<i>Gambierdiscus pacificus</i>	GIJQ01009298.1
Chromista	Myzozoa	Dinophyceae	<i>Gambierdiscus polynesiensis</i>	GETK01055910.1
Chromista	Myzozoa	Dinophyceae	<i>Gonyaulax spinifera</i>	HBNG01065451.1
Chromista	Myzozoa	Dinophyceae	<i>Gymnodinium catenatum</i>	HBLW01077801.1
Chromista	Myzozoa	Dinophyceae	<i>Gyrodinium shiwhaense</i>	GFHE01000685.1
Chromista	Myzozoa	Dinophyceae	<i>Heterocapsa arctica</i>	HBNJ01038395.1
Chromista	Myzozoa	Dinophyceae	<i>Heterocapsa rotundata</i>	HBLO01067633.1
Chromista	Myzozoa	Dinophyceae	<i>Heterocapsa triquetra</i>	HBLK01063662.1
Chromista	Myzozoa	Dinophyceae	<i>Karenia brevis</i>	GFLM01039285.1
Chromista	Myzozoa	Dinophyceae	<i>Karenia mikimotoi</i>	GISR01008935.1
Chromista	Myzozoa	Dinophyceae	<i>Lingulodinium polyedra</i>	HBQU01097259.1
Chromista	Myzozoa	Dinophyceae	<i>Lingulodinium polyedrum</i>	JO709806.1
Chromista	Myzozoa	Dinophyceae	<i>Noctiluca scintillans</i>	HBFG01012472.1
Chromista	Myzozoa	Dinophyceae	<i>Pelagodium bei</i>	HBNF01082217.1
Chromista	Myzozoa	Dinophyceae	<i>Prorocentrum minimum</i>	GHMX01159955.1
Chromista	Myzozoa	Dinophyceae	<i>Scrippsiella hangoei</i>	HBPM01101163.1
Chromista	Myzozoa	Dinophyceae	<i>Symbiodinium muscatinei</i>	GFDR03033769.1
Chromista	Myzozoa	Dinophyceae	<i>Symbiodinium</i> sp.	HBTG01057664.1
Chromista	Myzozoa	Dinophyceae	<i>Symbiodinium</i> sp. A1	GAKY01102437.1
Chromista	Myzozoa	Dinophyceae	<i>Symbiodinium</i> sp. A4	GFPM01010862.1
Chromista	Myzozoa	Dinophyceae	<i>Symbiodinium</i> sp. B2	GBRZ01003534.1
Chromista	Myzozoa	Dinophyceae	<i>Symbiodinium</i> sp. CCMP2430	HBTH01081069.1
Chromista	Myzozoa	Dinophyceae	<i>Symbiodinium</i> sp. clade A	HBSZ01019953.1
Chromista	Myzozoa	Dinophyceae	<i>Symbiodinium</i> sp. clade C	GBSC01004690.1
Chromista	Myzozoa	Dinophyceae	<i>Symbiodinium</i> sp. clade D	GAFP01017879.1
Chromista	Myzozoa	Dinophyceae	<i>Symbiodinium</i> sp. clade D	GBRR01002019.1
Chromista	Myzozoa	Dinophyceae	<i>Togula jolla</i>	HBKY01023746.1
Chromista	Ochrophyta	Pelagophyceae	<i>Chrysoreinhardia</i> sp.	HBSO01018369.1
Chromista	Ochrophyta	Bacillariophyceae	<i>Coscinodiscus wailiesii</i>	HBJZ01008141.1
Chromista	Ochrophyta	Bacillariophyceae	<i>Navicula</i> sp.	HBQT01035211.1
Chromista	Ochrophyta	Pelagophyceae	<i>Pelagomonas calceolata</i>	HBQU01000605.1
Chromista	Ochrophyta	Bacillariophyceae	<i>Pleurosigma</i> sp.	HBRE01034425.1
Chromista	Ochrophyta	Bacillariophyceae	<i>Proboscia alata</i>	HBOX01003438.1
Chromista	Ochrophyta	Bacillariophyceae	<i>Pseudo-nitzschia fraudulenta</i>	HBPFO1070060.1

(Continued)

TABLE 1 | Continued

Kingdom	Phylum	Class	Species	Accession
Chromista	Ochrophyta	Phaeophyceae	<i>Sargassum vulgare</i>	GEHA01001042.1
Chromista	Ochrophyta	Bacillariophyceae	<i>Synedra</i> sp.	HBQV01036945.1
Chromista	Ochrophyta	Bacillariophyceae	<i>Thalassiosira antarctica</i>	HBPL01059889.1
Plantae	Chlorophyta	Ulvophyceae	<i>Ulva lactuca</i>	GFUR01013571.1
Plantae	Chlorophyta	Chloropicophyceae	<i>Chloroparvula pacifica</i>	HBPX01006065.1
Plantae	Chlorophyta	Mamiellophyceae	<i>Crustomastix stigmatica</i>	HBLU01015603.1
Plantae	Rhodophyta	Floriellophyceae	<i>Laurencia pacifica</i>	GFZU01073384.1
Plantae	Rhodophyta	Floriellophyceae	<i>Lithophyllum</i> sp.	GHIV01139773.1
Plantae	Rhodophyta	Floriellophyceae	<i>Porolithon</i> sp.	GHIO01088530.1

*The origin of sequence is unknown, and may represent contamination from symbiotic/adhesive algae.

were from animal hosts, we further performed molecular phylogenetic analyses of sequences from cnidarian TSA databases together with *DL-L* genes from the Symbiodiniaceae, coccolithophores and prokaryotes (**Figure 4A**). Six distinct

clades were supported by strong bootstrap probabilities (93 ~ 100%). Most of the sequences belonging to the Hexacorallia clustered together in Clade 1 with *A. digitifera* *DL-L* genes, indicating that these originated from hexacorallian hosts.

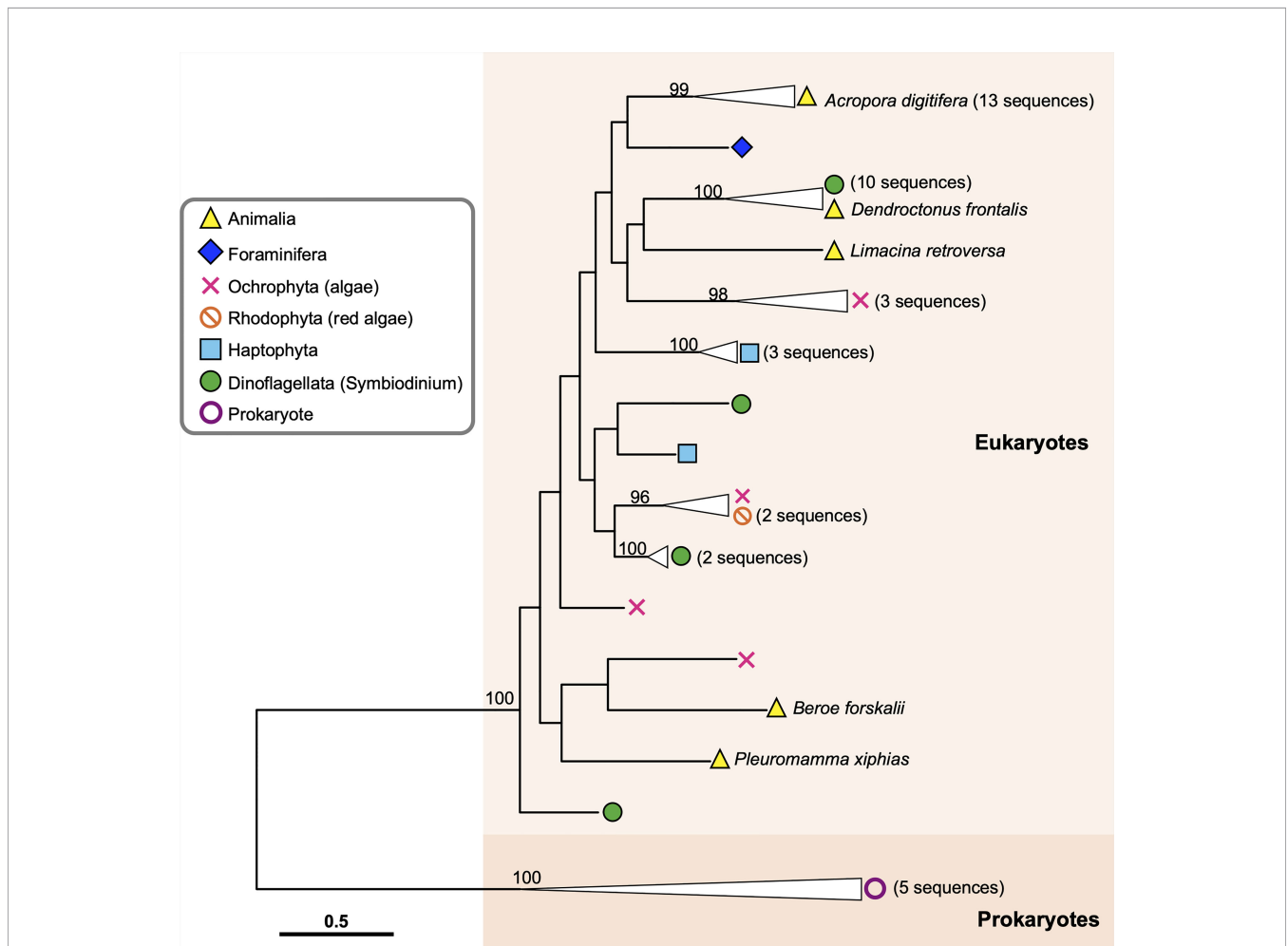


FIGURE 3 | Molecular phylogenetic analysis of *DL-L* genes identified from transcriptomic databases of eukaryotes. Possible *DL-L* genes from eukaryotic NCBI TSA databases were analyzed using the maximum likelihood method. 337 gap-trimmed aligned amino acids were used for phylogenetic analysis. Bootstrap support for representative nodes is shown. Eukaryotic and prokaryotic DMSP lyase genes clades are highlighted in different colors. *A. digitifera* *DL-L* genes cloned from cDNA are represented as animal genes in the analysis. *DL-L* genes from the Animalia, Foraminifera, Ochrophyta, Rhodophyta, Haptophyta, Dinoflagellata, and Prokaryota are colored in yellow (triangle), indigo (diamond), pink (cross), orange (prohibited), blue (square), green (circle), and purple (white circle), respectively. The bar indicates 0.5 substitutions per site in aligned regions. The complete phylogenetic tree is shown in **Supplementary Figure 2**.

TABLE 2 | *DL-L* genes in cnidarians excluding *Acropora*.

Class	Subclass	Order	Family	Genus	Species	Sequences originated from cnidarian hosts confirmed by molecular phylogenetic analysis (Figure 4)	Accession
Hydrozoa	Hydroidolina	Anthoathecata	Milleporidae	<i>Millepora</i>	<i>Millepora alcicornis</i>	No	GFAS01239487.1
Hydrozoa	Hydroidolina	Anthoathecata	Milleporidae	<i>Millepora</i>	<i>Millepora complanata</i>	No	GIXC01089652.1
Hydrozoa	Hydroidolina	Anthoathecata	Milleporidae	<i>Millepora</i>	<i>Millepora</i> sp.	No	GFGV01397967.1
Hydrozoa	Hydroidolina	Anthoathecata	Milleporidae	<i>Millepora</i>	<i>Millepora squarrosa</i>	No	GFGU01029924.1
Hydrozoa	Hydroidolina	Anthoathecata	Porpitidae	<i>Velella</i>	<i>Velella velella</i>	Yes	GHAZ01122917.1
Anthozoa	Octocorallia	Alcyonacea	Briareidae	<i>Briareum</i>	<i>Briareum asbestinum</i>	No	GHBD02057672.1
Anthozoa	Octocorallia	Alcyonacea	Clavulariidae	<i>Clavularia</i>	<i>Clavularia</i> sp.	Yes	GHAW01081527.1
Anthozoa	Octocorallia	Alcyonacea	Xeniidae	<i>Xenia</i>	<i>Xenia</i> sp.	No	GHBC01044802.1
Anthozoa	Octocorallia	Helioporacea	Helioporidae	<i>Heliopora</i>	<i>Heliopora coerulea</i>	No	IABP01030506.1
Anthozoa	Hexacorallia	Zoantharia	Sphenopidae	<i>Palythoa</i>	<i>Palythoa caribaeorum</i>	Yes	GESO01095871.1
Anthozoa	Hexacorallia	Zoantharia	Sphenopidae	<i>Palythoa</i>	<i>Palythoa</i> sp.	No	GGUI01140954.1
Anthozoa	Hexacorallia	Zoantharia	Sphenopidae	<i>Protospalythoa</i>	<i>Protospalythoa variabilis</i>	Yes	GCVI01065809.1
Anthozoa	Hexacorallia	Zoantharia	Zoanthidae	<i>Zoanthus</i>	<i>Zoanthus</i> sp.	No	GGTW01049612.1
Anthozoa	Hexacorallia	Actiniaria	Actiniidae	<i>Anemonia</i>	<i>Anemonia viridis</i>	No	GGLT01126584.1
Anthozoa	Hexacorallia	Actiniaria	Actiniidae	<i>Anthopleura</i>	<i>Anthopleura elegantissima</i>	No	GBXJ01017739.1
Anthozoa	Hexacorallia	Corallimorpharia	Discosomidae	<i>Rhodactis</i>	<i>Rhodactis indosinensis</i>	Yes	GELO01068433.1
Anthozoa	Hexacorallia	Scleractinia	Acroporidae	<i>Montipora</i>	<i>Montipora digitata</i>	Yes	GIVM01155846.1
Anthozoa	Hexacorallia	Scleractinia	Acroporidae	<i>Alveopora</i>	<i>Alveopora japonica</i>	Yes	GGJR01165973.1
Anthozoa	Hexacorallia	Scleractinia	Euphyllidae	<i>Fimbriaphyllia</i>	<i>Fimbriaphyllia ancora</i>	No	ICQS01038312.1
Anthozoa	Hexacorallia	Scleractinia	Agariciidae	<i>Agaricia</i>	<i>Agaricia lamarcki</i>	No	GGLC03011859.1
Anthozoa	Hexacorallia	Scleractinia	Siderastreidae	<i>Siderastrea</i>	<i>Siderastrea siderea</i>	Yes	GIYO011329375.1
Anthozoa	Hexacorallia	Scleractinia	Poritidae	<i>Porites</i>	<i>Porites astreoides</i>	Yes	GIYN01600157.1
Anthozoa	Hexacorallia	Scleractinia	Poritidae	<i>Porites</i>	<i>Porites australiensis</i>	Yes	FX437344.1
Anthozoa	Hexacorallia	Scleractinia	Poritidae	<i>Porites</i>	<i>Porites lutea</i>	Yes	GGER01067412.1
Anthozoa	Hexacorallia	Scleractinia	Merulinidae	<i>Cyphastrea</i>	<i>Cyphastrea serailia</i>	Yes	GETH01074762.1
Anthozoa	Hexacorallia	Scleractinia	Merulinidae	<i>Favites</i>	<i>Favites colemani</i>	Yes	GIVN01210226.1
Anthozoa	Hexacorallia	Scleractinia	Mussidae	<i>Favia</i>	<i>Favia lizardensis</i>	Yes	GDZU01025741.1
Anthozoa	Hexacorallia	Scleractinia	Pocilloporidae	<i>Pocillopora</i>	<i>Pocillopora acuta</i>	No	GJER01286462.1
Anthozoa	Hexacorallia	Scleractinia	Pocilloporidae	<i>Seriatopora</i>	<i>Seriatopora callendrum</i>	Yes	GIAR01012305.1

Interestingly, *Clavularia* sp. of the Octocorallia and *Velella velella* of the Hydroidolina were also relegated to Clade 1, indicating that these share a common ancestral gene with hexacorallian species. The family Symbiodiniaceae is genetically diverse, and includes multiple genera (LaJeunesse et al., 2018). As expected, some Cnidarian sequences clustered with sequences of symbiotic algae (Symbiodiniaceae) and were assigned to Clades 3-5 (Figure 4A; Supplementary Figure 3), indicating that these

were contaminant from symbiotic algae. Among them, a sequence from *Pocillopora acuta* was clustered into Clade 3, sequences from *Anthopleura elegantissima*, *Millepora squarrosa*, *Agaricia lamarcki*, *Heliopora coerulea*, *Zoanthus* sp., *Palythoa* sp., *M. alcicornis*, *Millepora* sp. were clustered in Clade 4, and sequences from *Fimbriaphyllia ancora*, *M. complanata*, and *Xenia* sp. were clustered in Clade 5 (Figure 4A; Supplementary Figure 3; Table 2). Different cnidarian species

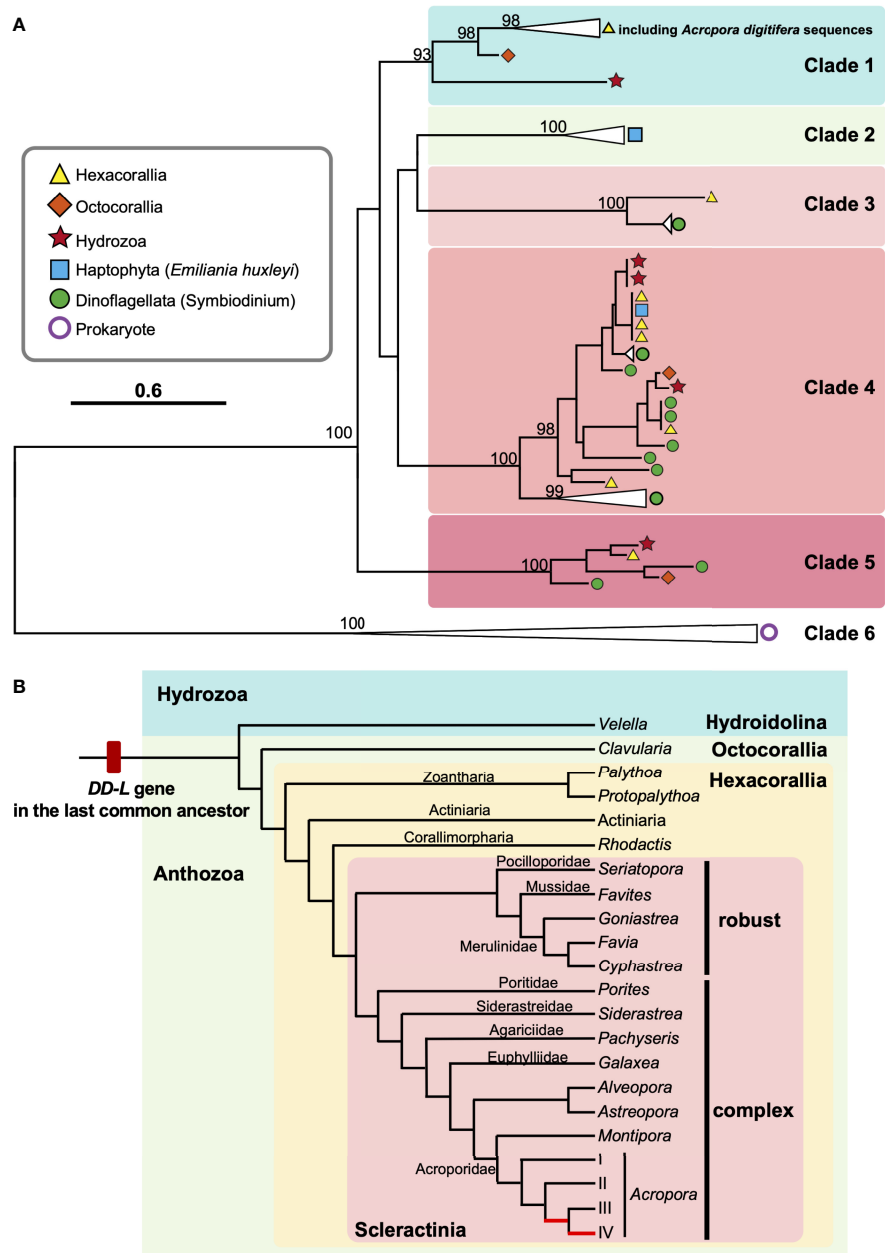


FIGURE 4 | Molecular phylogenetic analysis of *DL-L* genes identified from transcriptomic databases of Cnidaria. **(A)** Possible *DL-L* genes from cnidarian NCBI TSA databases were analyzed using the maximum likelihood method. 667 gap-trimmed aligned amino acids were used for phylogenetic analysis. Bootstrap support for representative nodes is shown. Clades 1-6 of *DL-L* genes of cnidarians, other eukaryotes and prokaryotes are highlighted in different colors. **(A)** *digitifera DL-L* genes identified from cDNA, which were all clustered in Clade 1, are also included. *DL-L* genes from Hexacorallia, Octocorallia, Hydrozoa, Haptophyta, Dinoflagellata, and Prokaryota are colored in yellow (triangle), orange (diamond), red (star), blue (square), green (circle), and purple (white circle), respectively. The bar indicates 0.6 substitutions per site in aligned regions. The complete phylogenetic tree is shown in **Supplementary Figure 3**. **(B)** Updated evolutionary history of *DL-L* gene in the Phylum Cnidaria. Only species of cnidarians possessing animal-type *DL-L* genes are shown. Two *Acropora*-specific gene expansion events proposed by Shinzato et al. (2021a) are shown in red in the phylogenetic tree. Phylogenetic relationships of cnidarians and scleractinian corals are derived from Kayal et al. (2018) and Kitahara et al. (2016).

harbor different types of symbiotic algae; thus, Clades 3-5, containing Symbiodiniaceae could reflect different types of symbiotic algae. All *DL-L* genes of the coccolithophore *E. huxleyi* within the Haptophyta clustered in Clade 2, and

bacterial DMSP lyase genes clustered in Clade 6. Taken together, all *DL-L* genes of Cnidaria, including scleractinian corals, soft corals, and jellyfishes, evolved from an ancestral gene that already existed in the last common ancestor of

Anthozoa and Hydrozoa, and have completely different evolutionary backgrounds from those of coccolithophores, the Family Symbiodiniaceae, or prokaryotes.

DISCUSSION

A Variety of Scleractinian Corals Possess *DL-L* Genes

It has been reported that coral reefs are hotspots for DMSP, which have been attributed to symbiotic algae of corals (Broadbent et al., 2002; Broadbent and Jones, 2004; Broadbent and Jones, 2006; Swan et al., 2012). Recent studies have shown that adult and juvenile *A. tenuis* and *A. millepora* without symbiotic algae both produce DMSP (Raina et al., 2013). *DL-L* genes have also been discovered, not only in *Acropora* genomes (Alcolombri et al., 2015; Shinzato et al., 2021a), but also in genomes of *Montipora*, *Astreopora*, *Goniastrea*, and two corallimorpharians, *Amplexidiscus* and *Discosoma* (Shinzato et al., 2021a).

In this study, we successfully identified full-length ORFs of 13 *DL-L* genes, which are expressed in *A. digitifera*, and we identified *DL-L* genes from a variety of scleractinian lineages (Figures 1, 4A; Supplementary Figure 3). The earliest coral fossil record of a Scleractinian dates to the middle Triassic (240 Ma) (Stanley, 2003). Most extant scleractinians are classified into two major clades, known as the Complexa (complex corals) and Robusta (robust corals), and are assumed to have diverged in the Late Carboniferous (300 Ma) (Romano and Palumbi, 1996; Romano and Cairns, 2000). In genomes of robust corals, a *DL-L* gene has been detected only in *Goniastrea aspera* to date (Shinzato et al., 2021a). However, in this study, we identified animal-type *DL-L* genes from four robust corals, including *Cyphastrea serailia*, *Favites colemani*, *Favia lizardensis*, and *Seriatoxypora caliendrum* (Figure 4B; Table 2), indicating that *DL-L* genes have been preserved in a variety of complex and robust corals, but were lost from some lineages.

Ancient Origin of *DL-L* Genes in Cnidarians

Although a large proportion of *DL-L* genes were identified in corals and cnidarians, we also identified similar sequences from non-cnidarian animals, *B. forskalii*, *P. xiphias* and *L. retroversa*. However, none of these share a common ancestry with coral *DL-L* genes (Figure 3). Although the origins of these sequences are not clear, we suggest that they may have come from symbiotic/adhesive algae, as in the case of a sequence from *D. frontalis* (Figure 3). Based on our phylogenetic analyses using currently available transcriptomic databases, we conclude that, to date, only cnidarians possess *DL-L* genes that are clearly of animal origin. Further addition of more phytoplankton *DL-L* genes may reveal the origins of these from non-cnidarian species.

The Phylum Cnidaria contains three clades (subphyla): Anthozoa (comprising the Octocorallia, Hexacorallia, and Ceriantharia), Endocnidozoa (a clade of parasites) and Medusozoa (consisting of the Cubozoa, Hydrozoa, Scyphozoa,

and Staurozoa) (Collins, 2009; Kayal et al., 2018). In this study, we identified eukaryotic *DL-L* genes, not only in the Scleractinia and Corallimorpharia but also in the Zoantharia (Hexacorallia), Alcyonacea (Octocorallia), and Hydrozoa (Anthoathecata, Hydroidolina) (Figure 4B; Table 2). This indicates that the last common ancestor of Anthozoa and Hydrozoa possessed a *DL-L* gene and that this gene has been inherited in a wide range of cnidarian species. The earliest cnidarian fossils occur in strata of the Ediacaran (560 Ma, Liu et al., 2014), and together with molecular and paleontological analyses, suggest that the phylum Cnidaria probably originated during the Precambrian Eon from the Cryogenian to the Ediacaran (700–595 Ma, Peterson et al., 2004; Erwin et al., 2011). Divergence of 2 major taxa (Anthozoa and Medusozoa) may have occurred before the Cambrian (543 Ma) (Cartwright et al., 2007; Park et al., 2012). Consequently, we hypothesize that the *DL-L* gene may be have originated from an ancient gene that already existed in the last common ancestor of Cnidaria in the pre-Cambrian (Figure 4B).

How did cnidarians, including corals, obtain *DL-L* genes? Shinzato et al. (2021a) hypothesized that *DL-L* genes may have been acquired by the common ancestor of scleractinians and corallimorpharians, both of which are hexacorallians (Anthozoa), via horizontal gene transfer from symbiotic Symbiodiniaceae or *Emiliana*. However, as mentioned above, a variety of anthozoans and hydrozoans possess these genes (Figure 4A). McFadden et al. (2021) suggested that the Anthozoa probably arose in the Cryogenian to Tonian periods (648–894 Ma) and lacked photosymbionts. In the Devonian (383 Ma) from the Palaeozoic Era, anthozoans of the Scleractinia first formed associations with photosymbionts, followed by alcyonacean octocorals (318 Ma) and corallimorpharians (312 Ma), and photosymbioses have been gained and lost repeatedly in all orders through the Jurassic (199–151 Ma, McFadden et al., 2021). In addition, the fossil record shows that scleractinian corals had photosymbionts in most of the upper Triassic since the Mesozoic Era (Stolarski et al., 2011; Frankowiak et al., 2016). Recent molecular dating estimates suggest that the earliest diversification of the Symbiodiniaceae occurred in the Jurassic (~160 Ma, LaJeunesse et al., 2018) and the first *E. huxleyi* appeared 270,000 years ago (Thierstein et al., 1977; Paasche, 2001), which were much later than the origin of the Anthozoa. Our phylogenetic analysis (Figure 4) confirms distinct ancestries of *DL-L* genes in Symbiodiniaceae and cnidarians, indicating that they have completely different evolutionary backgrounds. Therefore, acquisition of *DL-L* genes via horizontal gene transfer from symbiotic algae (Shinzato et al., 2021a) may not have occurred. Based on the present findings, we propose an updated hypothesis: *DL-L* genes in cnidarians are “ancient genes” in the animal kingdom, dating back to the pre-Cambrian.

DL-L Genes: Essential for Survival in Coral Reef or Shallow and Warm Water Environments?

As of 10th February 2022, 137 transcriptomic databases from 91 cnidarian species had been registered in NCBI TSA.

Interestingly, we realized that all cnidarian species, except *V. velella*, possessing animal type *DL-L* genes (15 species) are limited to coral reefs (**Table 1**). *V. velella* (**Figure 4**; **Table 2**), known as “by-the-wind sailor”, is a cosmopolitan, free-floating, colonial hydrozoan that lives mainly at the water/air interface and floats in temperate and tropical seas (Araya and Aliaga, 2018). This implies that *DL-L* genes may be essential for animals to survive in coral reef or warm, shallow-water environments, although we acknowledge that publicly available transcriptomic databases of cnidarians to date may be limited to coral reef species.

Comparative genomic analysis using reported scleractinian coral genomes showed that *DL-L* genes are the most diversified gene family among gene families that significantly increased number of genes in the last common ancestor of *Acropora* (Shinzato et al., 2021a). Why did gene duplication events of *DL-L* gene specifically occur in the *Acropora* lineage? The earliest fossil records of *Acropora* are known from the late Paleocene (65–54 Ma) in Somalia and Austria (Carbone et al., 1993; Baron-Szabo, 2006), indicating that *Acropora* has existed for more than 50 million years. *Acropora* was the main reef builder in the Oligocene (28–23 Ma) of Greece and Early Miocene of Egypt (Schuster, 2002), and was widely distributed throughout the Miocene in different regions, including the Indo-Pacific and Caribbean (Budd, 2000). It is suggested that *Acropora* began to spread throughout the world in the Cenozoic and species diversification occurred in the Eocene and Oligocene (around 25–50 Ma). Molecular dating analysis using whole-genome data indicates that the *Acropora* ancestor survived warm periods without sea ice from the mid or late Cretaceous to the Early Eocene, when gene expansion of *DL-L* genes occurred specifically in the *Acropora* ancestor (Shinzato et al., 2021a). In addition, *Acropora* species also have high concentrations of DMSP compared to other corals (Broadbent et al., 2002; Guibert et al., 2020), suggesting that *Acropora* corals actively utilize DMSP and that high concentrations of DMSP may have triggered *Acropora*-specific duplication of *DL-L* genes. Several studies have shown that DMSP is involved in a wide range of coral stress responses, including responses to heat, sunlight, air exposure, and hyposalinity (Sunda et al., 2002; Raina et al., 2009; Deschaseaux et al., 2014; Aguilar et al., 2017). Not all *A. digitifera* *DL-L* genes (5 out of 18) responded to increased sea water temperature and response patterns of differentially expressed genes vary (1 upregulated and 4 downregulated, **Supplementary Table 2**), suggesting that the functions of the *DL-L* genes in *A. digitifera* have also diverged. Taken together, diversified *DL-L* genes in *Acropora* may have acquired new or different functions, not only mediating cleavage of DMSP into DMS, but that they may assist *Acropora* in adapting to environmental changes, for example from intense heat, light, and salinity (Shinzato et al., 2021a). Eventually *Acropora* may become the dominant coral genus in extant coral reefs.

The functions of *DL-L* genes in corals are completely undetermined at this stage. Interestingly, although overexpression of the *Alma 1* genes from *E. huxleyi* and *Symbiodinium A1* in *E. coli* cells had high DMSP lyase activities, an *Alma1* homolog from *A. millepora* showed almost no DMSP lyase activity (Alcolombri et al., 2015), indicating that not all *DL-L* genes in eukaryotes retain their DMSP lyase function, and that acquisition of other functions or functional differentiation may have occurred during the process of gene duplication. In particular, duplicated *DL-L* genes in *Acropora* will need to be investigated to determine which genes have DMSP lyase activity. We identified expressed sequences of *DL-L* genes from *A. digitifera* RNA, and these could be used for molecular and functional characterization in DMSP lyase assays. We also found that expression levels of *DL-L* genes were indeed diverse in *A. digitifera*. Therefore, even if some *DL-L* genes in corals do not function as DMSP lyases, they may have other functions enabling adaptation to coral reef or warm, shallow-water environments. Identifying their actual biological functions in *Acropora* corals will be important to understand not only adaptation mechanisms to shallow and warmer environments, but also the impact of *Acropora* corals on the sulfur cycle in the oceans.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

CS conceptualized, commenced and supervised the project. Y-LC performed the lab work, database searches and molecular phylogenetic analyses. Y-LC and CS analyzed the data and wrote the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.889866/full#supplementary-material>

Supplementary Figure 1 | Domain structure of the 13 deduced amino acid sequences of *A. digitifera* and *Emiliana huxleyi*, Alma1 (KR703620.1). Lengths of amino acid sequences are shown at the right and positions of the Asp/Glu/hydantoin racemase superfamily conserved domain are shown in gray boxes. Scale bar=20 aa, aa: the number of amino acids.

Supplementary Figure 2 | Maximum likelihood analysis of *DL-L* genes identified from transcriptomic databases of eukaryotes. A total of 65 *DL-L* genes from prokaryotes and eukaryotes, including *A. digitifera DL-L* genes, were aligned using MAFFT v7.310. Then, 337 gap-trimmed aligned amino acid sequences were used for the phylogenetic analysis. Each species name is followed by a different symbol indicating the taxonomy of the species. The bar indicates 0.5 substitutions per site in aligned regions.

Supplementary Figure 3 | Maximum likelihood analysis of *DL-L* genes identified from transcriptomic databases of cnidarians. A total of 65 *DL-L* genes from cnidaria

and prokaryotes including, *A. digitifera DL-L* genes, were aligned using MAFFT v7.310. Then, 337 gap-trimmed aligned amino acid sequences were used for the phylogenetic analysis. Each species name is followed by a different symbol indicating the taxonomy of the species. The bar indicates 0.6 substitutions per site in aligned regions.

Supplementary Table 1 | List of the primers for cloning PCR analysis.

Supplementary Table 2 | Gene expression levels (counts per million) of *Acropora digitifera DL-L* genes in different developmental stages (Shinzato et al., 2021a and Yoshioka et al., 2021) and increased sea water temperature (Shinzato et al., 2021b).

Supplementary Table 3 | *DL-L* genes in Eukaryotes, excluding cnidarians. *Emiliana huxleyi* Alma1 (Accession: KR703620.1) and *Symbiodinium* A1 DMSP lyase (Accession: PODN22) were used as query sequences in homology searches against the TSA at NCBI using tBlastn (e-value cutoff $1e^{-5}$, query range >70%).

Supplementary Table 4 | *DL-L* genes in cnidarians excluding *Acropora. Emiliana huxleyi* Alma1 (Accession: KR703620.1) and *Symbiodinium* A1 DMSP lyase (Accession: PODN22) were used as query sequences in homology searches against the TSA at NCBI using tBlastn (e-value cutoff $1e^{-5}$, query range >70%).

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