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Cyanosiphovirus S-ESS1 Infecting Marine *Synechococcus* (*Chroococcales*) Almost Shows No Genetic Relationship to Known Cyanosiphoviruses

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Abstract Cyanosiphoviruses are a group of viruses with long tail that infect cyanobacteria. In this study, we described a cyanosiphovirus S-ESS1 infecting *Synechococcus* SJ01, both isolated from samples of coastal waters from the East China Sea. The genome of this cyanosiphovirus had a 60,362 bp genetic map, with 282 predicted open reading frames (ORFs), among which only 56 ORFs had homologues in Genbank. According to the result of BLASTP, S-ESS1 had no ORF with any similarity to the eight known cyanosiphoviruses. Moreover, according to the phylogenetic tree of TerL, S-ESS1 was not closely related to known cyanosiphoviruses either, indicating a low genetic homology level of TerL, further proofing the biological diversity of cyanosiphovirus S-ESS1. Cyanosiphovirus S-ESS1 shared common host with reported cyanosiphoviruses S-CBS1, S-CBS2, S-CBS3, S-CBS4 and KBS2A, but as the only cyanosiphovirus separated from East China Sea, regional distribution might contribute to such genetic differences. Cyanosiphovirus S-ESS1's genetic characteristics provided an evidence for the study of the common origin of cyanophage and bacteriophage.

Keywords Cyanosiphovirus; Biological diversity; Regional distribution

Introduction

Cyanophages have been shown to be a key component of aquatic microbial communities because of their abundance, ubiquity, and potential impact on the microbial loop (Huang et al., 2012). Cyanophage–cyanobacterium interactions may have important implications for global biogeochemical cycles (Sullivan et al., 2003; Bailey et al., 2004; Paul and Sullivan, 2005). Cyanophages also mediate the horizontal transfer of genetic material between host microbes, and thereby the genetic diversity of microorganisms is affected (Mann, 2003).

All known cyanophages belong to three families: Myoviridae, Siphoviridae, and Podoviridae. Cyanosiphoviruses are a group of viruses that infect cyanobacteria, and receive much less attention than cyanomyoviruses and cyanopodoviruses (Huang et al., 2012). To date, only eight cyanosiphovirus genomes (S-CBS1, S-CBS2, S-CBS3, S-CBS4, P-SS2, KBS2A, A-HIS1, and A-HIS2) have been reported (Wang and Chen, 2008; Sullivan et al., 2009; Huang et al., 2012; Ponsero et al., 2013; Chan et al., 2015). The first genome of a cyanosiphovirus, P-SS2, isolated from Atlantic slope waters, infecting the Prochlorococcus S.W. Chisholm et al host MIT9313, was described in 2009 (Sullivan et al., 2009). Five more cyanosiphoviruses (SCBS1, S-CBS2, S-CBS3, S-CBS4 and KBS2A), infecting *Synechococcus* strains and isolated from Chesapeake Bay, were reported by Huang (Huang et al., 2012) and Ponsero (Ponsero et al., 2013). Recently, two cyanosiphoviruses, A-HIS1 and A-HIS2, which infect a Caryochloris marina H. Miyashita & M. Chihara strain MBIC11017, were isolated from reef waters off Heron Island, Australia (Chan et al., 2015). The genome sizes of the aforementioned eight cyanosiphoviruses range from 30 kb to 108 kb with 40 to 105 ORFs.

The large terminase subunit (TerL), a protein responsible for phage DNA packaging, is essential for double-stranded DNA (dsDNA) phages. For cyanophages, phylogenetic clustering of TerL not only reflects the relative genetic conservation among the three cyanophage families, but also supports the separation of four subtypes of cyanosiphoviruses (Huang et al., 2012; Chan et al., 2015).

Here we sequenced the genome of a dsDNA cyanosiphovirus S-ESS1 infecting marine *Synechococcus* isolated from the East China Sea, and analyzed the phylogenetic relationship to the known marine cyanosiphoviruses by building the phylogenetic tree of the TerL.

1 Materials and Methods

1.1 Phage isolation and purification

Synechococcus sp. SJ01 was isolated from the East China Sea by using sterilized artificial seawater media (Zhang et al., 2013), and the strain was identified as *Synechococcus* sp WH8102, according to its partial 16S rRNA sequence (Accession: BX569694.1). Lytic cyanosiphovirus S-ESS1 that can infect *Synechococcus* sp. SJ01 was isolated from coastal water samples of the East China Sea (33°44’38″N, 122°25’44″E) by a serial dilution method (Middelboe et al., 2010). Phage purification was performed using sucrose density gradient centrifugation. The lysate was initially centrifuged at 4 ℃, 10,000 g for 1 h to remove cells (Eppendorf 5810R centrifuge equipped with a 20270 rotor and several 125-mL centrifuge tubes) before the supernatant was centrifuged at 4 ℃, 120,000 g for 2 h to precipitate phages (Beckman L-100XP ultracentrifuge equipped with an SW28Ti rotor and several 38.5-mL centrifuge tubes); then five sucrose steps of 20%, 30%, 40%, 50%, and 60% were used for centrifugation at 4 ℃, 450,000 g for 3 h (Beckman SW60Ti rotor and several 4-mL centrifuge tubes). A visible band at the 50% step was collected and washed twice by centrifugation at 4 ℃ and 250,000 g (Beckman SW41Ti rotor and several 13.2-mL centrifuge tubes) for 1.5 h to obtain purified phage particles.

1.2 TEM observation cyanophage

A total of 20 μL of sucrose density gradient purified phage concentrate was transferred to 200 mesh Formvar carbon-coated copper grids and then negatively stained with 2% sodium phosphotungstate (pH 7.0). The grids were viewed using a Hitachi 3H-7000FA TEM.

1.3 DNA extraction, genome sequencing, and ORF annotation

DNA was prepared from sucrose density gradient-purified phages following the method of Wilson (Wilson et al., 1993). Sequencing of the phage DNA was performed using Illumina’s Hiseq 2000 (sequencing platform produced by Illumina company) platform to generate 2 G of average 2×100 bp original data and then spliced using software velvet (Version 1.2.07) by Sangon Biotech company. The genomic sequence was then subjected for ORF prediction by ORF finder (ORF finder: https://www.ncbi.nlm.nih.gov/orffinder/). Next, predicted ORFs were considered as hypothetical proteins and function annotations were assigned when BLASTP E-values were ≤ 0.001 (Huang et al., 2012) (BLASTP: https://blast.ncbi.nlm.nih.gov/Blast.cgi?PROGRAM=blastp&PAGE_TYPE=BlastSearch&BLAST_SPEC=&LINK_LOC=blasttab).

1.4 Phylogenetic tree of TerL

A neighbor-joining phylogenetic tree based on the TerL was built by MEGA5.1(http://www.megasoftware.net/). Distance analyses were used to test the bootstrap support. A heuristic search with 1000 bootstrap replications was conducted in this analysis.

2 Results

2.1 Siphovirus morphology

Using liquid dilution cultures and sucrose density gradient centrifugation, we isolated and purified a lytic marine *Synechococcus* siphovirus S-ESS1, infecting strain SJ01 (Figure 1). The morphology of negatively stained S-ESS1, as observed with TEM, revealed an icosahedral capsid that was ~65 nm in diameter and exhibited a long tail (~210 nm long and ~20 nm in diameter) (Figure 2).

Figure 1 Color change in the S-ESS1-infected Synechococcus cultures. Uninfected cultures are blue-green (Normal), and cyanophage-infected cultures are chlorotic yellow (S-ESS1 infected)

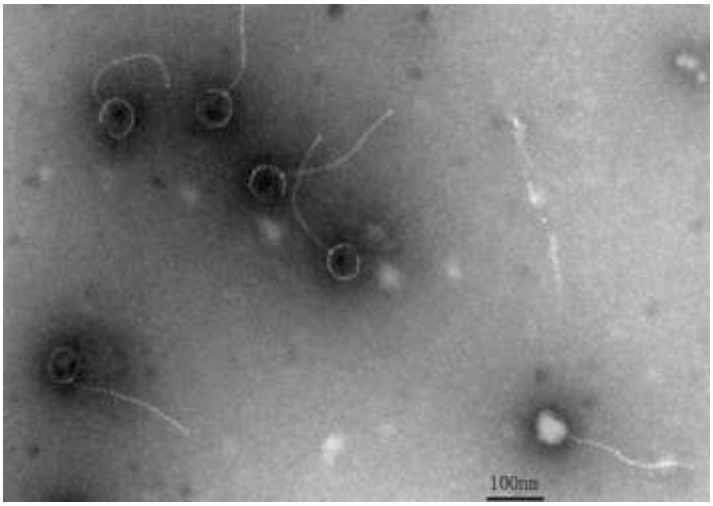

Figure 2 TEM of the negatively stained cyanosiphovirus S-ESS1, 50,000×

2.2 Gene content and ORF information

The complete sequence of the *Synechococcus* siphovirus S-ESS1 genome can be accessed under the GenBank accession no. KY249644. The linearly assembled dsDNA genome of S-ESS1 was 60,362 bp in length, and the G+C content of S-ESS1 was 60.9%. Fifty-six of 282 ORFs in the S-ESS1 genome had recognizable homologues by BLASTP, among which 20 are hypothetical proteins that having unknown function and 36 had ascribed functions (Table 1). No similarity was found to ORFs of known cyanosiphoviruses, and no tRNA sequence was identified in the S-ESS1 genomes. Cyanosiphovirus S-ESS1 was most similar to cyanosiphovirus KBS2A (Ponsero et al., 2013) among the known eight cyanosiphoviruses in terms of gene capacity and ORF content (Table 2). However, the predicted genetic distribution of cyanosiphovirus S-ESS1 was similar to that of cyanosiphovirus PSS2 (Sullivan et al., 2009), with a shared structural gene in the middle, and replication and metabolism-related genes at both ends of the DNA (Figure 3).

2.3 TerL phylogenetic tree

From TerL phylogenetic tree (Figure 4), cyanosiphovirus S-ESS1 had far genetic distance from known cyanosiphoviruses but, unexpectedly, had a relatively close genetic distance with the *E. coli* bacteriophage T7 and a *Ruegeria* bacteriophage DSS3-P1.

Table 1 Predicted ORFs of S-ESS1 genome and their presumed functions (identified by online BLASTP)

ORF	Strand	Start	Stop	size(aa)	Predicted protein	Related phage(s) or microbes	E-value (<0.001)
3	+	4476	5417	313	hypothetical protein		2.00E-36
8	+	13824	15515	563	phage portal protein	Bradyrhizobium sp,Ruegeria phage DSS3-P1,Labrenzia,Xylella phage Sano,Enterobacter phage Enc34,Proteus phage pPM_01,Salmonella phage Chi],Salmonella phage iEPS5]	0
11	+	20010	20597	195	minor tail protein	Burkholderia phage AH2	2.00E-22
12	+	22686	24635	649	phage tape measure protein	Sinorhizobium meliloti,Bradyrhizobium sp. WSM3983,Loktanella phage pCB2051-A,Burkholderia phage AH2,Asticcacaulis sp,Salmonella phage FSL,Salmonella phage	6.00E-74
13	+	27024	28217	397	hypothetical protein DSS3P1_47		4.00E-85
16	+	30444	31400	318	tail assembly protein	Caldimonas manganoxidans,Providencia phage Redjac,Gulbenkiania mobilis,Pseudomonas aeruginosa,Hydrogenophaga sp	6.00E-32
34	+	5605	6294	226	DUF2815 domain-containing protein	Klebsiella variicola,Enterobacter aerogenes,Serratia marcescens	7.00E-16
35	+	6637	8607	656	DNA polymerase I	Silicibacter phage DSS3-P1,Ruegeria phage DSS3-P1,Burkholderia phage,Enterobacter phage,Providencia phage,Xylella phage,Salmonella phage,	1.00E-165
36	+	9274	9990	238	DEAD/DEAH box helicase	Lactobacillus fermentum,Megamonas funiformis,Listeria monocytogenes,Anaerovibrio lipolyticus	3.00E-25
37	+	10558	11463	301	putative terminase small subunit	Ruegeria phage DSS3-P1,Burkholderia phage BcepNazgul,Xylella phage Salvo,Enterobacter phage Enc34,Burkholderia phage AH2,Proteus phage,Achromobacter phage	4.00E-26
38	+	13591	13824	77	head-tail joining protein	Labrenzia sp,Ruegeria phage,Achromobacter phage,Agrobacterium,Loktanella phage,Enterobacter phage	1.00E-14
40	+	17695	18429	244	minor capsid protein E	Mesorhizobium plurifarium,Bradyrhizobium sp,Labrenzia,Burkholderia phage,Agrobacterium	2.00E-79
42	+	18913	19305	130	hypothetical protein		1.00E-11
45	+	24577	25962	461	tail tape measure protein	Ruegeria phage DSS3,Sinorhizobium ,Burkholderia phage,Roseivivax isoporae,Rhizobium sp	2.00E-67
46	+	26731	27024	97	tail length tape measure protein	Loktanella phage	2.00E-20
50	+	29323	29523	66	hypothetical protein DSS3P1_44		2.00E-15
51	+	31489	31857	122	tail assembly structural protein	Pseudomonas phage,Vibrio phage	7.00E-13

Continued Table 1

ORF	Strand	Start	Stop	size(aa)	Predicted protein	Related phage(s) or microbes	E-value (<0.001)
73	+	8429	8752	107	DNA polymerase	Ruegeria phage,Silicibacter phage,Burkholderia phage,Xylella phage,Selenomonas sp	2.00E-25
74	+	8825	9277	150	hypothetical protein		2.00E-13
75	+	9791	10768	325	SNF2-related protein		2.00E-95
76	+	11432	13582	716	terminase large subunit	Ruegeria phage DSS3-P1,Loktanella phage pCB2051-A,Salmonella phage FSLSP088,Pseudomonas aeruginosa	0.00E+00
77	+	15512	17323	603	peptidase S49	Sinorhizobium meliloti,Variovorax sp	1.00E-102
79	+	19307	19924	205	hypothetical protein		1.00E-43
80	+	19925	20230	101	minor tail protein	Salmonella phage	1.00E-04
81	+	20483	21262	259	tail length tape measure protein	Loktanella phage pCB2051-A	3.00E-49
86	+	25676	26578	300	tail length tape measure protein	Loktanella phage pCB2051-A	1.00E-26
87	+	28217	29065	281	hypothetical protein DSS3P1_46		1.00E-90
88	+	29075	29317	80	tail assembly structural protein	Pseudomonas phage MP1412	2.00E-09
89	+	29507	30208	233	putative tail protein	Ruegeria phage DSS3-P1,Loktanella phage pCB2051-A,Achromobacter phage phiAxp-2,Pseudomonas phage SM1	2.00E-09
91	+	32159	32863	234	putative tail protein	Ruegeria phage DSS3-P1,Loktanella phage pCB2051-A,Achromobacter phage phiAxp-2,Agrobacterium	7.00E-59
92	+	32879	33484	201	hypothetical protein DSS3P1		1.00E-32
94	+	36113	37294	393	Peptidoglycan-binding domain 1 protein	Sinorhizobium meliloti AK83	7.00E-92
106	+	48173	49624	483	hypothetical protein ruthe_00792		3.00E-14
107	+	49625	49939	70	hypothetical protein		5.00E-12
108	−	48149	49999	616	ribonucleoside-diphosphate reductase, adenosylcobalamin-dependent	Sulfitobacter donghicola,Sulfitobacter,	0.00E+00
111	−	43406	44356	316	FAD-dependent thymidylate synthase	Sulfitobacter donghicola,Sulfitobacter,Orientia tsutsugamushi	8.00E-108
114	−	39899	40630	243	DNA methyltransferase	Tetraselmis viridis virus,Geminicoccus roseus,Fodinicurvata fenggangensis	2.00E-57
145	−	46012	47130	372	DUF932 domain-containing protein	Rhizobium sp. YK2,Pelagibacterium sp,Bradyrhizobium elkanii	2.00E-99

Continued Table 1

ORF	Strand	Start	Stop	size(aa)	Predicted protein	Related phage(s) or microbes	E-value (<0.001)
148	—	42988	43416	142	dihydrofolate reductase	Rhizobium phage vB_RleM_P10VF,Methylobacterium ,Firmicutes bacterium,Escherichia coli	1.00E-11
150	—	40975	41283	102	hypothetical protein		4.00E-36
160	—	29131	29382	83	Uncharacterized conserved protein	Janthinobacterium sp	2.00E-04
179	—	3382	3633	83	Cro/Cl family transcriptional regulator	Acinetobacter,Moraxella bovoculi,Proteus mirabilis	6.00E-04
180	—	2341	3324	327	Phage associated DNA primase	Sulfitobacter geojensis,	1.00E-109
190	—	41871	42311	146	DUF3310 domain-containing protein	Pseudovibrio sp	1.00E-10
194	—	39678	39980	100	hypothetical protein P10VF_021		7.00E-05
195	—	38661	39167	168	collagen triple helix repeat family protein	Haemophilus parasuis	1.00E-04
218	—	483	2492	669	Phage associated DNA primase	Sulfitobacter geojensis]	0.00E+00
256	—	56643	56963	106	hypothetical protein	Actinobacteria,Bradyrhizobium retamae,uncultured Mediterranean phage uvMED,Synechococcus phage P60,uncultured Mediterranean phage uvMED	3.00E-11
260	—	53370	53597	75	hypothetical protein	Pseudomonas stutzeri,Yersinia aldovae,Alistipes putredinis,Pseudomonas aeruginosa,Bacteroides oleiciplenus	8.00E-10
261	—	52485	53030	181	hypothetical protein	Pseudoruegeria sabulilitoris,Methylosinus,Leptospirillum ferriphilum	6.00E-14
262	—	52011	52295	94	hypothetical protein	[Sinorhizobium meliloti,Enterobacter cloacae,Yersinia pseudotuberculosis	7.00E-06
263	—	51285	51554	89	hypothetical protein CAPSK01_001762	Candidatus Accumulibacter sp. SK-01	2.00E-08
265	—	50001	50636	212	ribonucleoside-diphosphate reductase, adenosylcobalamin-dependent	Rhodobacteraceae bacterium CY02, Nereida ignava,Paenirhodobacter sp. MME-103,Tateyamaria sp. ANG-S1,Donghicola sp. JL3646	2.00E-108
274	—	57556	59061	501	hypothetical protein	Caulobacter virus Karma,Caulobacter virus Magneto,Rhizobium phage RHEph01,Alistipes putredinis	6.00E-20
275	—	56893	57282	129	hypothetical protein	Bradyrhizobium retamae,Bradyrhizobium elkanii	2.00E-19
276	—	55660	56646	328	hypothetical protein	Agrobacterium,Caulobacter virus Magneto,Caulobacter virus Karma	2.00E-16

Table 2 Comparision of gene length, ORFs capacity, host and source between all reported 8 cyanosiphoviruses and cyanosiphovirus S-ESS1 ("+"is "greater than")

Name	Length	ORFs	Host	Isolation location	Reference
S-CBS1	30332	40+	*Synechococcus*	Chesapeake Bay	Huang S,2012
S-CBS2	72332	102	*Synechococcus*	Chesapeake Bay	Huang S,2012
S-CBS3	33004	40+	*Synechococcus*	Chesapeake Bay	Huang S,2012
S-CBS4	69420	105	*Synechococcus*	Chesapeake Bay	Huang S,2012
P-SS2	107595	38	*Prochlorococcus*	Atlantic Ocean slope waters	Sullivan MB et al., 2009
KBS2A	40658	43	*Synechococcus*	Chesapeake Bay	Alise J,2013
A-HIS1	55653	93	*Acaryochloris*	Reef waters off Heron island, Australia	Yi-Wah Chan et al, 2015
A-HIS2	57391	104	*Acaryochloris*	Reef waters off Heron island, Australia	Yi-Wah Chan et al, 2015
S-ESS1	60362	56	*Synechococcus*	East sea of China	This work

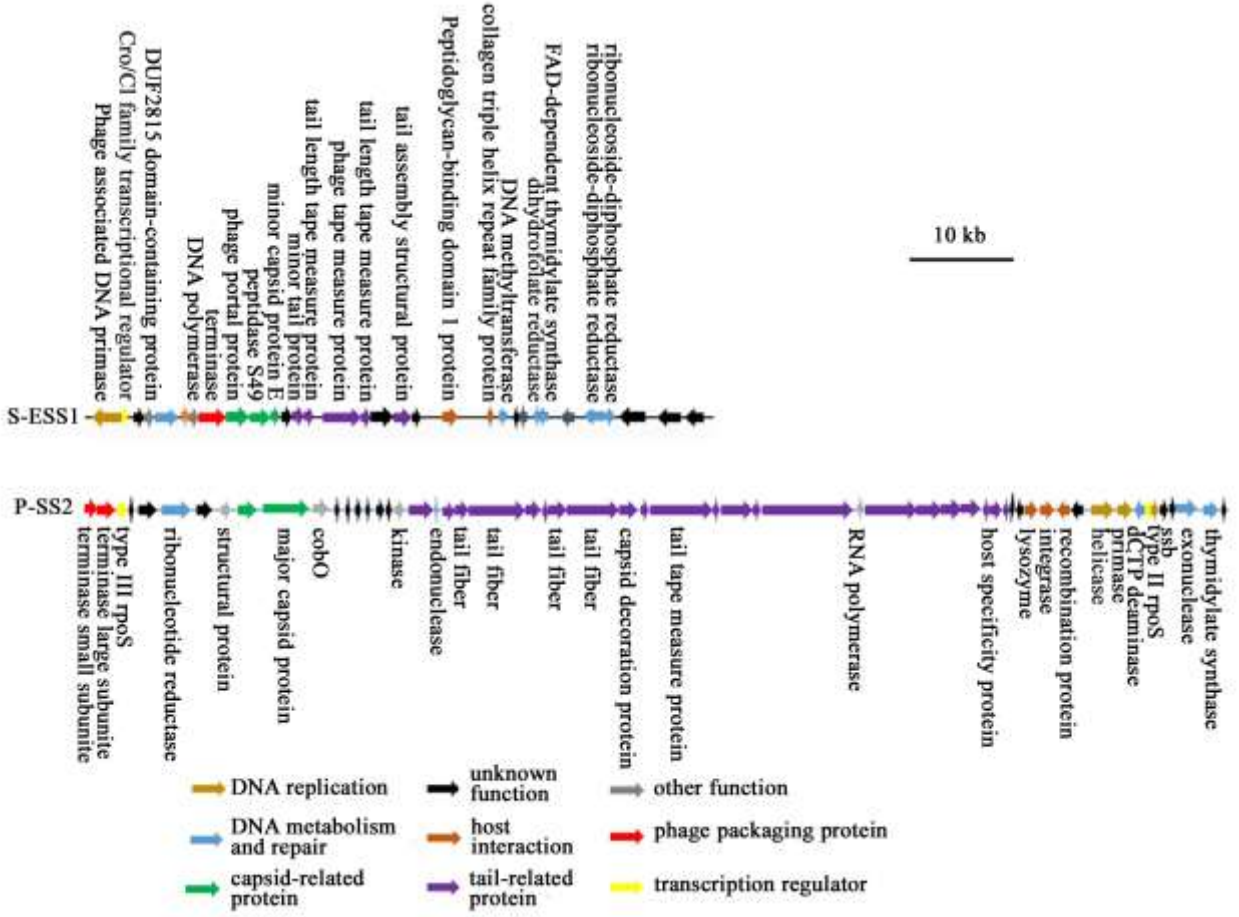

Figure 3 Comparative genomic structure analysis and putative function of phage ORFs between predicted S-ESS1 and P-SS2

3 Discussion

S-ESS1 had an icosahedral capsid and a long non-contractile tail, which are often seen in siphoviruses. S-ESS1 was morphologically similar to S-CBS4, a cyanosiphovirus infecting marine *Synechococcus* CB0101, which also had an isometric head (~72 nm) and a long flexible tail (~200 nm) (Huang, 2012).

Although cyanosiphovirus S-ESS1 has some similarity with cyanosiphoviruses KBS2A and PSS2 in terms of sequence length, ORF capacity, and gene distribution, the predicted ORFs of S-ESS1showed no homology with the other eight reported cyanosiphovirus genomes (including KSB2A and PSS2) (Sullivan et al., 2009; Huang et al., 2012; Ponsero et al., 2013; Chan et al., 2015). In other words, S-ESS1 showed very obvious genetic diversity

from known cyanosiphoviruses. Moreover, only 36 of the 56 predicted ORFs have ascribed functions by BLASTP, which means that there is still much genetic information remaining to be described.

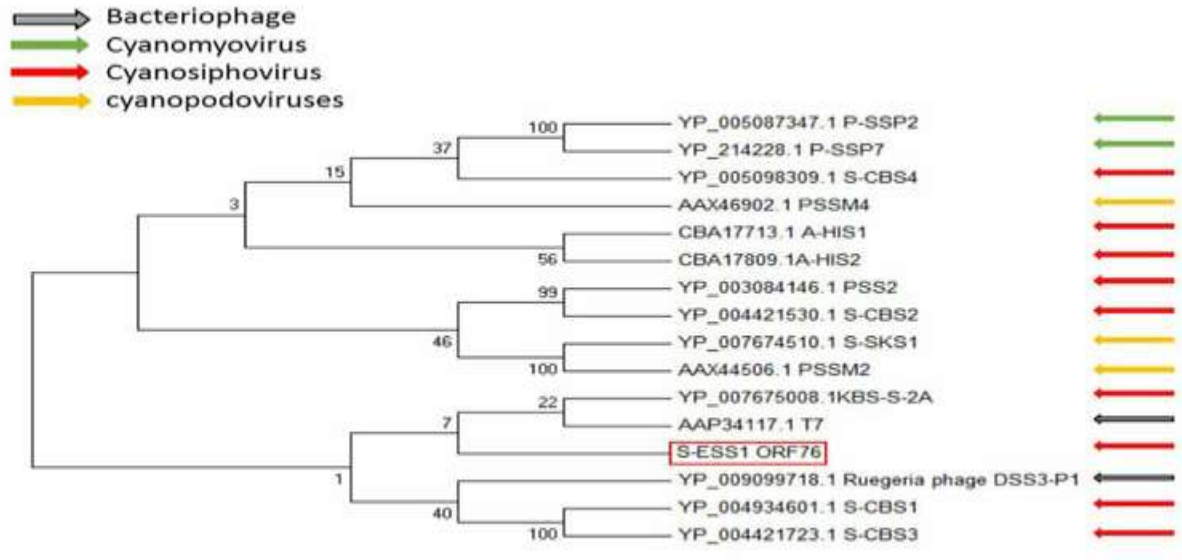

Figure 4 Phylogenetic analysis based on TerL protein sequences showing the clustering of cyanosiphovirus subtypes
Note: A neighbor-joining tree is shown. Distance analyses were used to test the bootstrap support (1000 replicates). Number means the support for the specific node branching of the tree. Cyanosiphoviruses are indicated by red arrows, cyanopodoviruses by yellow arrows, cyanomyoviruses by green arrows, and bacteriophages by grey arrows

According to the sequence of TerL, cyanosiphovirus S-ESS1 was more related to *E. coli* bacteriophage T7 and *Ruegeria* phage DSS3-P1 compared to other cyanosiphoviruses, and the extremely low value for the specific node branching of the tree stated that S-ESS1 was not closely related to the eight known cyanosiphoviruses. The TerL protein-based phylogeny showed that cyanosiphoviruses could fall into three distantly related phyletic groups among the five-known marine siphoviruses (S-CBS1, S-CBS2, S-CBS3, S-CBS4 and P-SS2) by 2012 (Huang et al., 2012). And the latest reported cyanosiphoviruses, A-HIS1 and A-HIS2, became the fourth distantly related phyletic group (Chan et al., 2015). Here, the distant phylogenetic kinship between S-ESS1 and the other eight cyanosiphoviruses, together with their different ORF annotations, reconfirms that S-ESS1 can be classified into a new fifth cyanosiphovirus subtype.

4 Conclusions

Our study aims to identify and classify the cyanophage we isolated from East China Sea. This cyanophage turn out to belong to long-tailed cyanophage which relatively receive less attention and coverage in the current study. From the genome length and content S-ESS1 is defined as a new number of the 8 reported cyanosiphoviruses, but from the TerL phylogenetic tree S-ESS1 have hardly gene homology with reported 8 cyanosiphovirus, thus greatly enriching the genetic diversity of existing cyanosiphovirus. Those results reveal that more work worth investing in cyanosiphoviruses' diversity research. Since different virus–host lifestyles (i.e. broad host vs. narrow host, lytic vs. lysogenic) pose different selection pressures on gene acquisition between virus and host (Huang et al., 2012), and S-ESS1 (as well as its host) was the only cyanosiphovirus isolated from the East China Sea (western part of the Pacific Ocean), this suggests that the regional difference might be the reason for such congeneric genetic variation.

Authors' contributions

HY performed data analyses and wrote the first draft of the manuscript with input from all co-authors. ZY and HY conducted the experiments. ZYJ and CK performed data analyses and wrote the final version of the manuscript. CK conceived of the study.

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