Hydrogenimonas urashimensis sp. nov., a hydrogen-oxidizing chemolithoautotroph isolated from a deep-sea hydrothermal vent in the Southern Mariana Trough

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Abbreviations

ANI, average nucleotide identity; *in silico* DDH, *in silico* DNA-DNA hybridization; AAI, average amino acid identity; SGC, single-copy core gene

Nucleotide sequence data

The 16S rRNA gene sequence and the genome sequence of strain SSM-sur55^T were deposited in DDBJ/EMBL/GenBank under LC469141and AP023212, respectively.

Strain repositories

JCM 19825 = KCTC 15926

Abstract

A novel thermophilic bacterium, strain SSM-sur55^T, was isolated from a chimney structure at the Urashima site on the Southern Mariana Trough in the Pacific Ocean. Growth was observed at temperatures between 25 and 60°C (optimum, 55°C; 180 min doubling time), at pH values between 5.3 and 7.2 (optimum, pH 5.9) and in the presence of between 1.6 and 5.6% (w/v) NaCl (optimum, 3.2%). The isolate used molecular hydrogen as its sole energy source, carbon dioxide as its sole carbon source, ammonium as its sole nitrogen source, and elemental sulfur as its sole sulfur source. Thiosulfate, molecular oxygen (0.1%, v/v) or elemental sulfur was utilized as its sole electron acceptor. Phylogenetic analysis based on 16S rRNA gene sequences indicated that strain SSM-sur55^T belonged to the genus *Hydrogenimonas* of the class "*Campylobacteria*", and its closest relative was *Hydrogenimonas thermophila* EP1-55-1%^{T} (94.9%). On the basis of the phylogenetic, physiological and molecular characteristics, strain SSM-sur55^T represents a novel species within the genus *Hydrogenimonas*, for which the name *Hydrogenimonas urashimensis* sp. nov. is proposed, with the type strain SSM-sur55^T (JCM 19825 = KCTC 15926).

Introduction

The class "*Campylobacteria*" is one of the ecologically important chemolithoautotrophic primary producers in deep-sea hydrothermal systems, where they are often found to be dominant in bacterial communities [1, 2]. Species of the class "*Campylobacteria*" from hydrothermal environments with validly published name fall into two mesophilic (*Thiovulaceae* and *Sulfurovaceae*) and three thermophilic (*Hydrogenimonadaceae*, *Nitratiruptoraceae*, and *Nautiliacea*) families [3, 4]. *Hydrogenimonadaceae* is presently a monogeneric family comprised solely of a validly described hydrogen-oxidizing thermophile, *Hydrogenimonas thermophila*, which was isolated from a deep-sea hydrothermal vent in the Central Indian Ridge [5]. Although sequences affiliated to the genus *Hydrogenimonas* have been detected from worldwide hydrothermal systems [6-9], physiological diversity and the ecological role of this group in hydrothermal ecosystems have not been fully elucidated yet due to the lack of additional cultivated strains within this genus.

The Southern Mariana Trough is a spreading back-arc basin, where geochemically diverse hydrothermal sites have been discovered [10]. The geochemical diversity would provide diverse habitats and a great metabolic potential of microbial communities [11]. In some hydrothermal sites, sulfur- and/or hydrogen-oxidizing mesophilic and thermophilic "*Campylobacteria*" such as the genera *Sulfurovum* and *Lebetimonas* have been detected as dominant in bacterial linages [11, 12]. A recent study successfully has enriched a member of the genus *Hydrogenimonas* that possessed the potential of global warming mitigation [13]. Although these previous studies imply that deep-sea hydrothermal environments in the Southern Mariana Trough are expected to be good candidates for obtaining new microbial species, "*Campylobacteria*" species from this area has never been validly described. Here, we succeeded to isolate a novel strain SSM-sur55^{T} from the hydrothermal field of the Urashima site in the Southern Mariana Trough, and determined its physiological and phylogenetic characteristics.

Methods

Sample collection, enrichment and purification

Sample collection and subsampling procedures were carried out as described previously [13]. The chimney structure was taken with *R/V Yokosuka* and *DSV Shinkai* 6500 from the Baltan chimney at the Urashima site (12º55.3'N, 143º38.9'E) in the Southern Mariana Trough in 2010. The physical and chemical characterization of the vent emissions has been described elsewhere [10]. After retrieval on board, the sample was anaerobically suspended in 20 ml sterilized MJ synthetic sea water [14, 15] containing 0.05% (w/v) sodium sulfide in a 100 ml glass bottle (Schott Glaswerke) tightly sealed with a butyl-rubber cap under a gas phase of 100% N_2 (0.1 MPa). The suspended slurry was used to inoculate a series of media, including MMJHS medium [16], under a gas phase of $H_2/CO_2/O_2$ (80:19:1; 0.3 MPa), and the cultures were incubated at 55°C in a dry oven. Growth of thermophiles was observed in MMJHS medium after 2 days incubation at 55°C. Enrichment cultures at 55°C contained rod-shaped cells. A pure culture was obtained by using the dilution-to-extinction technique at 55°C with the same medium as that used for the enrichment [17]. The culture in the tube showing growth at the highest dilution was designated strain SSM-sur55^T. Purity was confirmed with a routine microscopic examination and by repeated partial sequencing of the 16S rRNA gene using several PCR primers.

Growth characteristics

Growth of strain SSM-sur55^T was measured by direct cell counting after staining with 4',6-diamidino-2-phenylindole using the ZEISS Axiophot microscope (Carl Zeiss Co., Oberkochen, Germany). To determine optimum temperature, pH and NaCl concentrations, cultures were prepared in a 3 ml MMJHS medium under various conditions.

To determine combinations of a single electron donor and acceptor, the isolate was tested using MJ synthetic seawater containing 0.1% (w/v) $NaHCO_3$ as the basal medium. For testing the growth on hydrogen as an electron donor, H_2/CO_2 (80:20) was used as the gas phase. To examine the growth on thiosulfate (0.1%, w/v) or elemental sulfur (S^0) (1%, w/v) as an electron donor, N_2/CO_2 (80:20) was used as the gas phase. Nitrate (0.1%, w/v), thiosulfate (0.1%, w/v), nitrite (0.1 and 0.01%, w/v) sulfite (0.01%, w/v), elemental sulfur (1%, w/v) or molecular oxygen (0.1 and 1%, v/v) were tested as sole electron acceptors. The presence or absence of the cell growth was determined by microscopic observation.

For testing heterotrophic growth of strain SSM-sur55^T, experiments were conducted using MMJHS medium without $NaHCO_3$ under a gas phase of 100% H_2 (0.3 MPa). Each of the following potential carbon sources was tested: yeast extract, peptone, tryptone, casamino acids, D(+)-glucose, galactose, sucrose, fructose, lactose, maltose, starch (all 0.2%, w/v), formate, acetate, glycerol, citrate, tartrate, malate, succinate, propionate, lactate, oxalate, pyruvate (all 10 mM), methanol (0.05%, v/v), ethanol (0.1%, v/v) and 2-propanol (0.2%, v/v).

Potential nitrogen and sulfur sources required for the growth of the isolate were tested. To determine the nitrogen sources for growth of strain SSM-sur55^T, NH_4Cl (0.025%, w/v), $NaNO_3$ (0.1%, w/v) and $NaNO_2$ (0.1 and 0.01%, w/v) were added in MMJHS medium lacking all nitrogen sources, under a H_2/CO_2 (80:20) gas phase (0.3 MPa). In addition, utilization of N_2 was examined under a $H_2/N_2/CO_2$ (60:20:20) gas phase.

To examine the sulfur sources for the growth of the isolate, sulfate (0.42%, w/v), thiosulfate (0.1%, w/v), sulfite (0.01%, w/v) and elemental sulfur (1%, w/v) were examined in MMJHS medium in which sulfur compounds were removed and replaced with the chloride salts under an H_2/CO_2 (80:20) gas phase (0.3 MPa).

Morphological observation

The cell morphology of strain SSM-sur55^T was observed by phase-contrast microscopy with a Zeiss Axiophot microscope and a JEM-1011 transmission electron microscope (JEOL). Cells grown in MMJHS medium at 55°C in the mid-exponential phase of growth were used for microscopic observation. Cells were fixed with 2.5% glutaraldehyde, followed by several washes with 10mM PIPES buffer before negative staining with EM Stainer (Nisshin EM, Tokyo, Japan).

Genome sequencing and assembly

Genomic DNA of strain SSM-sur55^T was extracted from the cells grown in MMJHS medium with Wizard genomic DNA purification kit (Promega, Madison, Wisconsin, USA) according to the protocol provided by the manufacturer. The genome was sequenced using both Oxford Nanopore Technology (ONT) and Illumina platforms. For the ONT sequencing, library was prepared using the Rapid Barcoding Sequence kit (Oxford Nanopore Technologies, Oxford, UK) according to the standard protocol provided by the manufacturer. The constructed library was loaded into the FlowCell (FLO-MIN106) on a MinION device and a 48-hour sequencing run with MinKNOW 1.15.4 software was performed. After basecalling ONT reads with Guppy v1.1 (Oxford Nanopore Technologies) with following settings: --qscore_filtering and --calib_detect, basecalled reads were binned with Deepbinner [18]. For the Illumina sequencing, paired-end libraries were generated using Nextera library preparation methods. Genome sequencing was then performed on an Illumina MiSeq platform (2x300 bp paired-end). ONT and Illumina reads were then assembled using Unicycler version 0.4.7 [19]. The genome was annotated using DFAST [20]. KEGG pathway annotation and mapping were performed with BlastKOALA [21] and KEGG Mapper [22], respectively.

Phylogeny based on 16S rRNA gene sequences

Phylogenetic trees were constructed by using the almost full-length sequences of the 16S rRNA genes. The 16S rRNA gene of strain SSM-sur55^{T} was amplified by PCR using primers Eubac 27F and 1492R [23]. The nearly complete 16S rRNA gene sequence (1,422 bp) was obtained by direct sequencing of both strands. The 16S rRNA gene sequence was analyzed using BLAST search algorithm [24]. To conduct the phylogenetic analysis of the strain, the other "*Campylobacteria*" sequences were retrieved and aligned using Silva database [25] and Silva Incremental Aligner v1.2.11 [26], respectively. A phylogenetic tree was constructed by neighbor-joining algorism [27] with the MEGA 7.0.21 software [28] using 1,273 base pairs. Bootstrap analysis was done using 1,000 replications to provide confidence estimates for the phylogenetic tree topologies.

Pangenomic, phylogenomic, and genome sequence similarities analyses

Phylogenomic tree construction and pangenomic analysis were carried out with 16 thermophilic campylobacterial genomes using the anvi'o v5.5 [29]. The phylogenomics workflow (http://merenlab.org/2017/06/07/phylogenomics/) was followed to infer evolutionary associations bewteen genomes. Briefly, the fasta files containing nucleotide sequences of genomes was used for generating the database of each genome (anvi-script-FASTA-to-contigs-db). We then identified an HMM profiles (anvi-get-sequences-for-hmm-hits) and extracted 139 single-copy core genes (SCGs) proposed by Campbell et al. [30]. The amino acid sequences of 139 SCGs were concatenated in a fasta file (anvi-get-sequences-for-hmm-hits) and a phylogenomic tree was constructed (anvi-gen-phylogenomic-tree) using FastTree [31]. For pangenome analysis, we generated a storage database (anvi-gen-genomes-storage) from the genomes of thermophilic relatives and then computed the pangenome (anvi-pan-genome). COG-annotated strains-specific gene clusters were exported from pangenome (anvi-summarize) for the gene functional analysis. Average nucleotide identity (ANI) between genomes was calculated with PyANI (anvi-compute-ani) (https://github.com/widdowquinn/pyani/releases/tag/v0.1.2). The pangenome was visualized with anvi-display-pan. Average amino acid identity (AAI) and *in silico* DNA-DNA hybridization values were calculated using aai.rb script within the enveomics collection [32] and Genome-to-Genome Distance Calculator 2.1 [33], respectively.

Results and Discussion

Growth characteristics

With MMJHS medium, strain SSM-sur55^T grew at temperature between 25ºC and 60ºC, showing optimum growth at 55ºC. No growth was observed below 20ºC or above 65ºC. Growth occurred between pH 5.3 and 7.2, with optimum growth at pH 5.9. No growth was observed below pH 4.9 or above pH 7.7. Growth was observed between 1.6 and 5.6% (w/v) NaCl concentrations, with optimum growth at 3.2%. No growth was detected below 0.8% or above 7.2% NaCl concentration levels (Fig. S1). These growth characteristics of strain SSM-sur55^T were similar to those of *Hydrogenimonas thermophila* EP1-55-1%^{T} [5] (Table 1).

Strain SSM-sur55^T was unable to utilize any electron donors other than H_2. Thiosulfate (0.1%, w/v), elemental sulfur (1%, w/v) and molecular oxygen (0.1%, v/v) were able to serve as its sole electron acceptors. None of the organic compounds sustained growth of strain SSM-sur55^T as energy or carbon sources. These results indicated that strain SSM-sur55^T was a strictly hydrogen-oxidizing thermophilic chemolithoautotroph. Strain SSM-sur55^T utilized ammonium as its sole nitrogen source and did not utilize nitrate, nitrite and molecular nitrogen. Strain SSM-sur55^T utilized elemental sulfur as its sole sulfur source. Utilization of thiosulfate, sulfate and sulfite were not observed.

Cell morphology

Cells of strain SSM-sur55^T were Gram-stain negative and rod-shaped (Fig. S2). Flagella were not observed although motility was confirmed under the light microscopic observation (Fig. S2). A small percentage of cells grown in MMJHS medium exhibited spherical shape, as reported for *H. thermophila* EP1-55-1%^{T} [5]

Phylogenetic analysis based on 16S rRNA gene sequences

With a nearly full length 16S rRNA gene sequence of strain SSM-sur55^T as a query in BLAST search, the highest similarity with *Hydrogenimonas* sp. RS_Sur55-1 (96.2%), *Hydrogenimonas* sp. MAG (95.9%), and *H. thermophila* EP1-55-1%^{T} (94.9%) were obtained. More closely related sequence was retrieved from an environmental clone from the detritus from tubeworm in the East Pacific Rise (LF8GH2b132, 96.7% 16S rRNA gene sequence similarity). The phylogenetic tree based on 16S rRNA gene sequences showed that strain SSM-sur55^T formed a clade with *H. thermophila* (Fig. 1). These results indicated that strain SSM-sur55^T is a novel species belonging to the genus *Hydrogenimonas*.

Genome properties and genome relatedness

The complete genome of strain SSM-sur55^T was reconstructed. The genome size was 2,297,889 bp with an average G + C content was 52.8% (Table 1). In total, 2,270 coding sequence regions, 48 tRNA genes, and 3 set of rRNA genes were respectively predicted. The G + C content of strain SSM-sur55^T was higher than that of previously sequenced genome of *H. thermophila* (33.5%) and comparable with that of *Hydrogenimonas* sp. MAG (50.2%) [13].

Genome analysis of the strain SSM-sur55^T supported its phenotypic characteristics. The H_2-uptake hydrogenase gene cluster for H_2 oxidation was present in strain SSM-sur55^T. The ability to utilize oxygen as a sole electron acceptor was ensured by the presence of four genes encoding the CcoNOQP proteins, which constitutes a *cbb*$_3$-type terminal cytochrome oxidase. A gene encoding putative thiosulfate sulfurtransferase was found in its genome, supporting the ability to utilize thiosulfate as a sole electron acceptor. Although strain SSM-sur55^T showed no ability to use nitrate and N_2O as a sole electron acceptor under hydrogen-oxidizing condition, the complete set of denitrification genes such as *nap*, *nir*, *nor*, *and nos* was found on its genome, that might allow to the strain to contribute to the nitrogen cycle as a denitrifier in deep-sea hydrothermal vent environments.

The ANI and *in silico* DDH values between strain SSM-sur55^T and *H. thermophila* EP1-55-1%^{T} were found to be 72.7% and 17.4%, respectively, well below the species threshold (95-96% and 70%, respectively) [34]. Strain SSM-sur55^T shared AAI values of 71.4% with *H. thermophila* EP1-55-1%^{T} that considerably above the recently proposed AAI genus threshold among "*Campylobacterota*" (60-62%) (35). These results also support the proposal that the isolate is a novel species within the genus *Hydrogenimonas*.

Table 1. Comparison of physiological characteristics of SSM-sur55^T with species of "*Campylobacteria*" from deep-sea vents.

Characteristics	*Hydrogenimonas* sp. SSM-sur55^T (This study)	*Hydrogenimonas thermophila* EP1-55-1%^{T} [5]	*Nitratiruptor tergarcus* MI55-1^T [36]	"*Nitrosophilus labii*" HRV44^T [35, 37]	"*Nitrosophilus alvini*" EPR55-1^T [35]
Origin	Southern Mariana Trough	Central Indian Ridge	Mid-Okinawa Trough	Mid-Okinawa Trough	East Pacific Rise
Temperature range (°C)	25-60	35-65	40-55	45-60	50-60
Temperature optimum (°C)	55	55	55	53	60
pH range	5.3-7.2	4.9-7.2	5.4-6.9	5.4-6.4	5.4-8.6
pH optimum	5.9	5.9	6.4	6.0	6.6
NaCl range (%, w/v)	1.6-5.6	1.6-5.6	1.5-4.0	2.0-4.0	2.4-3.2
NaCl optimum (%, w/v)	3.2	3.2	2.5	2.5	2.4
Electron donors	H_2	H_2	H_2	H_2	H_2
Electron acceptors	$S_2O_3^{2-}$, O_2, S^0	NO_3^-, O_2, S^0	NO_3^-, O_2, $S^{0\dagger}$	NO_3^-, N_2O, O_2, S^0	NO_3^-, N_2O, $S_2O_3^{2-}$, O_2, S^0
Carbon sources other than CO_2	-	-	-	-	-
Nitrogen sources	NH_4^+	NO_3^-, NH_4^+	NO_3^-, NH_4^+	NO_3^-, NH_4^+	NH_4^+
DNA G+C content (%)	52.8	33.5	36.9	33.4	37.7

-, negative; ND, not determined.

†S^0 did not serve as a sole electron acceptor to support growth.

Pangenomic and pylogenomic analyses

The pangenome of thermophilic campylobacteria revealed a total of 8,272 gene clusters comprising 35,198 genes (Fig. 2). 557 gene clusters were represented core genome, and 468 of those were SCGs. 577 gene clusters were found to be unique to the strain SSM-sur55^T. Although we searched gene clusters enriched in *Hydrogenimonas* genomes, the statistically significant trends were not obtained (corrected p≥ 0.25), possibly due to the small number of genomes in each genus. The COG functional annotation of the strain-specific gene clusters showed that relatively abundance of genes related to energy production and conversion (C) in SSM-sur55^T is higher (9.6% in without poorly characterized categories) than those in *H. thermophila* EP1-55-1%^{T} and *Hydrogenimonas* sp. BAL40 [13] (Fig. S3). Further pangenomic analyses with additional genome sequences could provide us a better understanding on genus-specific genomic traits of thermophilic "*Campylobacteria*".

Conclusion

On the basis of physiological and molecular characteristics of strain SSM-sur55^T, the strain is considered to represent a novel species in the genus *Hydrogenimonas*, for which the name *Hydrogenimonas urashimensis* sp. nov. is proposed. Its Protologue description is listed in Table 2.

Table 2. Protologue description of *Hydrogenimonas urashimensis* sp. nov.

Genus name	*Hydrogenimonas*
Species name	*Hydrogenimonas urashimensis*
Specific epithet	*urashimensis*
Species status	**sp. nov.**
Species etymology	u.ra'shi men'sis. N.L. fem. adj. *urashimensis* pertaining to the Urashima deep-sea hydrothermal site in the Southern Mariana Trough
Description of the new taxon and diagnostic traits	Cells are gram-negative, motile, and rod-shaped. The temperature range for growth is 25-60ºC (optimum, 55ºC; 180 min doubling time). The pH range for growth is 5.3-7.2 (optimum, pH5.9). NaCl in the concentration range 1.6-5.6% (w/v) is an absolute growth requirement; optimum growth occurs at 3.2%. Strain SSM-sur55^T is hydrogen-oxidizing, facultatively anaerobic and chemolithoautotroph with molecular hydrogen as its sole electron donor and with thiosulfate, molecular

	oxygen or elemental sulfur as its sole electron acceptors. Ammonium is utilized as its sole nitrogen source. Elemental sulfur is utilized as its sole sulfur source.
Country of origin	USA
Region of origin	The Southern Mariana Trough
Date of isolation (dd/mm/yyyy)	17/12/2010
Source of isolation	deep-sea hydrothermal vent
Sampling date (dd/mm/yyyy)	23/08/2010
Latitude (xx°xx′xx″N/S)	12°55'18"N
Longitude (xx°xx′xx″E/W)	143°38'54"E
Altitude (meters above sea level)	-2,922 m
16S rRNA gene accession nr.	LC469141
Genome accession number [RefSeq; EMBL; …]	GenBank = AP023212
Genome status	Complete
Genome size	2,297 kbp
GC mol%	52.8 (based on the complete genome sequence)
Number of strains in study	1
Source of isolation of non-type strains	not applicable
Information related to the Nagoya Protocol	not applicable
Designation of the Type Strain	SSM-sur55^{T}
Strain Collection Numbers	JCM 19825^{T} = KCTC 15926^{T}

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Figure Legends

Fig. 1. Phylogenic tree based on 16S rRNA gene sequences. Phylogenetic tree of the members of thermophilic "*Campylobacteria*", inferred by the neighbor-joining algorism using 1,229 homologous sequence positions. Numbers at branches are bootstrap values (%) based on 1,000 replicates.

Fig. 2. Pangenome of thermophilic "*Campylobacteria*". Pangenomic analysis of 16 sequenced thermophilic "*Campylobacteria*" revealing 468 SCGs among 8,272 total gene clusters along with their distribution and ANI.

Supplementary

Fig. S1. Growth rates of strain SSM-sur55^T. Growth rates of temperature (a), pH (b) and NaCl concentration (c) in MMJHS medium.

Fig. S2. Transmission electron micrograph of a rod-shaped cell of strain SSM-sur55^T. Bar, 1 µm.

Fig. S3. The COG category annotation of strain-specific gene clusters. All COGs (a) and without poorly characterized categories, "R", "S", and "-".

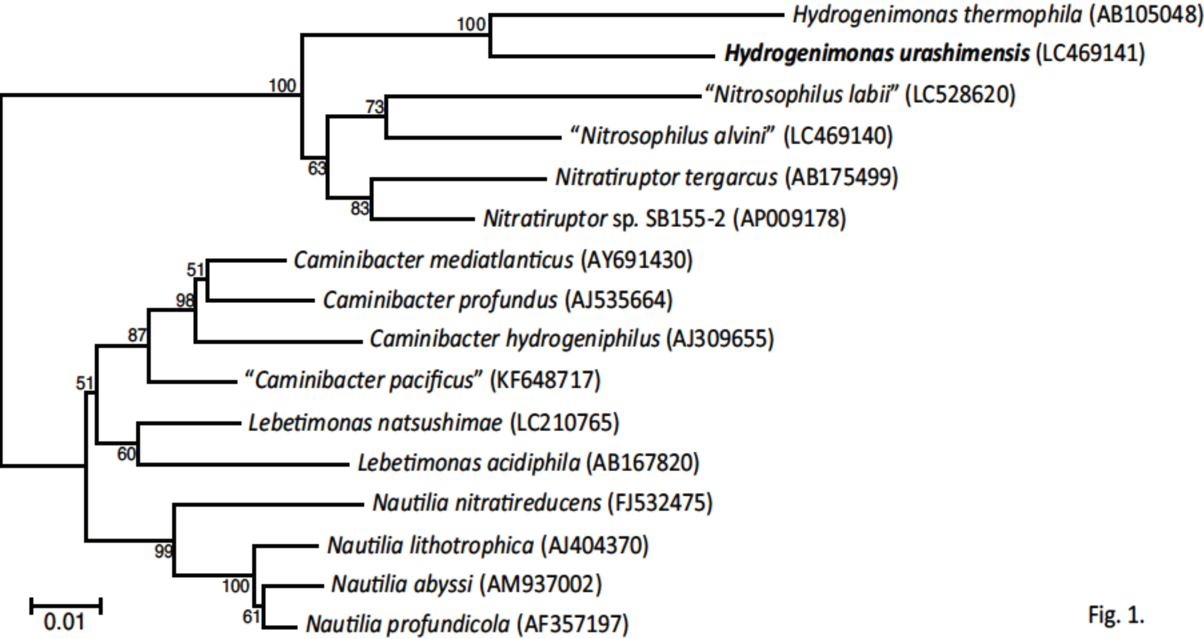
Hydrogenimonas thermophila (AB105048)
Hydrogenimonas urashimensis (LC469141)
"Nitrosophilus labii" (LC528620)
"Nitrosophilus alvini" (LC469140)
Nitratiruptor tergarcus (AB175499)
Nitratiruptor sp. SB155-2 (AP009178)
Caminibacter mediatlanticus (AY691430)
Caminibacter profundus (AJ535664)
Caminibacter hydrogeniphilus (AJ309655)
"Caminibacter pacificus" (KF648717)
Lebetimonas natsushimae (LC210765)
Lebetimonas acidiphila (AB167820)
Nautilia nitratireducens (FJ532475)
Nautilia lithotrophica (AJ404370)
Nautilia abyssi (AM937002)
Nautilia profundicola (AF357197)
100
100
73
63
83
51
98
87
51
60
99
100
61
0.01

Fig. 1.

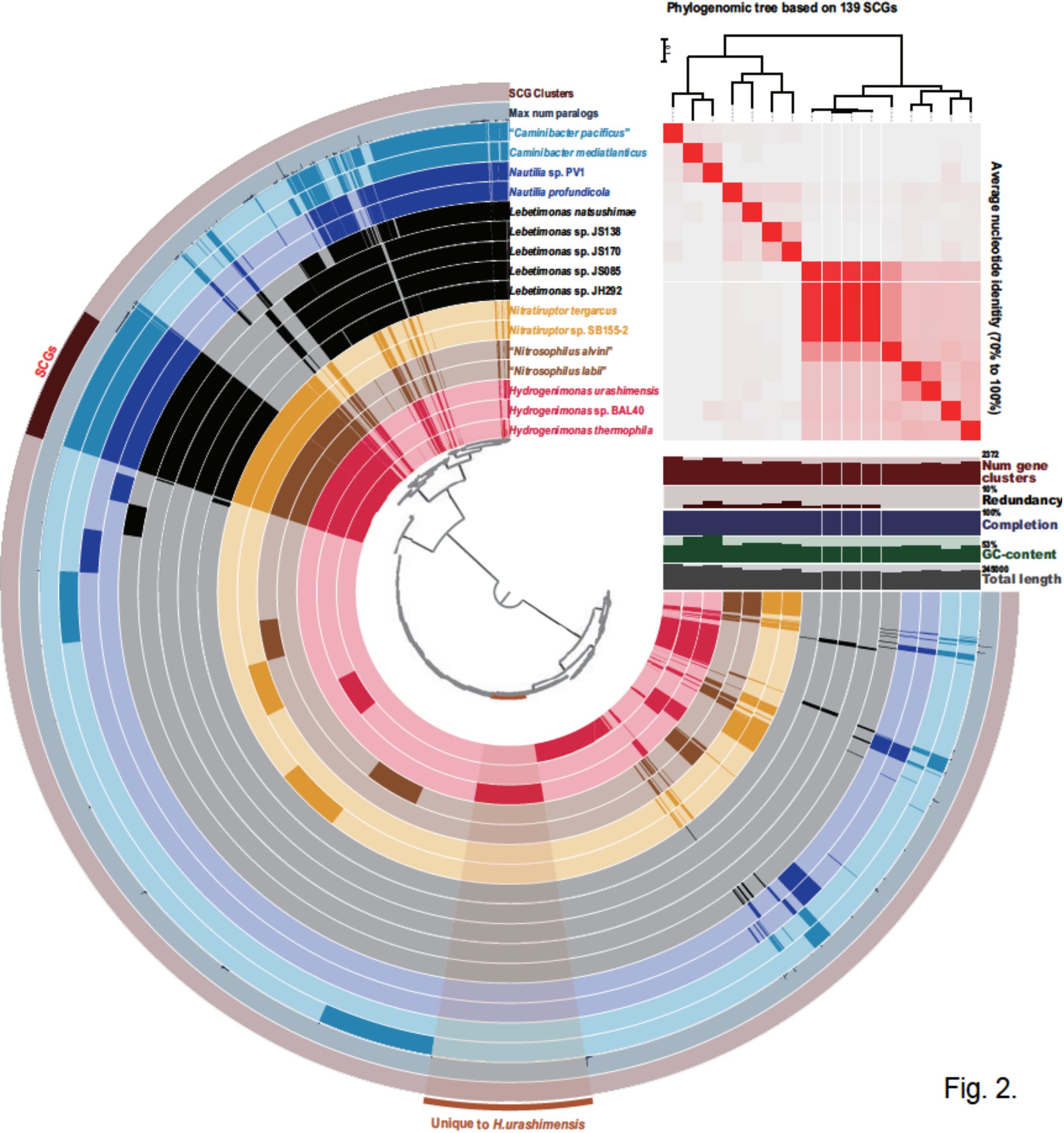
Phylogenomic tree based on 139 SCGs
SCG Clusters
Max num paralogs
"Caminibacter pacificus"
Caminibacter mediatlanticus
Nautilia sp. PV1
Nautilia profundicola
Lebetimonas natsushimae
Lebetimonas sp. JS138
Lebetimonas sp. JS170
Lebetimonas sp. JS085
Lebetimonas sp. JH292
Nitratiruptor tergarcus
Nitratiruptor sp. SB155-2
"Nitrosophilus alvini"
"Nitrosophilus labii"
Hydrogenimonas urashimensis
Hydrogenimonas sp. BAL40
Hydrogenimonas thermophila
Average nucleotide identity (70% to 100%)
Num gene clusters
Redundancy
Completion
GC-content
Total length
SCGs
Unique to H.urashimensis

Fig. 2.

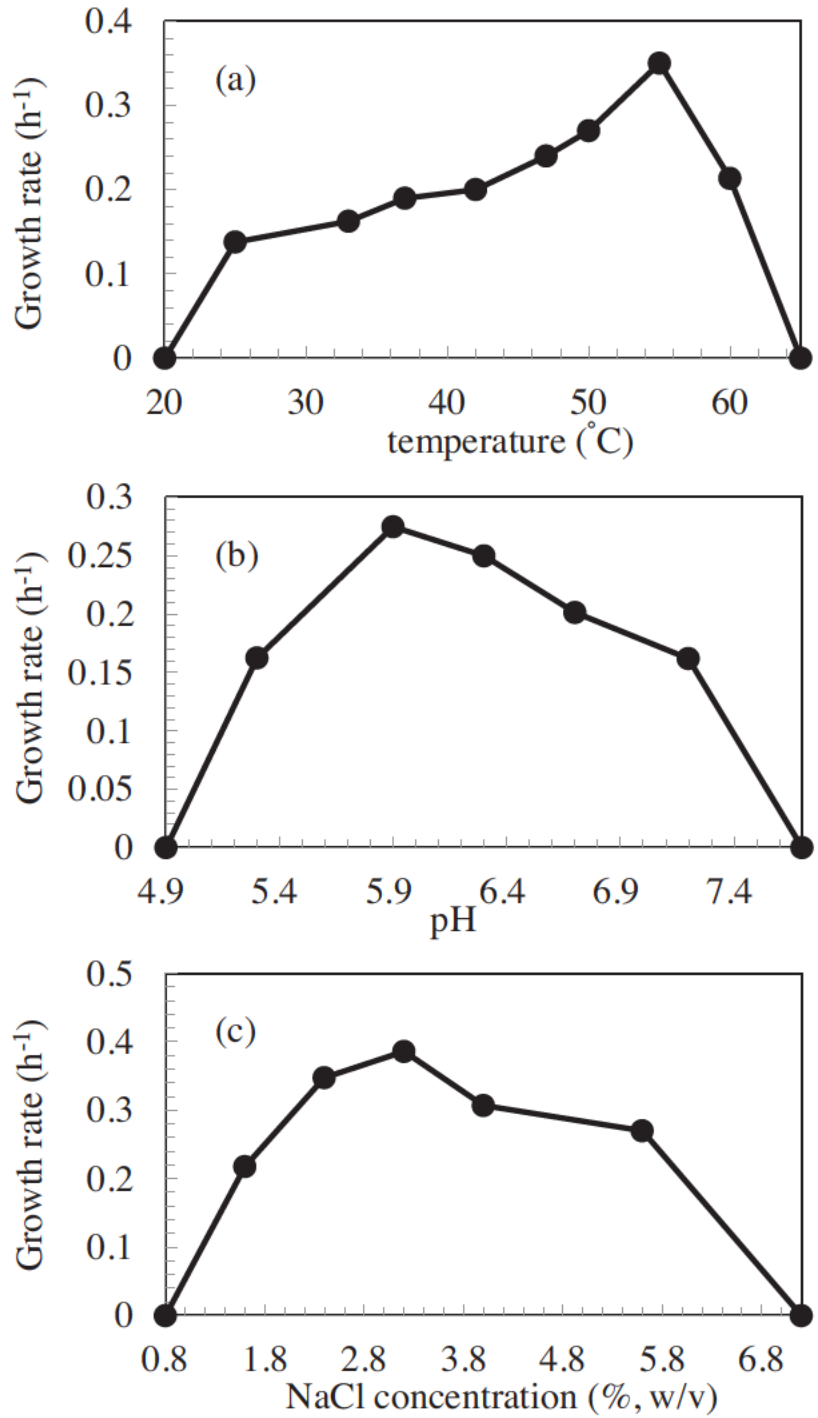
(a)
Growth rate (h-1)
0.4
0.3
0.2
0.1
0
20
30
40
50
60
temperature (˚C)
(b)
Growth rate (h-1)
0.3
0.25
0.2
0.15
0.1
0.05
0
4.9
5.4
5.9
6.4
6.9
7.4
pH
(c)
Growth rate (h-1)
0.5
0.4
0.3
0.2
0.1
0
0.8
1.8
2.8
3.8
4.8
5.8
6.8
NaCl concentration (%, w/v)

Fig. S1.

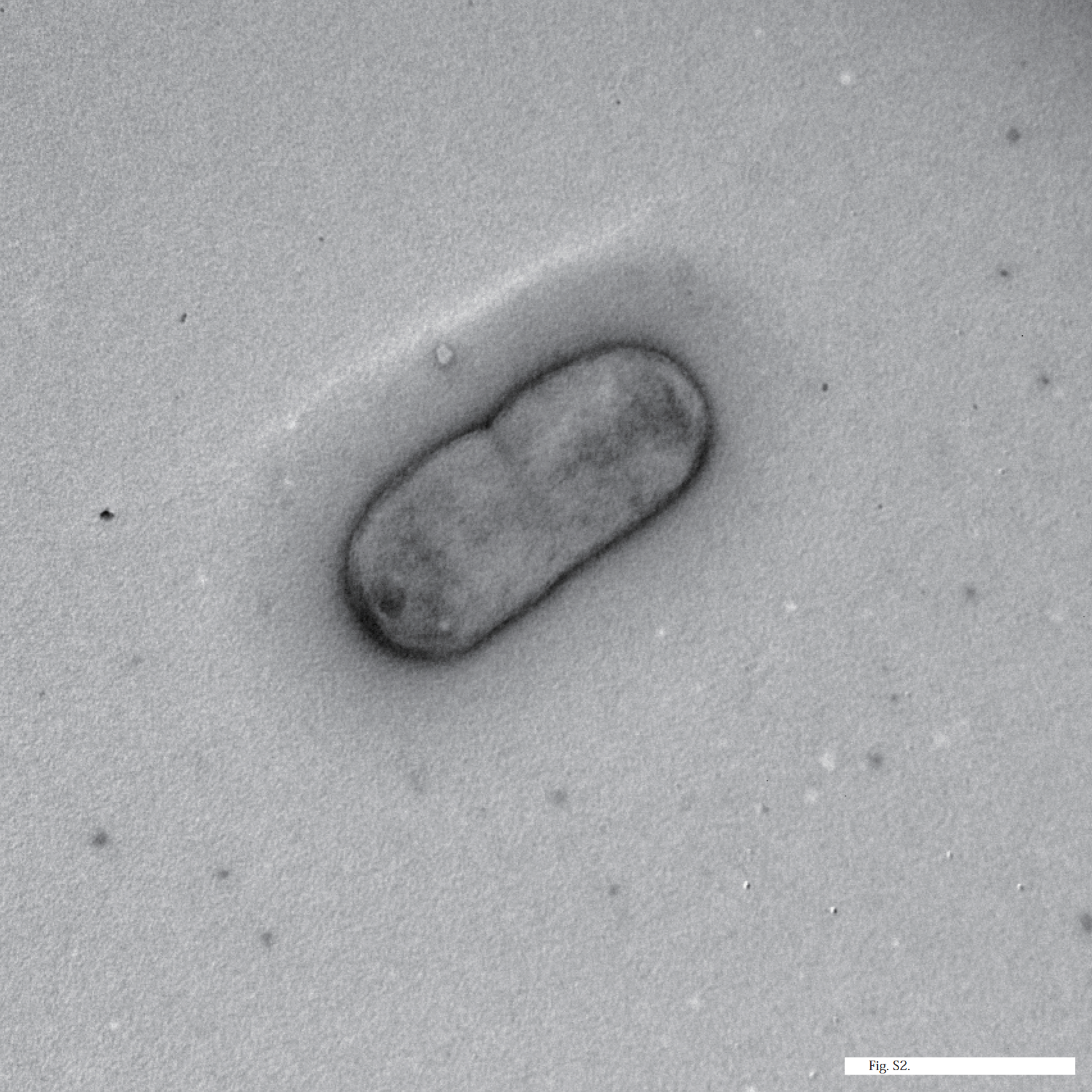

Fig. S2.

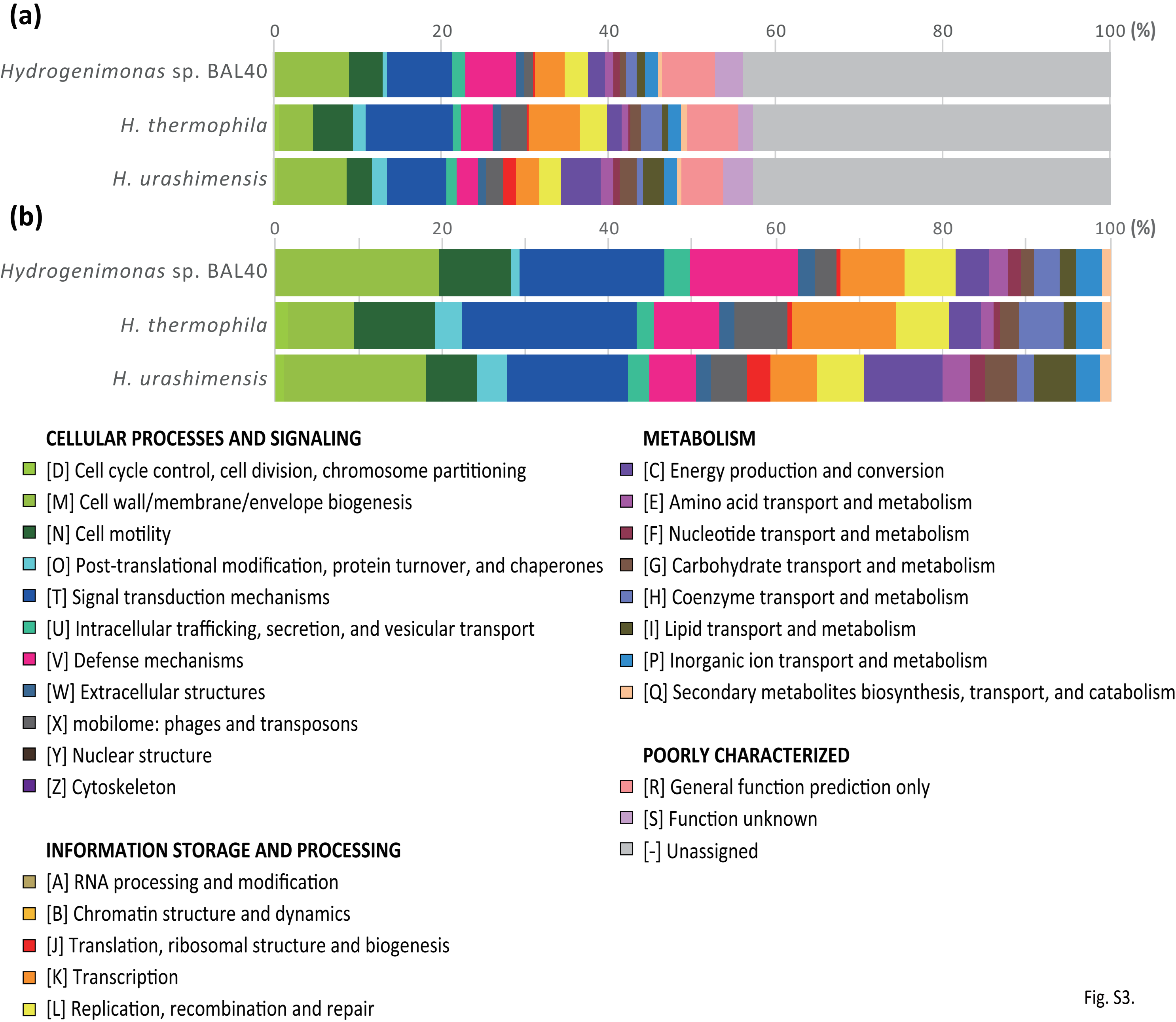
(a)
0
20
40
60
80
100 (%)
Hydrogenimonas sp. BAL40
H. thermophila
H. urashimensis
(b)
0
20
40
60
80
100 (%)
Hydrogenimonas sp. BAL40
H. thermophila
H. urashimensis
CELLULAR PROCESSES AND SIGNALING
[D] Cell cycle control, cell division, chromosome partitioning
[M] Cell wall/membrane/envelope biogenesis
[N] Cell motility
[O] Post-translational modification, protein turnover, and chaperones
[T] Signal transduction mechanisms
[U] Intracellular trafficking, secretion, and vesicular transport
[V] Defense mechanisms
[W] Extracellular structures
[X] mobilome: phages and transposons
[Y] Nuclear structure
[Z] Cytoskeleton
INFORMATION STORAGE AND PROCESSING
[A] RNA processing and modification
[B] Chromatin structure and dynamics
[J] Translation, ribosomal structure and biogenesis
[K] Transcription
[L] Replication, recombination and repair
METABOLISM
[C] Energy production and conversion
[E] Amino acid transport and metabolism
[F] Nucleotide transport and metabolism
[G] Carbohydrate transport and metabolism
[H] Coenzyme transport and metabolism
[I] Lipid transport and metabolism
[P] Inorganic ion transport and metabolism
[Q] Secondary metabolites biosynthesis, transport, and catabolism
POORLY CHARACTERIZED
[R] General function prediction only
[S] Function unknown
[-] Unassigned

Fig. S3.