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Abstract

Brown algae are important primary producers and ecosystem engineers in the ocean, and *Ectocarpus* has been established as a laboratory model for this lineage. Like most multicellular organisms, *Ectocarpus* is associated with a community of microorganisms, a partnership frequently referred to as holobiont due to the tight interconnections between the components. Although genomic resources for the algal host are well established, its associated microbiome is poorly characterized from a genomic point of view, limiting the possibilities of using these types of data to study host–microbe interactions. To address this gap in knowledge, we present the annotated draft genome sequences of seventy-two cultivable *Ectocarpus*-associated bacteria. A screening of gene clusters related to the production of secondary metabolites revealed terpene, bacteriocin, NRPS, PKS-t3, siderophore, PKS-t1, and homoserine lactone clusters to be abundant among the sequenced genomes. These compounds may be used by the bacteria to communicate with the host and other microbes. Moreover, detoxification and provision of vitamin B pathways have been observed in most sequenced genomes, highlighting potential contributions of the bacterial metabolism toward host fitness and survival. The genomes sequenced in this study form a valuable resource for comparative genomic analyses and evolutionary surveys of alga-associated bacteria. They help establish *Ectocarpus* as a model for brown algal holobionts and will enable the research community to produce testable hypotheses about the molecular interactions within this complex system.

Key words: brown algae, holobiont, alga-associated bacteria, biosynthetic gene clusters, detoxification, metabolic networks.

Introduction

Brown macroalgae are important primary producers and major ecosystem engineers on marine rocky shores, providing both shelter and nutrients for other forms of life (Brodie et al. 2017). They belong to the stramenopiles, an evolutionarily distinct lineage from the Achaeplastida, which comprise red and green algae as well as land plants (Charrier et al. 2008) and are of commercial importance in several regions of the world (Koru 2013; Raja et al. 2013; Venkatesan et al. 2015). *Ectocarpus* is a genus of brown algae that has been established as a laboratory model for this lineage (Peters et al. 2004) due to its small genome (Cock et al. 2010), the possibility of cultivation in the lab, and its short life cycle.

Like most if not all multicellular eukaryotes, brown algae, including *Ectocarpus*, are associated with bacteria (Paix et al. 2019). These interactions may be so intimate that the term holobiont has been suggested to describe the functional unit of a host and its associated microbiome (Zilber-Rosenberg and Rosenberg 2008; Douglas and Werren 2016). For instance, it has been estimated that approximately half of all algae (including 49 out of 83 surveyed stramenopiles) rely on their bacteria associated to provide them with vitamin B12 (Croft et al. 2005; Tang et al. 2010). In *Ectocarpus*, associated

bacteria are known to provide functions related to developmental transitions and growth of the algae (Pedersen 1968; Tapia et al. 2016). Furthermore, they may impact their capacity to tolerate environmental stressors (Dittami et al. 2016).

Collections of cultivable bacteria provide a valuable resource to study the mechanisms underlying these interactions, and in *Ectocarpus* three recent papers describe the generation of culture collections. In *Ectocarpus siliculosus* Tapia et al. (2016) have reported the isolation of 9 bacterial strains, and in *Ectocarpus subulatus* KleinJan et al. (2017) cultivated 46 strains corresponding to 33 different bacterial genera from algal surfaces. An additional 95 strains corresponding to 27 different genera have also recently been isolated from field material of *E. subulatus* (Dittami et al. 2019).

In present study, we describe genomic resources for 72 of these cultivable *Ectocarpus*-associated bacteria. Sixty-two genomes were sequenced specifically for this study, plus ten previously sequenced genomes from the same culture collection (Burgunter-Delamare et al. 2019) were also included. These genomes constitute a valuable resource both to study the genomic adaptations of bacteria to life on the surface of brown algae, but also to generate hypotheses on potential beneficial interactions between the bacteria and their host, for example, via metabolic complementarity-based approaches (Frioux et al. 2018). They furthermore constitute a first step toward filling a big gap in our current knowledge: The fact that currently (September 2019), based on our research through Marine Metagenomics Portal (Robertsen et al. 2017; Klemetsen et al. 2018), only ~100 draft and complete bacterial genomes isolated from algae/seaweed are publicly available in GenBank. Thus, the genomes from this study could add a great amount of information to algal microbiomes and will promote other studies aiming to decipher algal-microbial associations.

Materials and Methods

Bacterial Strains and DNA Extraction

Bacterial strains were isolated from a laboratory culture of *E.subulatus* (strain CCAP 1310/19; KleinJan et al. 2017) as well as from field samples of the same species (Dittami et al. 2019). Field samples were collected in March 2017 from two locations along the Hopkins River, Victoria, Australia, a few km upstream of Hopkins River falls, the original collection site of strain CCAP 1310/19 (West and Kraft 1996): Framlingham Forest reserve (–38.297064, 142.668291) and Kent's Ford (–38.191574, 142.698058). All bacterial strains were identified by Sanger-sequencing of the 16S rDNA gene using the 8F and the 1492R primer pair (Weisburg et al. 1991). Bacteria were grown on 90 mm Petri dishes with R2A medium (Reasoner and Geldreich 1985) Sigma–Aldrich at 19 °C for 4–7 days. Subsequently, a single colony was selected and grown at 25 °C in liquid R2A medium overnight. The bacterial genomic DNA was extracted using Promega Wizard Genomic DNA purification kit following the manufacturer's instructions. The extracted DNA was quantified using a Qubit and its quality was determined using agarose gel electrophoresis.

Genome Sequencing, Assembly, and Annotation

Paired-end DNA libraries with an average insert size of 500 bp were prepared using the Nextera XT DNA library kit (library average size ~1,100 bp). Libraries were then sequenced using the Illumina MiSeq technology (V3, paired-end, 2 × 300 bp reads) at GENOMER platform (Station Biologique de Roscoff), multiplexing ~20 bacterial genomes per run. Raw reads were first examined using FastQC (Andrews 2010). Low-quality sequences were trimmed or removed using Trimmomatic v.0.38 and a sliding window with a quality score of 15 as well as a minimal read length of 36 bp as filters. Trimmed read pairs were used for genome assembly with SPAdes v.3.12.0 (Bankevich et al. 2012) using default parameters. Genomic sequences encoding parts of the ribosome were identified using Barrnap v. 0.8 (https://github.com/tseemann/barrnap) and 16S rDNA sequences used to search for complete reference genomes in the GenBank. These reference genomes were used for scaffolding with Medusa version 1.6. Finally, gaps in the scaffolds were filled wherever possible using GapCloser 1.12 (Li et al. 2010) and the resulting draft genomes were annotated and prepared for submission to public databases using the MicroScope platform (Vallenet et al. 2017). The genomes were deposited at the European Nucleotide Archive.

Phylogenomic Analyses

Phylogenomic relationships among all studied strains were confirmed by running genome clustering based on pairwise distances and Average Nucleotide Identity (ANI) between all selected genomes using the Neighbor-Joining algorithm in MicroScope. Furthermore, the closest genome has been provided for all genomes, based on their resulting Tetranucleotide signature correlation index via the JSpeciesWS tool (Richter et al. 2016).

In Silico Analysis of Bacterial Metabolism

Models of primary metabolism for each sequenced bacterium were generated using the Pathway tools pipeline implemented in the MicroScope platform. The output of this pipeline is a pathway completion value, that is, the ratio between the number of reactions for a specific pathway in a bacterium and the total number of reactions for that pathway defined in the MetaCyc (Caspi et al. 2018) or KEGG (Kanehisa et al. 2008) databases. In addition, secondary metabolite-related gene clusters were predicted using antiSMASH (Blin et al. 2017).

Results and Discussion

Genome Characteristics

Here, we report the sequencing of 62 and the analysis of 72 genomes of *Ectocarpus*-associated bacterial strains corresponding to 43 different genera and 16 different orders. The individual strains as well as key attributes of their genome sequences are listed in table 1. The genome size of all strains ranged from 2.4 Mb to 6.8 Mb. The largest genome was that of *Imperialibacter* sp. strain SDR9 from the *Bacteroidetes* and the smallest was that of *Micrococcus* sp. strain 11B from the *Actinobacteria*. The analyzed genomes showed diverse GC contents with strains belonging to the *Bacteroidetes* and *Firmicutes* exhibiting GC contents <40% (e.g., 30% in *Flavobacterium* sp. 9AF) contrary to *Actinobacteria*, where most strains exhibit GC contents over 70%. Overall, the GC content was positively correlated with genome size (Pearson correlation $r = 0.73$, $P = 0.042$). CheckM analyses (Parks et al. 2015) suggest that the sequenced genomes are nearly complete (>98%, table 1) and free of or with very low levels of contamination (<2.5%; supplementary table S1, Supplementary Material online). The only exception was *Arthrobacter* sp. strain 9V with 4.8% contamination (22 marker genes). This indicates that, overall, the presented genomes are suitable for downstream analyses such as comparisons of metabolic capacities.

Phylogenomic Tree

Several of the sequenced bacteria in this study correspond to bacteria with no or only few closely related sequences in the databases. Notably, *Enterobacterales* bacterium 8AC, and *Moraxellaceae* bacterium 17A could be confidently identified only to the family level through RDP classifier (supplementary table S1, Supplementary Material online), making these strains candidates for new species or genera. Besides, fifteen strains including *Imperialibacter* sp. EC-SDR9, *Marinoscillum* sp. 108, *Sphingomonas* sp., AX6, and *Novosphingobium* sp., and *Burkholderiales* bacterium 8X have low similarity (*z*-score below cutoff < 0.989) with their closest genome-sequenced relatives (based on the tetra-nucleotide signature correlation index, table 1 and supplementary fig. S1, Supplementary Material online). This phylogenomic analysis yielded a tree generally grouping together bacteria from the same taxon (supplementary fig. S1, Supplementary Material online). However, *Imperialibacter* sp. EC-SDR9 and *Sphingobacterium* sp. 8BC from *Bacteroidetes* clustered with *Firmicutes*.

Secondary Metabolic Activities and Potentially Symbiosis-Related Metabolites

Algal-associated microbes are likely to interact with both the host and other microbes within the community. Secondary metabolites are metabolites not essential for normal growth of microorganisms, but they play a major role as chemical signals for interaction with other microorganisms (Netzker et al. 2015), restriction of pathogens (antimicrobial activities), and biofouling (Wiese et al. 2009; Nasrolahi et al. 2012; Susilowati et al. 2015). For instance, terpenes as the largest class of natural compounds have protective roles against competitors and are involved in interspecies signaling (Gershenzon and Dudareva 2007; Yamada et al. 2015). Similarly, bacteriocins, peptidic toxins produced by bacteria, have been suggested to play a role in pathogenesis by induction of cell lysis (Li and Tian 2012). The annotation of the 72 bacterial genomes with respect to genes involved in secondary metabolism obtained from AntiSMASH via the MicroScope platform showed that all analyzed strains except *Oceanicaulis* sp. strain 350, had at least one secondary biosynthetic gene cluster. Furthermore, 68% of genomes have at least one predicted terpene cluster gene, followed by bacteriocin (40.2%), nonribosomal Peptide Synthetases (NRPS, 36%), Type 3 polyketide synthases (PKS-t3, 33.33%), siderophores (23.6%), Type 1 polyketide synthases (PKS-t1, 20.8%), and homoserine lactone synthesis genes (16.6%; fig. 1 and supplementary table S1, Supplementary Material online). These genes are likely to be at least partially involved in the communication with the host and between microbes.

Detoxification Role of Symbionts and Provision of Vitamins

In terms of detoxification mechanisms, one pathway that was complete in all studied genomes was the capacity to degrade superoxide radicals. Moreover, 46 strains of 72 possessed the complete pathway for glutaredoxin synthesis (fig. 1). This mechanism is important for the degradation reactive oxygen species (ROS), which are formed by the algae through metabolic processes and in response to different stressors (Cosse et al. 2007). ROS can cause significant damage to the cell; thus, microorganisms have developed defense systems to detoxify ROS in order to survive.

Furthermore, the cyanate degradation pathway was complete or semicomplete in all bacteria except in strains 8BE, 8AC, and 8AQ. Cyanate is a common compound in marine environments and may serve as both an energy source for marine microbes (Palatinszky et al. 2015) as well as a potential source of nitrogen (Kamennaya et al. 2008; Sáez et al. 2019). Whether this pathway also plays a role during the interactions of microbes with their algal host, for example, by enabling the microbes to provide nitrogen to their host, remains to be tested.

Finally, most genomes analyzed encoded nearly complete or complete pathways for production of B vitamins like biotin (B7), folate (B9), riboflavin (B2), thiamine (B1), and pyridoxine (B6) (fig. 1). They may thus be contributors of vitamin B for the algal host, as has previously been suggested for diatom-bacteria associations (Behringer et al. 2018). All in all, these studied metabolic features highlight the possible contributions of the alga-associated bacteria to maintain host fitness and survival.

Table 1

Genome Features of Algal-Associated Bacteria Analyzed in This Study

Strain	Complete-ness (%)[a]	Genome Size (Mb)	Coverage (X)	N50 (Mb)	%GC	Scaffold Nb.	CDS Nb.	Mean CDS Length	tRNA Nb.	rRNA Nb.	Closest Relative	Accession Numbers
Actinobacteria												
Aeromicrobium sp. 9AM	99.7	4.2	144	2.98	68	9	4,422	897	46	3	*Aeromicrobium* sp. Root236	LR733303–LR733311
Arthrobacter sp. 8AJ	99.7	4.3	88	4.22	66	4	4,228	944	51	5	*Moraxella osloensis* NCTC10465	LR733289–LR733292
Arthrobacter sp. 9AX	99.7	4.4	230	4.41	66	7	4,453	918	50	6	*Pseudarthrobacter siccitolerans* 4J27	LR733289–LR733292
Arthrobacter sp. 9V	99.7	5.1	221	4.82	62	158	5,091	925	62	9	*Arthrobacter* sp. EpRS71	LR732912–LR733069
Citricoccus sp. K5	99.2	3.9	324	3.74	69	9	3,708	974	47	5	*Citricoccus muralis* DSM 14442	LR732817–LR732825
Curtobacterium sp. 8I–2	99	3.6	109	2.80	71	5	3,767	911	47	6	*Curtobacterium flaccumfaciens* UCD-AKU	LR732826–LR732830
Frigoribacterium sp. 9N	98.5	3.3	151	2.53	71	16	3,339	926	45	5	*Frigoribacterium* sp. Leaf8	LR733390–LR733405
Microbacterium sp. 8M	99.5	3.7	185	3.68	71	2	3,659	961	44	4	*Microbacterium azadirachtae* DSM 23848	LR733284–LR733285
Micrococcus sp. 116	98.6	2.6	215	2.49	73	19	2,526	943	48	5	*Micrococcus luteus* 2385	LR732370–LR732388
Micrococcus sp. 11B	98.1	2.4	450	1.89	73	52	2,398	952	48	5	*Micrococcus luteus* 2385	LR733070–LR733121
Micrococcus sp. 80W	98.1	2.5	224	1.78	73	80	2,521	942	48	4	*Micrococcus luteus* 2385	LR732389–LR732468
Nocardioides sp. AX2bis	98.7	4.2	221	3.96	73	37	4,397	915	45	4	*Marmoricola aurantiacus* DSM 12652*	LR733215–LR733251
Plantibacter sp. T3	99.5	4	287	3.98	69	3	4,131	924	48	4	*Plantibacter flavus* VKM Ac-2504	LR733286–LR733288
Pseudoclavibacter sp. 8L	98.2	4.1	98	1.43	68	30	4,137	921	45	4	*Microbacterium* sp. TS-1*	LR733185–LR733214
Bacteroidetes												
Imperialibacter sp. SDR9	100	6.8	111	0.96	47	65	5,767	1069	38	4	*Arcticibacter pallidi-corallinus* CGMCC 1.9313*	LR701573–LR701637
Marinoscillum sp. 108	99.1	5.2	83	3.73	46	12	4,489	1086	37	4	*Marinoscillum furvescens* DSM 4134*	LR734808–LR734819
Chryseobacterium sp. 8AT	100	4.7	114	4.43	34	31	4,483	931	70	7	*Chryseobacterium scophthalmum* DSM 16779	LR733314–LR733344
Flavobacterium sp. 9AF	98.9	4.2	101	2.95	30	74	3,871	992	51	5	*Flavobacterium* sp. 316*	LR733556–LR733629
Flavobacterium sp. 9R	99.6	3.6	184	3.42	35	16	3,175	1006	42	6	*Flavobacterium succinicans* DD5b*	LR733413–LR733428
Maribacter sp. 151	99.7	4.4	59	4.35	36	4	3,857	1044	36	6	*Maribacter litoralis* SDRB-Phe2	LR733271–LR733274
Sphingobacterium sp. 8BC	100	5.8	129	5.73	40	14	5,379	960	70	9	*Sphingobacterium multivorum* NCTC11343	LR733857–LR733870
Firmicutes												
Bacillus sp. 348	99.6	3.8	246	3.58	41	5	4,070	846	79	9	*Bacillus stratosphericus* LK33	LR732831–LR732835
Bacillus sp. 349Y	99.3	4.5	114	0.12	48	85	4,616	839	97	9	*Bacillus* sp. Leaf406	LR733732–LR733816
Bacillus sp. 71	99.3	5.7	116	5.69	35	14	6,092	796	98	18	*Bacillus* cereus HuA2-4	LR733376–LR733389
Bacillus sp. 9J	99.6	3.8	179	3.74	42	76	4,109	834	86	9	*Bacillus* sp. Leaf49	LR732836–LR732911
Exiguobacterium sp. 8A	99.3	3.1	184	2.87	48	77	3,234	868	63	13	*Exiguobacterium* sp. AT1b	LR733630–LR733706
Exiguobacterium sp. 8H	99.3	3	296	0.87	48	40	3,154	868	63	14	*Exiguobacterium* sp. AT1b	LR733429–LR733468
Exiguobacterium sp. 9Y	99.3	3	88	1.61	47	20	3,070	876	65	11	*Exiguobacterium oxidotolerans* JCM 12280	LR732308–LR732327
Staphylococcus sp. 8AQ	99.2	2.5	269	2.49	31	4	2,501	886	62	9	*Staphylococcus pasteuri* BAB3	LR733871–LR733874

Proteobacteria												
Aeromonas sp. 8C	100	4.6	345	4.57	59	3	4,769	899	114	11	*Aeromonas veronii* TTU2014-115ASC	LR732797–LR732799
Aeromonas sp. 9A	100	4.8	105	4.70	59	11	4,590	925	114	16	*Aeromonas salmonicida* Y577	LR732779–LR732789
Alteromonas sp. 38	100	4.7	209	4.70	44	3	4,324	975	62	6	*Alteromonas stellipolaris* LMG 21856	LR733300–LR733302
Marinobacter sp. HK377	100	4.4	172	4.34	57	7	4,176	976	45	6	*Marinobacter salarius* R9SW1	LR701480–LR701486
Marinobacter sp. N1	100	4.4	152	4.35	57	2	4,125	978	45	6	*Marinobacter salarius* R9SW1	LR733269–LR733270
Burkholderia sp. 8Y	100	6.3	61	2.36	63	37	6,403	874	52	8	*Burkholderia* sp. MR1	LR733519–LR733555
Limnobacter sp. 130	99	3.3	74	1.82	52	6	3,034	1007	37	3	*Limnobacter* sp. MED105*	LR732328–LR732333
Massilia sp. 9I	100	5.5	195	5.51	66	9	5,242	984	70	7	*Massilia alkalitolerans* DSM 17462	LR733275–LR733283
Burkholderiales bacterium 8X	99.8	4.8	141	4.78	67	3	4,776	973	44	5	*Variovorax* sp. WDL1*	LR732703–LR732705
Brevundimonas sp. G8	99.7	3.3	375	3.32	66	1	3,308	927	47	3	*Brevundimonas* sp. Leaf280	LR732816–LR732816
Oceanicaulis sp. 350	99.8	3.1	185	2.98	62	4	3,035	939	47	6	*Oceanicaulis alexandrii* DSM 11625	CABWMW010000001–CABWMW010000008
Pantoea sp. 111	100	4.9	62	4.09	56	35	4,807	890	73	9	*Pantoea brenneri* LMG 5343	LR733469–LR733503
Enterobacterales bacterium 8AC	100	5.3	134	4.81	53	63	4,858	936	74	10	*Serratia oryzae* J11-6	LR733916–LR733978
Halomonas sp. 153	100	5.5	35	5.44	55	11	5,045	972	59	5	*Halomonas titanicae* BH1	LR733721–LR733731
Halomonas sp. 98	100	5.5	109	5.43	55	14	5,029	975	59	6	*Halomonas titanicae* BH1	LR733707–LR733720
Acinetobacter sp. 8BE	100	4.4	144	3.94	41	35	4,368	891	61	7	*Acinetobacter* sp. NIPH 809	LR732744–LR732778
Acinetobacter sp. 8I-beige	100	3.5	138	2.08	41	7	3,452	895	73	7	*Acinetobacter johnsonii* DSM 6963	LR732790–LR732796
Moraxellaceae bacterium 17A	100	3	194	2.75	43	37	2,973	897	41	6	*Moraxella osloensis* CCUG 57516	LR732269–LR732305
Enhydrobacter sp. 8BJ	100	2.8	301	2.62	43	31	2,628	919	45	7	*Moraxella osloensis* NCTC10465	LR733345–LR733375
Enhydrobacter sp. AX1	99.7	2.7	350	2.65	44	16	2,517	943	49	6	*Enhydrobacter aerosaccus* SK60	LR732800–LR732815
Pseudomonas sp. 8AS	98.1	4.3	199	4.26	66	7	4,113	945	57	4	*Pseudomonas alcaligenes* NBRC 14159	LR733406–LR733412
Pseudomonas sp. 8BK	100	4.5	145	4.38	60	11	4,205	960	63	9	*Pseudomonas peli* DSM 17833	LR733252–LR733262
Pseudomonas sp. 8O	99.8	5.2	78	1.61	62	6	4,949	949	60	5	*Pseudomonas pseudoalcaligenes* AD6	LR733263–LR733268
Pseudomonas sp. 8Z	99.4	4.8	144	1.12	61	12	4,625	935	61	8	*Pseudomonas composti* CCUG 59231*	LR733824–LR733835
Pseudomonas sp. 9Ag	100	4.7	136	4.62	60	4	4,465	946	52	4	*Pseudomonas* sp. 10B238	LR733836–LR733839
Pseudomonas sp. 9AZ	99.7	4.5	235	4.46	60	4	4,260	961	60	8	*Pseudomonas peli* DSM 17833	LR733840–LR733843
Bosea sp. 125	99.1	6.3	46	6.12	67	63	6,435	899	46	3	*Bosea* sp. Root483D1	LR733122–LR733184
Bosea sp. 127	99.1	6.3	78	6.28	67	8	6,705	876	46	3	*Bosea* sp. Root483D1	LR733511–LR733518
Bosea sp. 29B	99.1	6.3	137	6.32	67	7	6,422	904	46	3	*Bosea* sp. Root483D1	LR733817–LR733823
Bosea sp. 62	99.1	6.3	154	6.28	67	7	6,411	905	46	3	*Bosea* sp. Root483D1	LR733504–LR733510
Bosea sp. HK365B	99.1	6.3	133	1.03	67	18	6,738	876	46	3	*Bosea* sp. Root483D1	LR701663–LR701680
Hoeflea sp. HK425	99.9	5.2	326	4.68	61	28	5,266	898	43	3	*Hoeflea halophila* KCTC 23107	LR701545–LR701572
Rhizobium sp. SD404	100	4.2	148	4.22	62	18	4,192	920	42	3	*Pararhizobium haloflavum* XC0140*	LR701442–LR701459
Roseovarius sp. SD190	99.3	4.7	80	3.89	61	17	4,794	902	44	3	*Roseovarius* sp. TM1035	LR701460–LR701476
Erythrobacter sp. HK427	99.1	3.1	157	3.12	63	3	3,097	947	45	3	*Porphyrobacter* sp. AAP60*	LR701477–LR701479
Novosphingobium sp. 9U	99.6	4.6	221	2.82	65	75	4,843	867	49	5	*Novosphingobium resinovorum* SA1*	LR732469–LR732543

(continued)

Table 1 Continued

Strain	Complete-ness (%)[a]	Genome Size (Mb)	Coverage (X)	N50 (Mb)	%GC	Scaffold Nb.	CDS Nb.	Mean CDS Length	tRNA Nb.	rRNA Nb.	Closest Relative	Accession Numbers
Sphingomonas sp. 8AM	99.7	3.8	119	3.66	67	13	3,739	929	48	4	*Sphingomonas phyllosphaerae* FA2	LR733844–LR733856
Sphingomonas sp. AX6	99.4	3	228	3.01	64	1	3,161	892	44	3	*Sphingomonas echinoides* ATCC 14820*	LR733857–LR733870
Sphingomonas sp. HK361	99.7	3.3	150	1.78	66	8	3,274	935	45	3	*Hephaestia caeni* DSM 25527*	LR701487–LR701494
Sphingomonas sp. SD391	99.5	4.6	114	4.15	66	34	4,682	903	49	5	*Sphingomonas* sp. Leaf28	LR701495–LR701528
Sphingomonas sp. T1	99.3	4.5	243	3.83	66	41	4,647	900	50	3	*Sphingomonas* sp. Leaf30	LR733875–LR733915
Sphingorhabdus sp. 109	99.2	3.6	97	3.56	58	5	3,585	928	45	6	*Sphingorhabdus* sp. M41*	LR732707–LR732711
Luteimonas sp. 9C	100	3.3	77	2.83	69	2	3,207	957	48	3	*Xanthomonas* sp. Mitacek01	LR733312–LR733313

Note.—The closest relative with the similarity below Cut-off [z-score (<0.98)] is marked with asterisk. Nb, number; CDS, coding sequence.
[a]Determined using the CheckM tool.

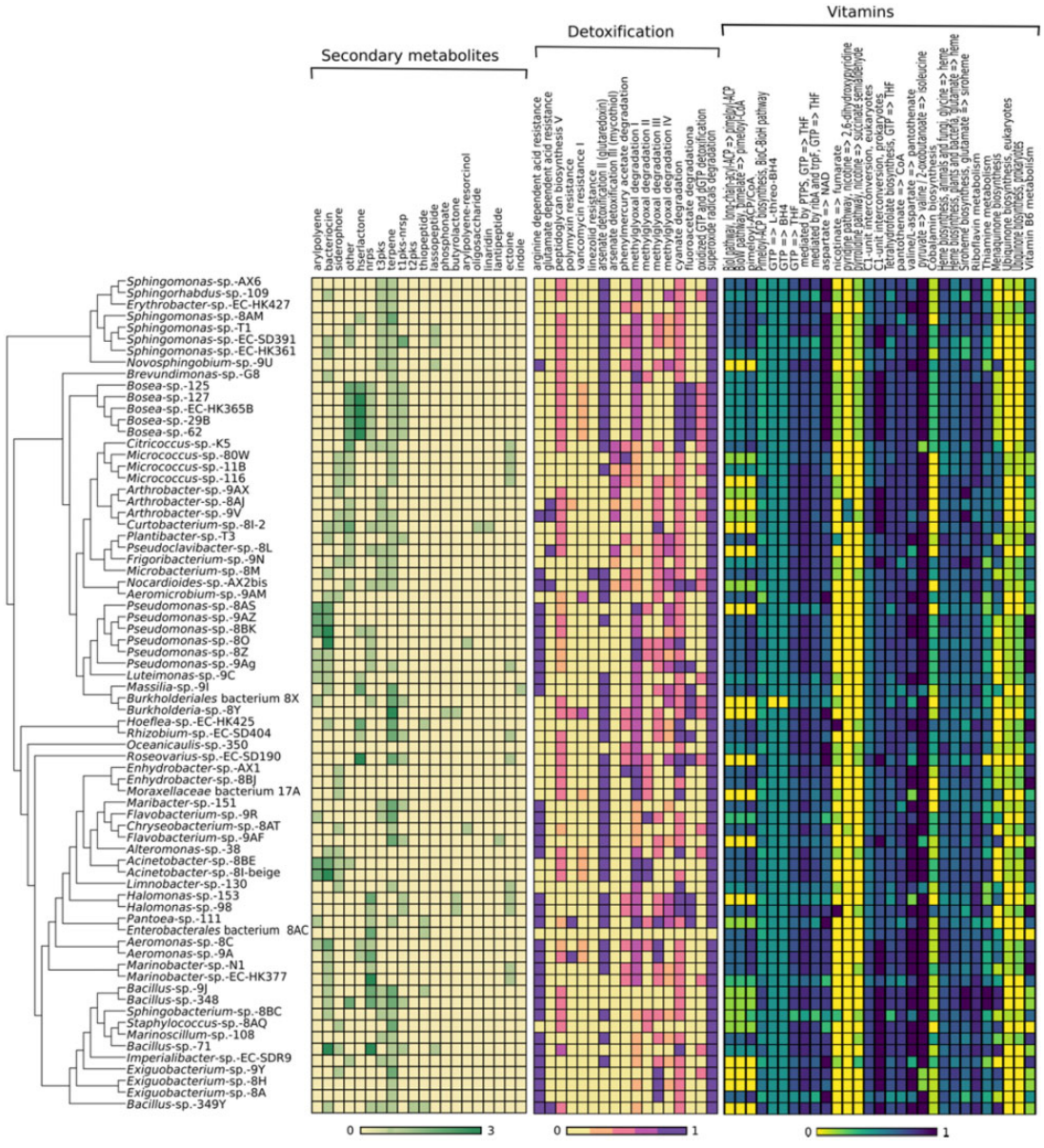

Fig. 1.—Heatmap of representative secondary metabolite clusters, detoxification-, and vitamin biosynthetic genes in the studied bacterial genomes. The dendrogram represents a whole-genome phylogeny, secondary metabolite gene clusters were predicted via AntiSMASH, detoxification genes were identified based on the MicroCyc database, and vitamin biosynthesis capacities were assess based on KEGG entries. The color code represents the number of genes per cluster (secondary metabolites) or the proportion of genes found in a particular organism and pathway.

The genomic resources provided here constitute a valuable resource for comparative genomic analyses and evolutionary surveys of alga-associated bacteria and will allow us to produce testable hypotheses about the molecular interactions between the microbes and their host. They may, among other uses, facilitate metabolic complementarity centered approach as proposed by Dittami et al. (2014), to identify potential beneficial interactions between the partners. They will also form the bases for more targeted molecular approaches, for example, gene knockouts or gene expression analyses once specific interactions are being targeted in coculture experiments.

Supplementary Material

Supplementary data are available at *Genome Biology and Evolution* online.

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Author Contributions

E.K. participated in the conception and design of the study, sample processing, genome sequencing and assembly, data analysis, writing the manuscript. E.G. participated in the genome assembling, submission of genomes to MicroScope, and helped with the preparation of the figures. H.K. participated in the isolation of bacteria and genome sequencing. G.T. and E.L. both contributed to the sequencing of the genomes. E.C. participated in the assembling protocol and revision. S.M.D. participated in the conception and design of the study, isolation of bacteria, genome assembly and writing the manuscript. All authors approved the final draft.

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