

Annual Review of Marine Science

The Physiology and Biogeochemistry of SUP05

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Annu. Rev. Mar. Sci. 2022. 14:261–75

First published as a Review in Advance on August 20, 2021

The *Annual Review of Marine Science* is online at marine.annualreviews.org

<https://doi.org/10.1146/annurev-marine-010419-010814>

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Keywords

Thioglobaceae, symbiosis, carbon, nitrogen, sulfur, oxygen minimum zones, OMZs

Abstract

The SUP05 clade of gammaproteobacteria (Thioglobaceae) comprises both primary producers and primary consumers of organic carbon in the oceans. Host-associated autotrophs are a principal source of carbon and other nutrients for deep-sea eukaryotes at hydrothermal vents, and their free-living relatives are a primary source of organic matter in seawater at vents and in marine oxygen minimum zones. Similar to other abundant marine heterotrophs, such as SAR11 and *Roseobacter*, heterotrophic Thioglobaceae use the dilute pool of osmolytes produced by phytoplankton for growth, including methylated amines and sulfonates. Heterotrophic members are common throughout the ocean, and autotrophic members are abundant at hydrothermal vents and in anoxic waters; combined, they can account for more than 50% of the total bacterial community. Studies of both cultured and uncultured representatives from this diverse family are providing novel insights into the shifting biogeochemical roles of autotrophic and heterotrophic bacteria that cross oxic–anoxic boundary layers in the ocean.

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INTRODUCTION

Like most of the major lineages of marine bacteria, SUP05 refers to the name of a 16S rRNA gene sequence recovered from an uncultured and previously unknown microorganism (Sunamura et al. 2004). Knowledge about the diversity, metabolic potential, and biogeochemistry of diverse marine bacteria related to SUP05 (the SUP05 clade) has expanded rapidly due to advances in sequencing, proteomics, metabolomics, and cultivation. Analyses of genomes, metagenome-assembled genomes, and single-cell amplified genomes indicate that the SUP05 clade represents a diverse family of marine bacteria with autotrophic and heterotrophic members (Ansorge et al. 2020, van Vliet et al. 2021). Functional studies have verified their activities across a range of marine ecosystems and suggest that their impact on marine biogeochemistry extends from strictly anoxic and sulfidic waters in marine oxygen minimum zones (OMZs) to oxic and nonsulfidic waters in the surface and deep ocean.

In this review, we adopt the SUP05 family name Thioglobaceae and the proposed genus names *Thiomultimodus* (Ansorge et al. 2020) and *Thioglobus* (Marshall & Morris 2013). The *Thiomultimodus* genus comprises host-associated and free-living thioautotrophic members that use sulfide and other forms of inorganic sulfur (sometimes hydrogen) and reduce oxygen, nitrate, nitrite, nitric oxide, or nitrous oxide for energy to fix inorganic carbon, depending on the bacterial species and redox conditions in seawater (Anantharaman et al. 2013, Callbeck et al. 2018, Shah et al. 2016, Walsh et al. 2009). The *Thioglobus* genus comprises free-living aerobic members that use a broad range of organic compounds for heterotrophic growth, including sulfonates and methylated compounds such as glycine betaine, choline, sarcosine, and trimethylamine *N*-oxide (Durham et al. 2019, Georges et al. 2014, Marshall & Morris 2013, Murillo et al. 2014, Spietz et al. 2019, Swan et al. 2011, van Vliet et al. 2021). Although some members of the *Thioglobus* genus have genes for thioautotrophic metabolisms, not all have key genes for carbon fixation, and their sulfur oxidation pathways are incomplete.

Thioglobaceae cells are cocci or amorphic, range in diameter from ~0.5 to 1.5 μm , are surrounded by a protein surface layer (S-layer), and lack a gene required for cell division in other proteobacteria (*ftsZ*) (Shah et al. 2019, Spietz et al. 2019). This suggests that cell division is more analogous to budding by Planctomycetes (Rivas-Marin et al. 2016, Wiegand et al. 2018), or by other FtsZ-less bacteria in the Planctomycetes, Verrucomicrobia, and Chlamydiae (PVC) superphylum, than it is to cytokinesis in most other bacteria (Coltharp et al. 2016, Xiao & Goley 2016)

S-LAYERS AND SYMBIOSIS

Most archaea and some bacteria are surrounded by an S-layer. These self-assembling polycrystalline structures are typically composed of only one or two proteins that produce uniform and regularly spaced pores. They form protective coats that act as molecular sieves or ion traps and have roles in surface recognition and adhesion, cell morphology and cell division, and virulence in pathogens (Rodrigues-Oliveira et al. 2017, Sleytr et al. 2014). The discovery of a single gene that codes for an S-layer protein in cultured *Thiomultimodus* and *Thioglobus* enabled the subsequent identification of homologous sequences in both uncultured endosymbionts and diverse free-living species (Shah et al. 2019, Spietz et al. 2019). Phylogenetic analyses of S-layer protein sequences distinguish among free-living *Thioglobus*, free-living *Thiomultimodus*, and the endosymbionts of clams, mussels, and sponges (Figure 1a). Evidence that the outermost structure of the cell is conserved and reflects known patterns in the diversity of free-living and endosymbiotic lineages suggests that S-layer proteins have a role in establishing symbiotic associations between sulfur-oxidizing gammaproteobacteria and deep-sea eukaryotic hosts. It also demonstrates the potential to use structural proteins to resolve close evolutionary relationships.

(see the sidebar titled S-Layers and Symbiosis). Members of this family are also capable of a remarkably diverse array of metabolic activities, including autotrophic, heterotrophic, phototrophic, and methylotrophic growth (Newton et al. 2007, Ponnudurai et al. 2017, Shah et al. 2016, Spietz et al. 2019, Walsh et al. 2009). Most cultured Thioglobaceae have a gene encoding ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the key enzyme for inorganic carbon fixation in the Calvin–Benson–Bassham cycle, but there are notable differences in the form and copy number of Rubisco genes in fully sequenced genomes (Shah et al. 2019, Spietz et al. 2019, Stewart et al. 2005). Differences in their carbon fixation and respiratory pathways suggest that dissolved oxygen concentrations in seawater are an important factor underlying the evolutionary divergence of the autotrophic and heterotrophic members that inhabit sulfidic and nonsulfidic marine environments, respectively.

BIOGEOGRAPHY AND METABOLIC DIVERGENCE

Phylogenetic analysis of 16S rRNA gene sequences from mixed communities in seawater suggested early on that sulfur-oxidizing gammaproteobacteria from the SUP05 clade belonged to one of two lineages, designated the SUP05 and Arctic96BD-19 subclades (Walsh et al. 2009), here and elsewhere renamed the *Thiomultimodus* and *Thioglobus* genera, respectively (Ansorge et al. 2020, Marshall & Morris 2013). Members of the *Thiomultimodus* genus form endosymbiotic associations with eukaryotic organisms at hydrothermal vents and often dominate anoxic waters in upwelling regions, fjords, and deep-sea hydrothermal vent environments (Anderson et al. 2013, Lavik et al. 2009, Zaikova et al. 2010), where they express genes and proteins for chemoautotrophic metabolisms (Anantharaman et al. 2013, Hawley et al. 2014, Lesniewski et al. 2012, Mattes et al. 2013, Williams et al. 2012). Members of the *Thioglobus* genus are common in the surface layer and throughout the deep ocean and are often more abundant at oxic–anoxic interfaces in marine OMZs (Beman & Carolan 2013, Carolan et al. 2015, Swan et al. 2011). Information about the organic compounds that support biosynthesis in heterotrophic members and the redox reactions that fuel energy demands in autotrophic members has been increasing dramatically in recent years due to advances in cultivation-independent (Callbeck et al. 2018, Crowe et al. 2018) and cultivation-based (Shah et al. 2019, Spietz et al. 2019) approaches, and there is evidence that the Thioglobaceae are optimized for growth at relatively low dissolved oxygen concentrations, where aerobic and anaerobic processes overlap (Mattes et al. 2021). Additional field and laboratory studies are still needed, however, to identify the range of organic and inorganic compounds that support growth under the variable conditions typical of marine OMZs.

Autotrophic and Heterotrophic Habitats

Members of the Thioglobaceae family have adapted to a range of marine environments, reflective of their divergence into two genera (**Figure 1a**). Host-associated members of the *Thiomultimodus* genus were first recognized as important endosymbiotic gammaproteobacteria in clams and mussels at hydrothermal vents (Distel et al. 1988) and have since been identified in deep-sea sponges, corals, and anemones (Goffredi et al. 2021, Nishijima et al. 2010, Rubin-Blum et al. 2019, Vohsen et al. 2020). The first complete Thioglobaceae genome sequence (“*Candidatus* Ruthia magnifica”) was obtained by extracting symbiont DNA from the gill tissues of a *Calypptogena* clam (Newton et al. 2007). The genome revealed metabolic pathways for sulfur oxidation and carbon fixation as well as the ability to synthesize all 20 amino acids, vitamins, and cofactors. One of the most striking findings was that the genome of “*Ca. R. magnifica*” was more similar to those of free-living thioautotrophic bacteria than to those of other endosymbionts with reduced genomes. Closely related and highly abundant representatives, originally designated SUP05 (*Thiomultimodus*), were

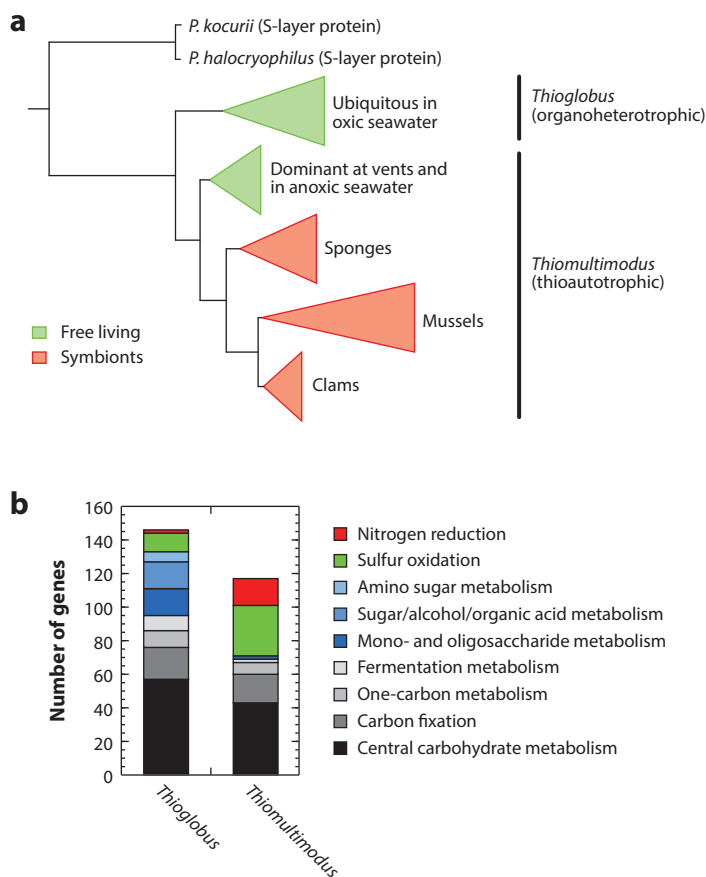


Figure 1

Habitat and metabolic divergence of the Thioglobaceae. (a) Maximum-likelihood phylogenetic tree constructed from full-length Thioglobaceae S-layer protein sequences identified in cultures, symbionts, and free-living representatives from the *Thiomultimodus* and *Thioglobus* genera, as identified by BLAST (Shah et al. 2019). Sequences were aligned using RAxML (Stamatakis 2014) with model GTRGAMMA to find the best tree topology (100 replicates). S-layer protein sequences from *Planococcus kocurii* and *Planococcus halocryophilus* were used as outgroups to root the tree. (b) Core carbon, nitrogen, and sulfur metabolisms associated with the *Thiomultimodus* and *Thioglobus* genera. Complete genome sequences for representatives from the *Thiomultimodus* genus (“*Candidatus* Thiomultimodus autotrophicus”) and the *Thioglobus* genus (“*Candidatus* Thioglobus singularis”) were used to identify core differences in gene content and are representative of differences in metagenomes, metagenome-assembled genomes, and single-cell amplified genomes. Abbreviations: BLAST, Basic Local Alignment Search Tool; RAxML, Randomized Axelerated Maximum Likelihood; S-layer, surface layer.

later identified as abundant community members that can exceed 30% of the bacterial community in seawater at hydrothermal vents and in fjords, enclosed seas, and other marine OMZs (Anderson et al. 2013, Glaubitz et al. 2013, Murillo et al. 2014, Sunamura et al. 2004, Zaikova et al. 2010). Members from a closely related subclade, designated Arctic96BD-19 (*Thioglobus*), were also identified in the ocean surface layer and throughout the deep ocean. They occur in relatively high abundance in seawater at oxic–anoxic interfaces near vents, reaching 64.7% of the bacterial community in hydrothermal vent plume waters and up to 25.5% in diffuse flow fluids (Anderson et al.

2013). They are also common in surface waters and throughout the deep ocean (Beman & Carolan 2013; Georges et al. 2014; Swan et al. 2011, 2013; Williams et al. 2012).

Autotrophic and Heterotrophic Physiologies

The Thioglobaceae family is a critical group of marine bacteria to understand given the potential for representatives to contribute to autotrophic and heterotrophic processes in the ocean and their involvement in carbon, nitrogen, and sulfur cycling (**Figure 1b**). Although there are known differences in the abundance and distribution of representatives from the two genera, they often co-occur at oxic–anoxic interfaces in marine OMZs (Anderson et al. 2013, Beman & Carolan 2013, Carolan et al. 2015), where aerobic and anaerobic processes overlap. Members of the *Thiomultimodus* genus are primary producers of organic carbon and can respire oxygen, nitrate, nitrite, nitric oxide, or nitrous oxide, depending on the bacterial species and redox conditions in seawater (Callbeck et al. 2018, Shah et al. 2016, Walsh et al. 2009). They can use the energy obtained from oxidizing hydrogen, sulfide, thiosulfate, or elemental sulfur to fix inorganic carbon, and like many other autotrophs, they lack key components of the oxoglutarate dehydrogenase complex in the tricarboxylic acid (TCA) cycle, forming a biosynthetic pathway that directs fixed inorganic carbon into central carbon metabolism (Wood et al. 2004). It is thought that this horseshoe TCA cycle is a way for organisms to conserve fixed organic carbon for biosynthesis rather than oxidize organic carbon intermediates for energy generation.

Members of the *Thioglobus* genus are primary consumers of organic carbon in the ocean. They have the ability to oxidize a diverse suite of organic carbon substrates for energy, including sulfonates and methylated compounds such as glycine betaine, choline, sarcosine, and trimethylamine *N*-oxide (Durham et al. 2019, Georges et al. 2014, Marshall & Morris 2013, Murillo et al. 2014, Spietz et al. 2019, Swan et al. 2011, van Vliet et al. 2021). They are also free living and aerobic and have genes for organic matter transport, sugar metabolism, and a complete TCA cycle, including both components of the oxoglutarate dehydrogenase complex that are missing from their autotrophic relatives. *Thioglobus* members residing in the surface ocean also have the genetic potential to harvest light energy using membrane-bound rhodopsins, which in other heterotrophic marine bacteria, like those from the ubiquitous alphaproteobacterial SAR11 clade, are used to maintain biomass and support organic matter transport when cells are starved for carbon (Giovannoni et al. 2005, Steindler et al. 2011). Genes to use alternative electron acceptors under anaerobic growth conditions have not yet been identified in *Thioglobus* genomes, metagenome-assembled genomes, or single-cell amplified genomes. Known members of this genus also lack key genes required to oxidize sulfide and have incomplete sulfur oxidation pathways. Some species have partial or incomplete pathways for sulfite reduction (*dsr*), sulfate activation (*sat*), and adenosine 5'-phosphosulfate (APS) reduction (*apr*) (Marshall & Morris 2015), but the ability to use reduced sulfur as a sole energy source has not been demonstrated. A preponderance of evidence suggests that organoheterotrophy is their metabolism, but it is also possible that they have retained partial sulfur oxidation and carbon fixation pathways for thioautotrophic growth under conditions that have not yet been identified.

ADAPTATIONS TO OXYGEN

Patterns observed in the global distributions of *Thiomultimodus* and *Thioglobus* suggest that seawater oxygen content is a key factor underlying the divergence of the two genera, as evidenced by adaptations to oxygen in their carbon fixation and respiratory pathways (**Figure 2**). Autotrophic bacteria that inhabit oxic and anoxic environments use distinct forms of Rubisco with different

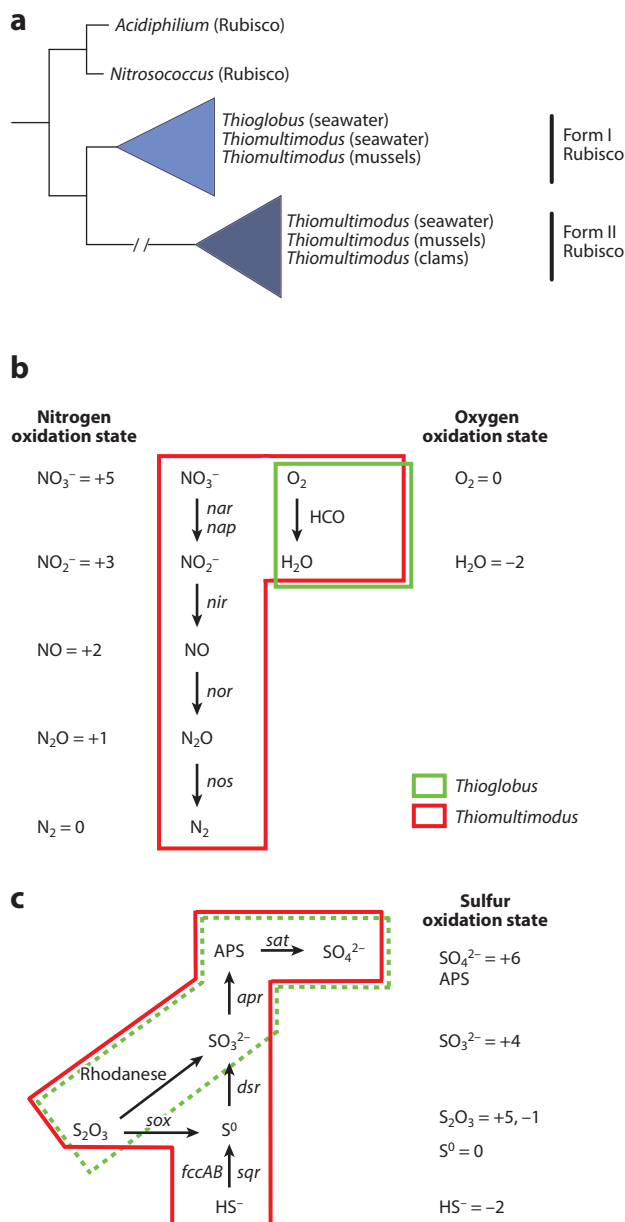


Figure 2

Thioglobaceae adaptations to carbon fixation and respiration. (a) Maximum-likelihood phylogenetic tree constructed from large-subunit Thioglobaceae Rubisco protein sequences identified in cultures, symbionts, and free-living representatives from the *Thiomultimodus* and *Thioglobus* genera. Sequences were aligned using RAXML (Stamatakis 2014) with model GTRGAMMA to find the best tree topology (100 replicates). Rubisco protein sequences from *Acidiphilium* and *Nitrosococcus* were used as outgroups to root the tree. (b) The collective respiratory potential of *Thiomultimodus* to use oxygen or reduced nitrogen, depending on the species, and of *Thioglobus* to use oxygen (red and green, respectively). (c) Sulfur oxidation pathways identified in the *Thiomultimodus* and *Thioglobus* genera (red and green, respectively). Dashed lines indicate unverified sulfur oxidation pathways in the *Thioglobus* genus. Abbreviations: APS, adenosine 5'-phosphosulfate; RAXML, Randomized Axelerated Maximum Likelihood; Rubisco, ribulose-1,5-bisphosphate carboxylase/oxygenase.

affinities for carbon dioxide and oxygen as substrates, which are present at varying ratios throughout the global ocean. Form I Rubisco enzymes in bacteria are more specific for carbon dioxide and have slower kinetics, which is better for high-oxygen environments; conversely, bacterial form II Rubisco enzymes are less specific for carbon dioxide and have faster kinetics, which is better in low-oxygen environments (Badger & Bek 2008, Tcherkez et al. 2006).

Phylogenetic analyses of the large subunit of Rubisco in the Thioglobaceae support patterns observed in the biogeography of aerobic, anaerobic, and facultatively anaerobic members (**Figure 2a**). Form I Rubisco genes related to those in cyanobacteria, which fix carbon in the ocean surface layer, are present in endosymbionts of mussels, in free-living *Thioglobus*, and in facultatively anaerobic *Thiomultimodus*, all of which can live in high-oxygen environments. Form II Rubisco genes related to those found in anaerobic or facultatively anaerobic bacteria are present in both endosymbionts and free-living *Thiomultimodus* but not in *Thioglobus*. Members of the *Thiomultimodus* genus have other key genes for growth in anoxic environments, including genes for different steps in denitrification (*narGH*, *napAB*, *nirK*, *norCB*, and *nosZ*) (**Figure 2b**) and sulfur oxidation (*sox*, *dsr*, *aprAB*, and *sat*) (**Figure 2c**). In combination, these genes confer the ability to oxidize sulfide, thiosulfate, and elemental sulfur and to reduce nitrate, nitrite, nitric oxide, and nitrous oxide.

Mattes et al. (2021) showed that the sole *Thiomultimodus* isolate, “*Ca. Thiomultimodus autotrophicus*,” respire oxygen and nitrate at low dissolved oxygen concentrations (3.8 μM), simultaneously contributing to aerobic and anaerobic respiration. They also demonstrated that the respiratory and carbon fixation processes of “*Ca. T. autotrophicus*” are highly active under low-dissolved-oxygen conditions, as compared with both high-dissolved-oxygen and anoxic conditions. It appears that this facultatively anaerobic strain optimizes its metabolism under low-oxygen conditions to take advantage of the overlapping resources that are present periodically or that are stable and persist at oxic–anoxic interfaces in hydrothermal vent plumes, and in fjords and oxyclines in OMZs. By contrast, members of the *Thioglobus* genus have key genes for aerobic organoheterotrophy and lack genes for strictly anaerobic respiration on nitrate and with an unknown capacity to oxidize reduced sulfur (Marshall & Morris 2015, Spietz et al. 2019).

BIOGEOCHEMICAL CYCLING

Advances in our understanding of the metabolic capabilities of bacteria and archaea have been greatly accelerated by metagenomics (Béjà et al. 2000, Gilbert & Dupont 2011, Rusch et al. 2007, Venter et al. 2004) and single-cell genomics (Stepanauskas & Sieracki 2007; Swan et al. 2011, 2013). Similar advances in our understanding of ecological niches have been made following cultivation of some of the most abundant bacteria and archaea in the ocean (Chis olm et al. 1992, Könneke et al. 2005, Rappe et al. 2002).

Similar cultivation studies seeking to elucidate the balance between autotrophy and heterotrophy in the Thioglobaceae have provided information about their contribution to the global carbon sink, as well as the availability of nitrogen, sulfur, and other nutrients (Marshall & Morris 2013; Mattes et al. 2021; Shah et al. 2016, 2019; Spietz et al. 2019). The first cultured representative from the Thioglobaceae family was isolated from Puget Sound on natural seawater media amended with labile sources of organic matter obtained from a diatom lysate, suggesting a heterotrophic growth requirement (Marshall & Morris 2013). Spietz et al. (2019) later verified heterotrophy on defined seawater media and identified specific organic substrates that support heterotrophic metabolisms in an isolate from the North Pacific Gyre. Shah and colleagues obtained the first autotrophic isolate from Effingham Inlet, an anoxic fjord in British Columbia (Shah et al. 2016), and showed that the size and morphology of cells shifted depending on oxygen and sulfur availability and that

the shift to aerobic growth enhanced sulfur storage and the chemolithoautotrophic production of organic carbon (Shah et al. 2019). Continued efforts to study both mixed communities in the ocean and pure culture in the laboratory are needed to elucidate factors controlling the shifting biogeochemical roles of the Thioglobaceae in the ocean.

Carbon, Nitrogen, and Sulfur Cycling in Sulfidic Waters

Global models of biogeochemical cycles are becoming more sophisticated and now include parameterizations for the activities of microbial groups (Mock et al. 2016). The inclusion of these details has improved predictions of the response of the ocean's biota to ocean change. Nevertheless, major gaps remain, and observations and models still deliver contradictory scenarios of the balance of major ocean processes, such as the balance between primary production and respiration as well as that of denitrification in the present and future ocean (Babbin et al. 2014, 2015; Duarte et al. 2013). Filling gaps will require a deeper understanding of the key metabolisms carrying out chemical transformations in the ocean.

Free-living *Thiomultimodus* members often dominate anoxic and sulfidic waters, where they can account for a significant fraction of the microbial community (Lavik et al. 2009, Walsh et al. 2009). Their thioautotrophic activities are particularly important in marine carbon and nitrogen cycling under anoxic conditions (Anantharaman et al. 2013; Callbeck et al. 2018, 2021; Hawley et al. 2014). Estimates of dark carbon fixation by *Thiomultimodus* range from 10 to 120 nmol C L⁻¹ d⁻¹ (Hawley et al. 2014) and from 1.3 to 592 nmol C L⁻¹ d⁻¹ (Callbeck et al. 2018). Estimates of sulfur-dependent denitrification by *Thiomultimodus* are also filling a critical gap in knowledge needed to understand nitrogen loss. Estimates of *Thiomultimodus* denitrification are high, ranging from 830 to 2,180 nmol N L⁻¹ d⁻¹, which is at the upper limit for in situ measurements of marine denitrification (Callbeck et al. 2018). However, *Thiomultimodus* members are diverse in their abilities to carry out the different steps in denitrification. They can contribute directly by sequential reduction of nitrate to nitrogenous gases (nitrous oxide and dinitrogen) (Canfield et al. 2010, Hawley et al. 2014, Murillo et al. 2014, Walsh et al. 2009) or indirectly by respiring nitrate and expelling nitrite, which then becomes available as a substrate for other processes, such as heterotrophic denitrification (Castro-Gonzalez et al. 2005, Jayakumar et al. 2004, Ward et al. 2009) and anaerobic ammonia oxidation (Hamersley et al. 2007, Kuypers et al. 2005, Lam et al. 2009, Thamdrup et al. 2006). Future studies that identify factors that regulate the shifting activities of diverse *Thiomultimodus* in sulfur-driven dark carbon fixation and autotrophic denitrification will further advance efforts to parameterize this important group of bacteria.

Influences on Nutrient Cycling in Nonsulfidic Waters

Thiomultimodus cells influence marine biogeochemistry in nonsulfidic marine waters, where tightly coupled sulfur oxidation and reduction reactions fuel a cryptic sulfur cycle (Canfield et al. 2010) or where cells transported offshore survive using stored elemental sulfur to sustain their thioautotrophic activities (Callbeck et al. 2018). Sulfur and nutrient storage are key physiological traits that extend the biogeochemical effects of thioautotrophic metabolisms to nonsulfidic waters through eddy and hydrothermal vent plume transport (see the sidebar titled Sulfur Storage and a Sinking Hypothesis). In hydrothermal vent systems, *Thiomultimodus* members also have important roles in the biological iron pump that disperses iron emitted from vents, potentially providing iron to nutrient-limited phytoplankton communities in distant surface waters (Li et al. 2014). Furthermore, genes for iron-sulfur cluster formation have been identified in phages that infect *Thiomultimodus* (Anantharaman et al. 2014, Zhou et al. 2019), which suggests that they are laterally

SULFUR STORAGE AND A SINKING HYPOTHESIS

Many bacteria and archaea, including some cyanobacteria and phototrophic bacteria, regulate their buoyancy by producing intracellular gas vesicles (Pfeifer 2012). Gas vesicles enable phototrophic cells to float to the surface, where sunlight is available as an energy source, and can increase their surface-to-volume ratio. The Thioglobaceae use sulfide released from sediments or produced in anoxic waters as their primary energy source and store the elemental sulfur that they produce as a sulfur oxidation intermediate in internal globules. The sulfide they need persists in anoxic bottom waters but is oxidized abiotically in oxygenated waters closer to the surface ocean. Our estimates of “*Ca. Thiomultimodus autotrophicus*” buoyancy, based on differences in cell sizes and stored elemental sulfur content under oxic and anoxic growth conditions, suggest that stored sulfur can increase sinking rates from 0.0006 to 0.08 m d⁻¹ in coastal OMZs and up to 0.15 m d⁻¹ at hydrothermal vents. Although these are relatively minor differences in the context of ocean mixing, we have found that “*Ca. T. autotrophicus*” cells sink on the order of hours under aerobic growth conditions, forming a white precipitant at the bottom of culture bottles (V. Shah & R.M. Morris, personal observation). The ability to increase sulfur storage and surface-to-volume ratios under nutrient-limiting conditions could also enable cells to sink toward a more favorable energy source. If so, this suggests that free-living *Thiomultimodus* cells actively transport carbon, trace metals, and other nutrients toward the seafloor.

transferred in habitats where dissolved iron concentrations are high relative to background seawater and there is enhanced incorporation into organic matter. Fitzsimmons et al. (2017) found that particulate iron in plume waters exceeded background concentrations 4,000 km from the vent source. If hydrothermal plume waters enriched in iron are also enriched in *Thiomultimodus* members (Mattes et al. 2013) that scavenge iron, then the Thioglobaceae are a potential source of organic carbon, trace metals, and other nutrients to nonsulfidic waters beyond vents.

Dissolved Organic Matter Cycling

Thioglobus members are often more abundant in oxic waters relative to anoxic waters (van Vliet et al. 2021, Wright et al. 2012), which further implicates their reliance on oxygen and not reduced nitrogen as an electron acceptor. *Thioglobus* members that have the Rubisco gene also code for form I, the more oxygen-tolerant form found in cyanobacteria (Figure 2a). However, evidence from both laboratory and environmental studies suggests that *Thioglobus* does not rely primarily on carbon fixation or sulfur oxidation for growth (Spietz et al. 2019). Instead, members of this genus take advantage of the dilute pool of methylated compounds residing in the upper ocean. The marine osmolytes glycine betaine, choline, trimethylamine *N*-oxide, and other methylated amines produced by phytoplankton and other marine organisms are among the most abundant methylated compounds in the surface pool of dissolved organic carbon and are readily metabolized by marine bacteria (Barrett & Kwan 1985; Diaz et al. 1992; Lidbury et al. 2014, 2015; Sun et al. 2011). Recent studies have suggested the importance of methylated amines for energy acquisition in abundant heterotrophic bacteria, including SAR11 and Roseobacter species (Lidbury et al. 2014, 2015; Sun et al. 2011). The genome of cultured *Thioglobus* from the North Pacific Gyre (strain NP2) contains the genes necessary for the complete oxidation of methylated amines, tetrahydroformate-linked substrates, and the marine osmolytes glycine betaine and choline, and growth has been demonstrated on these carbon compounds (Spietz et al. 2019). Methylated amines from phytoplankton can also provide a source of organic nitrogen, indicating a role in the secondary production and transformation of organic nitrogen. Organic sulfur compounds (sulfonates) produced by phytoplankton also serve as key substrates for some of the ocean's most abundant heterotrophic bacteria

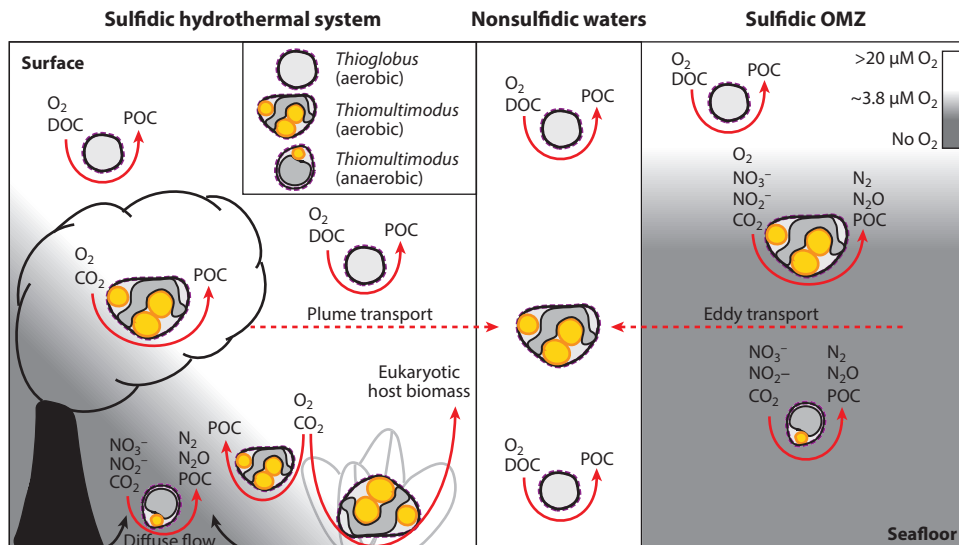


Figure 3

Schematic diagram of Thioglobaceae cells in diverse marine ecosystems and their shifting contributions to nutrient cycling along oxygen gradients. Differences in cell sizes, sulfur stores, and contributions to biogeochemistry are shown with curved arrows around cells. Straight arrows highlight the potential for the thioautotrophic activities of free-living *Thiomultimodus* cells to be transported from hydrothermal systems and OMZs to nonsulfidic waters, where the cells can remain active by using their stored elemental sulfur as an energy source. Abbreviations: DOC, dissolved organic carbon; OMZ, oxygen minimum zone; POC, particulate organic carbon. Cell illustrations adapted from Shah et al. (2019) under a CC BY 4.0 license (<https://creativecommons.org/licenses/by/4.0>).

(Durham et al. 2019). SAR11, Roseobacter, and *Thioglobus* were among the major lineages identified with desulfonation pathways, and growth on sulfonated substrates was verified in a SAR11 isolate from the North Pacific (Durham et al. 2019).

CONCLUSION

Members of the Thioglobaceae family often dominate microbial communities in anoxic waters where sulfide persists (Figure 3). At hydrothermal vents and cold seeps, *Thiomultimodus* members have formed close associations with a diverse array of eukaryotic hosts, including clams, mussels, corals, sponges, and anemones. Organoheterotrophic members of the *Thioglobus* genus are often present at relatively high abundances (>1%) throughout much of the ocean, where their metabolic activities resemble those of other abundant heterotrophs with the potential to use single-carbon compounds, volatile organic compounds, and sulfonated osmolytes produced by phytoplankton for carbon and energy. Thioautotrophic members of the *Thiomultimodus* genus that are transported to nonsulfidic waters by offshore eddies in coastal systems and by neutrally buoyant hydrothermal vent plumes in the deep ocean have the potential to impact marine biogeochemistry far beyond sulfidic waters, where stored elemental sulfur provides the energy needed to sustain growth for extended periods of time.

Adaptations to carbon, nitrogen, sulfur, and oxygen concentrations in seawater underlie patterns that have been observed in the abundance and distribution of thioautotrophic and organoheterotrophic genera and that reflect their diverse roles in marine biogeochemistry

(Figure 3). Evidence of genome streamlining in the Thioglobaceae (Rogge et al. 2017, Swan et al. 2013) suggests that the reduced genomes of organoheterotrophic members of the *Thioglobus* genus have lost, or are in the process of losing, genes for sulfur oxidation, carbon fixation, and nitrate reduction, and that the reduced genomes of thioautotrophic members of the *Thiomultimodus* genus have lost genes for the oxoglutarate dehydrogenase complex in the TCA cycle. Future studies that elucidate the physiology and biogeochemistry of the Thioglobaceae will further enhance understanding of niche adaptation, intracellular symbioses, and nutrient cycling in the ocean.

SUMMARY POINTS

1. The Thioglobaceae family comprises an autotrophic genus with both symbiotic and free-living species and a heterotrophic genus with free-living species.
2. Thioglobaceae cells are cocci, range in size from ~0.5 to 1.5 μm in diameter, are surrounded by a protein surface layer (S-layer), and lack a key gene required for cell division in other free-living proteobacteria (*ftsZ*).
3. To varying degrees, the diverse members of this group have adapted to niches associated with anoxic, suboxic, and oxic environments and the boundaries between them.
4. Symbiotic and free-living members of the *Thiomultimodus* genus are a primary source of organic carbon in eukaryotic hosts and in seawater where energy from sulfide, thiosulfate, or elemental sulfur fuels dark carbon fixation.
5. Members of the *Thiomultimodus* genus have an outsized impact on carbon, nitrogen, and sulfur cycling at hydrothermal vents and in marine oxygen minimum zones.
6. Free-living *Thioglobus* members resemble other abundant marine heterotrophs that can use single-carbon compounds, volatile organic compounds, and sulfonated osmolytes produced by phytoplankton for growth.
7. Enhanced sulfur storage under oxic growth conditions supports thioautotrophic activities of *Thiomultimodus* cells in nonsulfidic waters.
8. The physical transport of *Thiomultimodus* cells and the stored sulfur they contain has the potential to impact carbon and sulfur cycling in nonsulfidic waters.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Work on this review was funded by a grant from the National Science Foundation awarded to R.M.M. and Anitra Ingalls (OCE-1558483). We would like to thank members of the Center for Environmental Genomics at the University of Washington for their support and valuable feedback. We would like to give special thanks to Dr. Katharine Lalish, who initiated cultivation work on the first isolate from the Thioglobaceae family and *Thioglobus* genus and who prepared some of the figures, and to Dr. Vega Shah, who initiated cultivation work on the first isolate from the *Thiomultimodus* genus.

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