Folia Microbiologica
https://doi.org/10.1007/s12223-026-01464-8

REVIEW

# Comparative microbial lipidomics: structural diversity, adaptive strategies, and analytical advances

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Received: 9 February 2026 / Accepted: 17 March 2026


## Abstract

Lipids are essential biomolecules that play central roles in membrane structure, energy storage, and cellular signaling. During the past two decades, lipidomics has developed into a powerful analytical approach for systematic characterization of lipid composition, metabolism, and function across biological systems. Although early lipidomic studies focused primarily on animals and vascular plants, increasing attention has been directed toward microorganisms, whose lipid diversity reflects exceptional physiological and ecological adaptability across evolutionary timescales. This review focuses specifically on the comparative structural diversity of lipids across the main microbial groups – archaea, bacteria, yeasts, fungi, cyanobacteria, algae, and viruses—and on how mass spectrometry-based lipidomics has revealed adaptive strategies to environmental stress, temperature, salinity, pH, and availability of nutrients. Microorganisms exhibit pronounced variability in lipid structures and biosynthetic pathways. Archaeal membranes are characterized by ether-linked isoprenoid lipids that provide stability under extreme environmental conditions. In contrast, bacterial membranes contain diverse phospholipids, glycolipids, and hopanoids that enable rapid membrane remodeling in response to environmental stress. Fungi and algae synthesize characteristic sterols, glycolipids, and polyunsaturated fatty acids that are essential for membrane function, cellular signaling, photoprotection, and adaptation to fluctuating growth conditions. Recent advances in high-resolution mass spectrometry, particularly liquid chromatography-mass spectrometry, gas chromatography-mass spectrometry, and ion mobility spectrometry, have enabled detailed profiling of complex microbial lipidomes and their dynamic responses to physiological and environmental stimuli. Integration of lipidomics with transcriptomic, proteomic, and metabolomic data further enhances understanding of lipid biosynthesis and regulation. This review demonstrates that microbial lipidomics provides valuable insights into microbial physiology and adaptation and supports applications in chemotaxonomy, and environmental microbiology.

**Keywords** Lipidomic analysis · Archaea · Bacteria · Fungi and Yeast · Cyanobacteria and Algae

**Abbreviations**

| | |
|---|---|
| APCI | Atmospheric pressure chemical ionization |
| APPI | Atmospheric pressure photoionization |
| AR | Archaeol |
| DAG | Diacylglycerol |
| DESI | Desorption electrospray ionization |
| DG | Diacylglycerol |
| DGCC | Diacylglycerylcarboxyhydroxymethylcholine |
| DGDG | Diglycosyldiacylglycerol |
| DGMG | Digalactosyl monoacylglycerol |
| DGTA | Diacylglyceryl hydroxymethyl trimethylalanine |
| DGTS | Diacylglyceryltrimethylhomoserine |
| ESI | Electrospray ionization |
| $ESI^+/ESI^-$ | Positive/negative mode |

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Published online: 01 April 2026

| | |
|---|---|
| FA | Fatty acid |
| FAHFA | Fatty acyl esters of hydroxy fatty acid |
| GC-MS | Gas chromatography-mass spectrometry |
| GDGT | Glycerol dibiphytanyl glycerol tetraether |
| GIPC | Glycosylinositolphosphorylceramides |
| Gly | Glycine |
| HexCer | Hexosylceramide |
| HILIC | Hydrophilic interaction chromatography |
| HPLC | High performance liquid chromatography |
| HPTLC | High performance thin-layer chromatography |
| HRMS | High resolution mass spectrometry |
| ICP-MS | Inductively coupled plasma MS |
| IMS | Ion mobility separation |
| IPL | Intact polar lipid |
| LC-MS | Liquid chromatography-mass spectrometry |
| LPC | Lysophosphatidylcholine |
| LPE | Lysophosphatidylethanolamine |
| LPG | Lysophosphatidylglycerol |
| LPI | Lysophosphatidylinositol |
| LPS | Lysophosphatidylserine |
| LUCA | Last universal common ancestor |
| MAG | Monoacylglycerol |
| MALDI | Matrix-assisted laser desorption/ionization |
| MGDG | Monogalactosyldiacylglycerol |
| MGMG | Monogalactosylmonoacylglycerol |
| MGTS | Monoacylglyceryl-*N,N,N*-trimethylhomoserine |
| MS | Mass spectrometry |
| MS/MS | Tandem mass spectrometry |
| NARP | Non-aqueous reverse phase |
| NGAP | *N*-Glyceroyl alkylamine phosphoglycolipid |
| PA | Phosphatidic acid |
| PC | Phosphatidylcholine |
| PCA | Principal component analysis |
| PE | Phosphatidylethanolamine |
| PG | Phosphatidylglycerol |
| PI | Phosphatidylinositol |
| PIS | Precursor ion scan |
| PS | Phosphatidylserine |
| PUFA | Polyunsaturated fatty acid |
| QqTOF | Hybrid quadrupole time-of-flight |
| QTOF | Quadrupole time-of-flight |
| RP | Reversed-phase |
| SA | Sphinganine |
| SA1P | Sphinganine-1-phosphate |
| Ser | Serine |
| SQDG | Sulfoquinovosyldiacylglycerol |
| SQMG | Sulfoquinovosylmonoacylglycerol |
| TAG | Triacylglycerol |
| TLC | Thin-layer chromatography |
| TOF | Time-of-flight |
| UHPLC | Ultra-high performance liquid chromatography |
| UPLC | Ultra-performance liquid chromatography |

## Introduction to lipidomics – analysis of microorganisms

Lipids are fundamental components of all living systems, fulfilling essential structural, energetic, and signaling functions required for cellular function and adaptation. In recent years, lipidomics-the comprehensive study of lipid species and their interactions within biological systems-has emerged as a key discipline for understanding the complexity of lipid metabolism. Although lipidomic research has traditionally focused on mammals and vascular plants, an increasing number of studies now emphasize the importance of lipidomics in microorganisms, including bacteria, archaea, fungi (particularly yeasts), microalgae, and protozoa. These organisms exhibit extraordinary diversity in lipid structures and biosynthetic pathways, often reflecting distinct evolutionary strategies for survival in extreme or fluctuating environments.

Microbial lipidomes differ profoundly from those of plants and animals in both composition and biological function (Řezanka et al. 2020). A prominent example is the fundamental divergence in membrane architecture between bacteria and archaea, where *sn*-glycerol-3-phosphate-based ester lipids contrast with *sn*-glycerol-1-phosphate-based ether lipids. This represents a deep biochemical divide that likely dates back to the last universal common ancestor (LUCA). Likewise, the lipid composition of fungi and microalgae reveals remarkable adaptive capacity, such as the accumulation of polyunsaturated fatty acids under low-temperature or nutrient-limited conditions, or the synthesis of unusual glycolipids and phospholipids involved in stress tolerance and cellular signaling. Investigation of this lipidomic diversity, therefore, provides valuable insights into both the evolutionary trajectories of lipid metabolism and the ecological and biotechnological roles of microorganisms.

Modern lipidomic analysis integrates advanced chromatographic separation with high-resolution mass spectrometry (HRMS), enabling comprehensive profiling of lipid classes and individual molecular species. Techniques such as liquid chromatography-mass spectrometry (LC–MS), gas chromatography-mass spectrometry (GC–MS), and shotgun lipidomics have been successfully adapted to the often complex and variable lipid matrices of microorganisms. Recent advances in ion mobility spectrometry, tandem mass spectrometry (MS/MS), and data-independent acquisition approaches have substantially improved the differentiation of isomeric and isobaric lipid species, which is particularly important for the characterization of atypical lipid structures found in non-model organisms. Furthermore, integrating

lipidomic data with transcriptomic, proteomic, and metabolomic analyses within multi-omics frameworks has greatly enhanced our understanding of lipid biosynthesis and regulation across diverse taxa.

Lipidomic investigations of microorganisms also hold considerable applied potential. Microbial lipids (Fig. 1) represent renewable sources of nutritionally and industrially valuable compounds, including polyunsaturated fatty acids, sterols, carotenoids, and bioactive glycolipids. Lipidomic profiling supports the optimization of microbial production systems by identifying metabolic bottlenecks and adaptive responses to environmental or genetic perturbations. In environmental microbiology, lipidomics serves as a chemotaxonomic and ecological tool, enabling the characterization of microbial communities through lipid biomarkers and facilitating the study of symbiotic or pathogenic interactions.

In summary, lipidomic analysis of microorganisms is a rapidly advancing field at the interface of evolutionary biology, analytical chemistry, and biotechnology. The unique lipid architectures and metabolic capabilities of microorganisms not only challenge existing paradigms of lipid biochemistry, but also provide a foundation for novel discoveries and applications. Understanding microbial lipidomes thus contributes to a more comprehensive view of molecular diversity and supports both fundamental and applied research in lipid science. Although the functional roles of specific lipids in membrane physiology, stress signaling, and host–pathogen interactions are touched on where directly relevant, a comprehensive treatment of lipid function, regulation, and biotechnological exploitation lies beyond the scope of this review. These dimensions are noted as important directions for future synthesis.

Wood (2024) provided a comprehensive overview of metabolic and lipid biomarkers across a broad range of microorganisms, including algae, pathogenic fungi, cyanobacteria, mycobacteria, and Gram-positive and Gram-negative bacteria.

A comparative lipidomic analysis of the bacterium *Kocuria rhizophila*, the green alga *Chlamydomonas reinhardtii*, and bottom-fermenting brewing yeast *Saccharomyces*

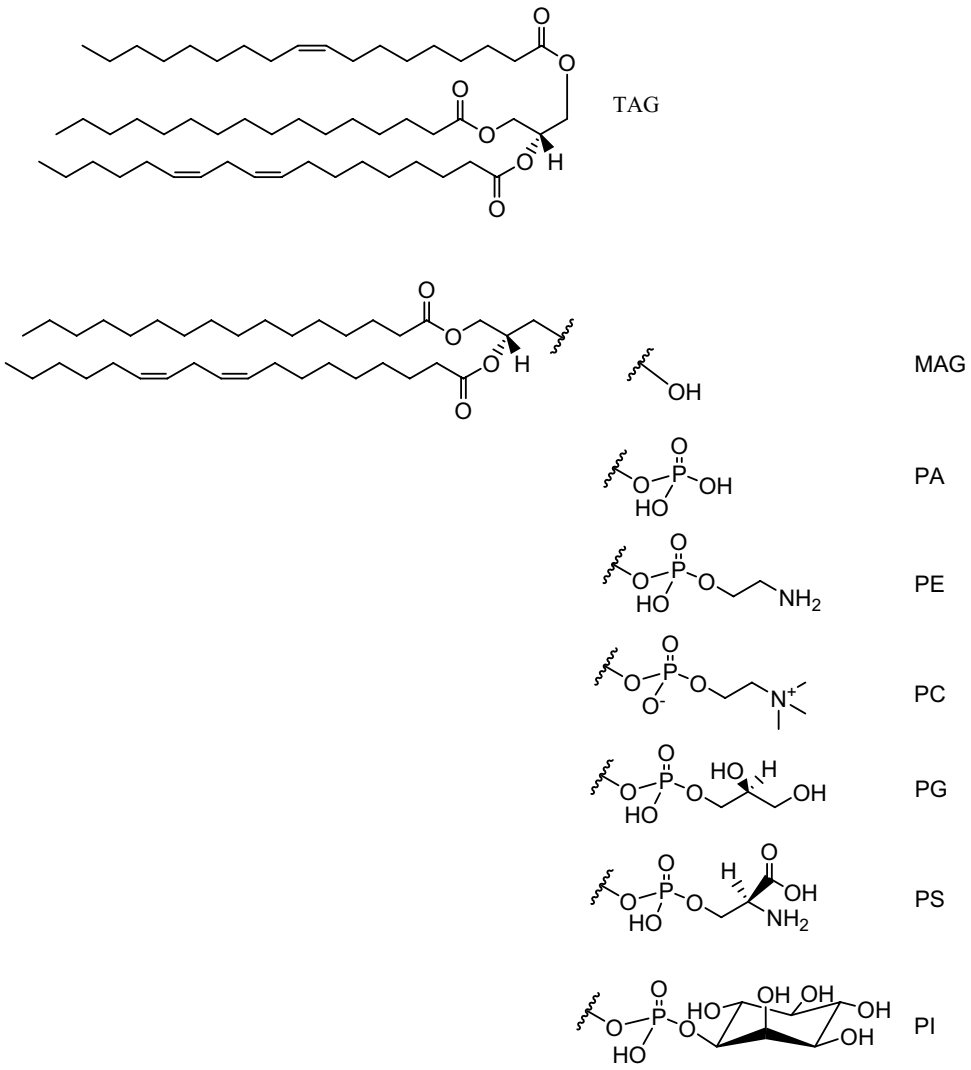


**Fig. 1** Structures of 'simple' and 'complex' microbial lipids (explanation of abbreviations, see below). TAG triacylglycerol, MAG monoacylglycerol, PA phosphatidic acid, PE phosphatidylethanolamine, PC phosphatidylcholine, PG phosphatidylglycerol, PS phosphatidylserine, PI phosphatidylinositol

*pastorianus* was performed using RPLC-MS/ESI$^-$, leading to the identification of a mixture of cardiolipin (CL) molecular species (Vítová et al. 2021a). An overview of LC–MS methodologies applied in lipidomics was presented by Harrieder et al. (2022).

## Archaea—general characteristics of membrane lipids

Archaea (from Greek archaia—ancient) represent a separate domain of prokaryotic unicellular organisms, whose independence from bacteria and eukaryotes was recognized only in 1977 (Garrett and Klenk 2008). The size of archaeal cells ranges from approximately 0.1 to 15 µm. Although they reproduce by binary fission and have a cytoplasmic membrane surrounded by a cell wall, similar to Gram-positive bacteria (Thomas et al. 2001), their molecular and biochemical properties differ fundamentally (Fig. 2).

Archaea represent an ancient lineage dating back approximately 3–3.5 billion years and are often associated with extreme environments such as high temperatures, extreme pH values, or high salinity (Garrett and Klenk 2008). The chemical composition of their membranes is fundamentally different from bacteria and eukaryotes. Whereas bacterial and eukaryotic membranes are composed of glycerol-ester lipids, archaeal membranes contain lipids with glycerol-ether bonds (De Rosa et al. 1986), which provide higher chemical stability under extreme conditions (Albers et al. 2000). The hydrophobic chains of archaeal lipids are composed of isoprenoid units, not fatty acids, increasing the rigidity and thermal resistance of the membrane (Damsté et al. 2002). Archaea also use *L*-glycerol-1-phosphate, while bacteria and eukaryotes use *D*-glycerol-3-phosphate, reflecting fundamentally different enzymatic machinery (Koga and Morii 2005, 2007). Some archaea contain tetraether lipids that form monolayer membranes with extreme resistance to physical and chemical stresses (Hanford and

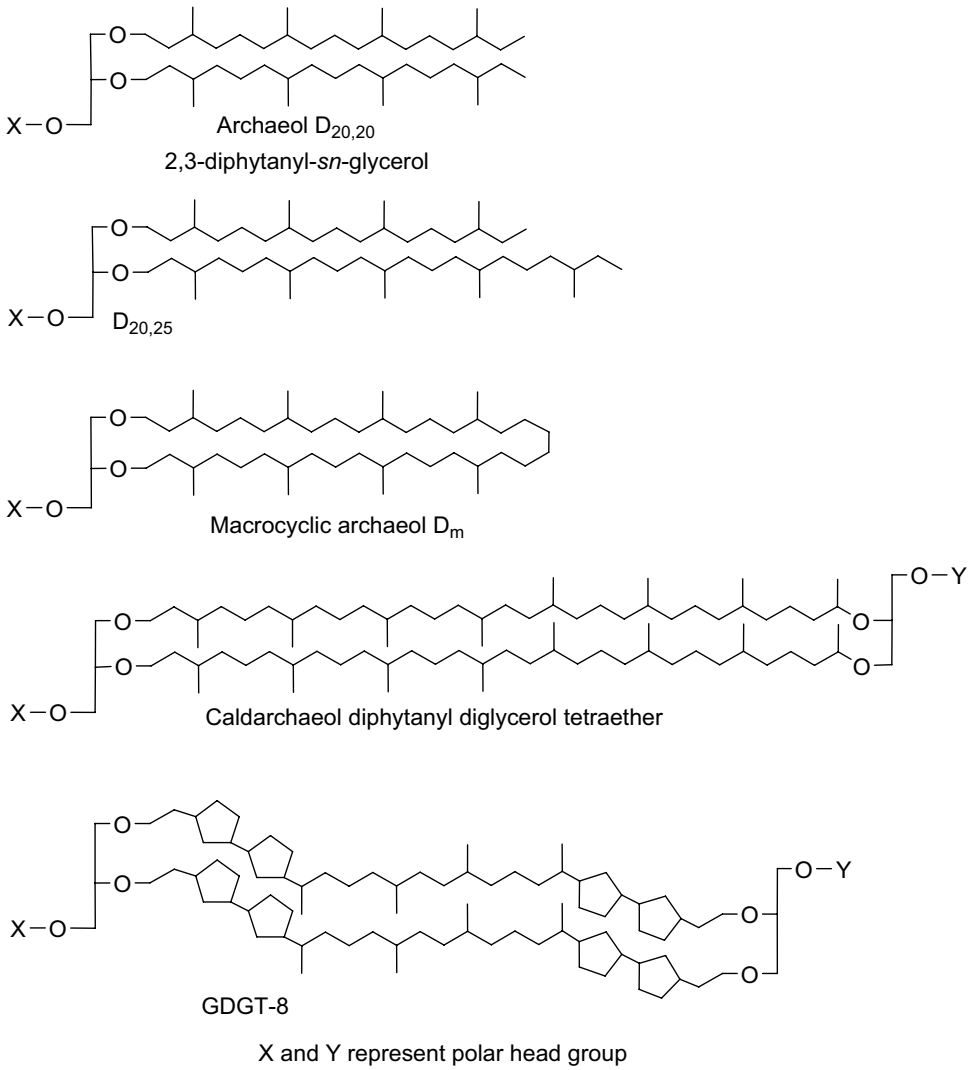


**Fig. 2** Archaea lipids, representative structures of major archaeal membrane lipids. Archaeal membranes are dominated by ether-linked isoprenoid glycerolipids with diverse polar headgroups. Phospholipid headgroups largely parallel those of bacteria and eukaryotes and include phosphodiester-linked ethanolamine, *L*-serine, glycerol, myo-inositol, and choline, whereas glycolipids predominantly contain glucosyl and gentiobiosyl (β-*D*-glucosyl-(1→6)-β-*D*-glucosyl) residues. Shown are diether lipids (archaeol $D_{20,20}$ and $D_{20,25}$), including a macrocyclic variant, and glycerol dibiphytanyl glycerol tetraethers (GDGTs). Archaeol $D_{20,20}$ exhibits an effective hydrocarbon length of ~C16, comparable to typical bacterial and eukaryotic membrane lipids, whereas archaeol $D_{20,25}$ contains mixed $C_{20}/C_{25}$ isoprenoid chains. Caldarchaeol (GDGT-0) consists of two covalently linked biphytanyl chains spanning the membrane and forming a monolayer architecture. Crenarchaeol (GDGT-8) is a cyclized GDGT containing eight cyclopentane rings, (e.g., Zeng et al. (2019)), conferring increased membrane rigidity and stability under extreme environmental conditions

Peeples 2002), for example, in the acidophilic archaea of the genus *Ferroplasma* (Macalady et al. 2004).

## Hyperthermophilic and thermoacidophilic archaea

Hyperthermophilic archaeon *Pyrococcus furiosus* isolated from geothermally heated marine sediments was analyzed by thin-layer chromatography and matrix-assisted laser desorption/ionization – time of flight (MALDI-TOF) MS, and archaeal and calarchaeal lipids were identified (Lobasso et al. 2012). These lipids contribute significantly to membrane stability at extremely high temperatures.

The genus *Sulfolobus* is one of the best studied thermoacidophilic archaea. In *Sulfolobus islandicus*, common archaeal lipids as well as a unique sulfonated tri-hexosyl-GDGT-inositol phosphate (GDGT, i.e., glycerol dibiphytanyl glycerol tetraether, Fig. 3) were identified using shotgun lipidomics (Jensen et al. 2015a). Additionally, a temperature-induced increase in the number of cyclopentane rings in tetraether lipids was observed in *S. islandicus* and *S. tokodaii*, which reduces membrane permeability (Jensen et al. 2015b). Detailed structural characterization of ether lipids was performed using the ion trap tandem MS-Orbitrap and QqTOF (Jensen et al. 2015a).

In *Thermococcus kodakarensis*, the lipid composition changed during growth, leading to increased production of tetraether lipids. UHPLC—MS/ESIA analyses suggest regulation of synthesis by a carbon–nitrogen hydrolase or a membrane-bound hydrogenase complex (Meador et al. 2014; Gagen et al. 2016). In piezophilic and hyperthermophilic *T. barophilus*, more than 80 intact polar lipids were characterized by LC–MS based on five core lipids and ten phosphatidylhexose head groups (Tourte et al. 2022).

## Halophilic and haloalkaliphilic archaea

Ether lipids, including phosphatidylglycerol (PG), phosphatidylglycerol phosphate methyl ester, and new cardiolipin lipids with four isoprenoid chains, have been identified in the haloalkaliphilic archaea *Natronococcus occultus* and *Natronococcus amylolyticus* (Angelini et al. 2012).

Studies on *Halobacterium salinarum* using MALDI-TOF MS without prior lipid extraction revealed the presence of phospholipids and glycolipids, including complex sulfated glycolipids (Angelini et al. 2010). Glycosylcardiolipins and unusual sulfated bis-diglycosyl-diether lipids with high molecular weights, probably related to adaptation to high salinity, have been identified in *Halorubrum trapanicum* and *Haloferax volcanii* (Lobasso et al. 2015).

The psychrotrophic archaeon *Halorubrum lacusprofundi* exhibited an increased unsaturation of ether lipids, including phosphatidylglycerol, phosphatidylglyceryl sulfate, and mono and diglycosylated archaeol derivatives, when cultured at 12 and 25 °C, as analyzed by ESI–MS (Gibson et al. 2005). Extensive analysis of the molecular network of halobacterial strains (*Haloarcula, Haloferax, Haloterrigena, Natrialba, Natrinema*) identified more than 100 molecular lipid species (Yao et al. 2023).

## Marine Thaumarchaea and GDGT lipids

The marine thaumarchaeon *Nitrosopumilus maritimus* was identified by LC–MS with characteristic GDGT lipids (Elling et al. 2014), which form the basis of the organic paleothermometer $TEX_{86}$ (Kim et al. 2008). GDGT biosynthesis and degradation significantly influence paleothermal reconstructions (Elling et al. 2014). Ion mobility coupled with LC–MS has enabled the resolution of crenarchaeol and its stereoisomers (Law et al. 2021). Comparative lipidomic analysis of ten ammonia-oxidizing thaumarchaeal strains and 19 euryarchaeal and crenarchaeal strains identified over 100 molecular species of archaeal lipids using UPLC-MS/$ESI^+$ (Elling et al. 2017).

## Methanogen and psychrophilic archaea

In the psychrophilic methanogen *Methanococcoides burtonii,* LC–ESI–MS revealed that adaptation to low temperatures is associated with increased unsaturation of ether lipids, especially archaeal and hydroxyarchaeal derivatives of phosphatidylglycerol and phosphatidylinositol (Nichols et al. 2004).

The lipidome of three autotrophic hydrogenotrophic methanogens (*Methanothermobacter marburgensis, Methanothermococcus okinawensis, and Methanocaldococcus villosus*) showed a pronounced dependence of lipid composition on temperature and nutrient availability (Taubner et al. 2023). Extremely halo(alkali)philic methanogenic euryarchaea of hypersaline lakes (*Methanonatronarchaeum, Methanosalsum, Methanocalculus*) contained a wide spectrum of polar main groups of archaeal lipids analyzed by HPLC–MS/APCI (Bale et al. 2019).

## Archaeal lipids in environmental samples

A significant portion of studies focus on environmental samples. Archaeal lipids have been analyzed in cold seep sediments in the South China Sea (Zhang et al. 2023), radioactive springs (Řezanka et al. 2025) and soil matrices, where approximately 17,000 lipid features were detected using LC-HRMS (Samrat et al. 2025). In the euxinic waters of the Black Sea, a depth-dependent distribution of archaeal IPLs has been demonstrated using UHPLC-HRMS (Sollai et al. 2019). GDGTs and bacteriohopanpolyols have also

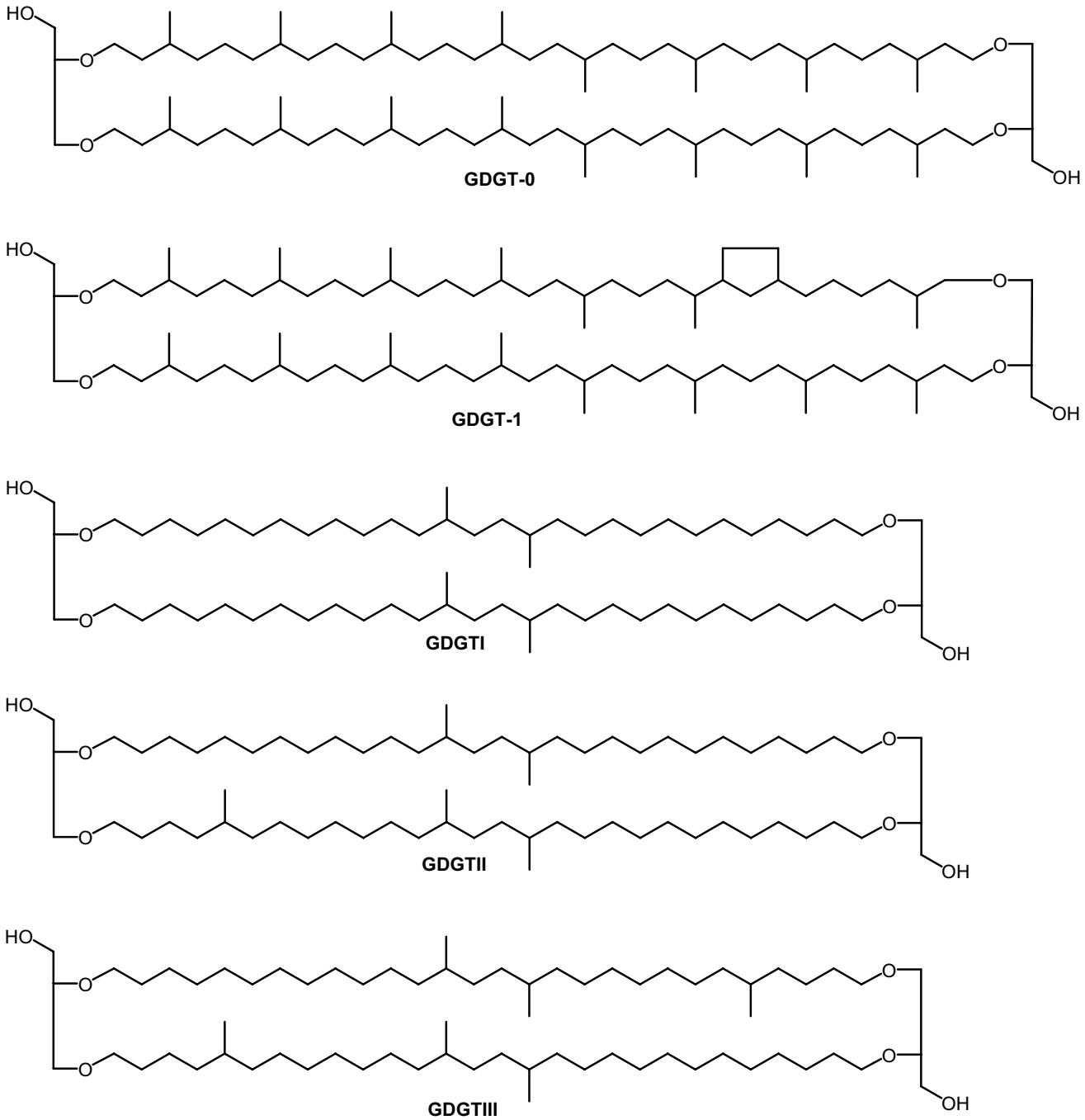


**Fig. 3** Archaea lipids, structures of five of the most widespread glycerol dialkyl glycerol tetraether (GDGT)-derived lipids in the archaea. GDGT-0 has a C32 carbon branched chain with no cyclopentane moieties, GDGT-1 has a C32 carbon branched chain with one cyclopentane moiety, GDGTI, GDGTII and GDGTIII each have a C28 carbon chain with different branching arrangements

been identified in marine sediment samples from the Antarctic Prydz Bay (van Kemenade et al. 2025).

## Concluding remarks on archaeal lipids

Despite significant progress, archaeal lipid research remains limited by the difficulty of culturing archaea (Woese et al. 1990; Rafiq et al. 2023), sample contamination, and the lack of reference databases (Blum 2008). Further methodological development of lipidomics and culture approaches will be crucial for a deeper understanding of the function, evolution, and environmental significance of archaeal membranes (Law et al. 2020; Edwards 2023; Řezanka et al. 2020, 2023; Law and Zhang 2019).

## Bacteria—general characteristics and lipid repertoire

Bacteria constitute a domain of unicellular prokaryotic organisms, typically 1–10 μm in size, with predominantly spherical (coccoid) or rod-shaped (bacillus) morphologies. The characteristic structural feature of the bacterial cell wall is peptidoglycan, which is organized into several layers. The cytoplasmic membrane, the key structure of all bacteria, is formed by a phospholipid bilayer containing transmembrane proteins and glycoproteins and, unlike eukaryotic membranes, generally does not contain sterols.

Bacteria exhibit an extraordinarily wide spectrum of lipid classes, reflecting their position as the most numerous and diverse group of organisms on Earth. The lipidome of a single bacterial cell can include up to 100,000 different molecular types of lipids (Yetukuri et al. 2008). Bacteria are capable of synthesizing all known lipid types, including polyunsaturated fatty acids (PUFAs), which were long thought to be exclusive to eukaryotes (Russell and Nichols 1999). Lipids containing cyclobutane rings, such as the ladderane phospholipids (Fig. 4) typical of anammox bacteria (Lanekoff and Karlsson 2010), are a particularly interesting group.

Comprehensive reviews of bacterial lipids, their metabolism, and mechanisms of membrane homeostasis were provided by Parsons and Rock (2013), while the structural diversity and biosynthetic pathways of bacterial membrane lipids were summarized by Sohlenkamp and Geiger (2016).

## Methodological reviews of bacterial lipidomics

The essential methodological reference in the field of bacterial lipid analysis is the publication mass spectrometry-based lipopolymers: methods and protocols (Hsu 2021). This volume contains 20 chapters devoted to detailed experimental procedures for lipid extraction and their structural characterization. It covers a wide range of analytical platforms, including ion mobility mass spectrometry, high-resolution LC–MS, shotgun analysis of bacterial lipid A using MALDI-TOF MS, and methods based on desorption electrospray ionization and post-photoionization MS.

Since the publication of this monograph, several review papers have appeared on the progress in lipidomics, and only those that specifically focus on the analysis of bacterial lipids are considered here. The review by Hsu (2023) focuses on the application of multi-step linear ion trap mass spectrometry to the characterization of native bacterial lipids. Unusual lipid classes are highlighted, including mycolic acid-containing phosphatidylglycerols, lysylcardiolipins (lysyl-CL), and amino acid-derived lipids such as lipocyclopeptides and dihydroceramide phosphoryl inositols. The review also details the fragmentation pathways observed by high-resolution multi-step MS and collision-induced dissociation.

Garrett (2017) provided additional insights into the structural diversity and mass spectrometric characterization of bacterial lipids. A medically oriented perspective was provided by Larrouy-Maumus et al. (2019), who focused on lipid biomarkers of bacterial infections and cancer, including cardiolipins as diagnostic indicators of mitochondrial-rich oncocytic thyroid tumors and prostate cancer.

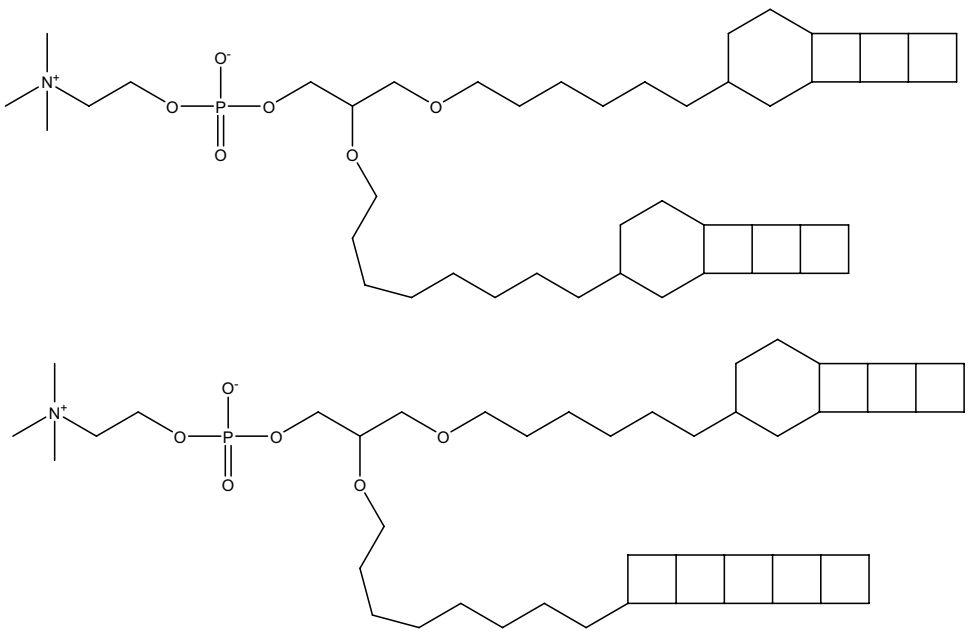

**Fig. 4** Ladderane phosphatidylcholine. Ladderane lipids are a structurally unique class of bacterial phospholipids characterized by acyl chains containing linearly concatenated cyclobutane rings, forming a rigid ladder-like architecture. They are found exclusively in anaerobic ammonium oxidation (anammox) bacteria, where they serve as the primary structural component of the anammoxosome membrane — a specialized intracellular compartment in which the toxic intermediate hydrazine is produced and contained. The extraordinary density and impermeability of ladderane membranes are thought to prevent hydrazine from leaking into the cytoplasm. Shown is a representative ladderane phosphatidylcholine (PC) species

A comprehensive review by Appaly et al. (2020) summarizes the applications of mass spectrometry in bacterial lipidomics, focusing on MALDI-based lipid profiling for bacterial strain identification and the relationship between lipid composition and antibiotic resistance. Characteristic lipidomic signatures of major pathogens are highlighted, including *Enterococcus faecium, Staphylococcus aureus, Klebsiella pneumoniae, Acinetobacter baumannii, Pseudomonas aeruginosa, Enterobacter* spp., as well as *Mycobacterium tuberculosis* and *Corynebacterium striatum*. Lipidomic analysis has thus become a commonly used approach in bacterial research, as summarized in the monograph introduction to lipidomics (Leray 2012) and reviews (Řezanka et al. 2012a; Crick and Guan 2016; Wood 2024).

## Model organisms

One of the first studies using lipidomic profiling analyzed *Escherichia coli* and *Bacillus subtilis* as representative Gram-negative and Gram-positive species. The mass spectra obtained by MALDI-TOF MS and tandem TOF/TOF MS differed significantly between the two bacteria. Lysylphosphatidylglycerol and diglucosyl diglycerides were identified in *B. subtilis*, which were absent in *E. coli*, reflecting fundamental differences in the structure of their cell membranes. In contrast, a unique cyclopropane fatty acid was found in *E. coli* (Gidden et al. 2009).

Subsequently, positive and negative desorption electrospray ionization (DESI) were used to analyze lipids in 16 bacterial samples without prior extraction. The analyzed samples included two Gram-positive species (*B. subtilis* and *S. aureus*) and fourteen Gram-negative bacteria (*E. coli* and 13 *Salmonella* species). Verification by MS/ESI up to 1000 Da revealed only minor differences between DESI and ESI data. Tandem MS allowed for the identification of lipids, and principal component analysis (PCA) demonstrated clear species differentiation, suggesting that the composition of the growth medium did not significantly affect the lipid profiles (Zhang et al. 2011).

*E. coli* culture further induced significant changes in the lipid composition of the surface and inner membrane of outer membrane vesicles (OMVs). Using UPLC-IMS-MS/QTOF, 10,165 components were detected, and 820 lipids were confidently identified across the classes of glycerolipids, fatty acids, sphingolipids, glycerophospholipids, saccharolipids, and sterol lipids (Song et al. 2025).

## Gram-positive pathogens

*Staphylococcus aureus*, one of the best-studied human pathogens, has been extensively analyzed using lipidomics methods. Hewelt-Belka et al. (2014) performed LC–MS/QTOF analysis, which resulted in a comprehensive database comprising 18 major lipid classes, 36 subclasses, and over 7,000 molecular species. Particular attention was paid to lipids containing odd-chain fatty acids, which are relatively rare. The study further showed that lipidomic differences at the strain level correlate with antibiotic susceptibility and phenotypic characteristics.

*S. aureus* infection on bacterial endophthalmitis was further investigated using both positive and negative ESI modes. The analysis demonstrated that *S. aureus* infection significantly alters the lipid profile of the retina, which may contribute to the pathogenesis of bacterial endophthalmitis (Ahmad et al. 2024).

Analysis of *Enterococcus faecalis* by UHPLC-HRMS identified 30 lipid species that incorporated fatty acids labeled with deuterium oxide and/or the isotope $^{13}C$. Tandem MS of isolated lipids allowed the localization of acyl chains, confirming the activity of glycerol-3-phosphate acyltransferase in the incorporation of $^{13}C$-labeled fatty acids into membrane lipids (Woodall et al. 2023).

Structural lipidomics has further enabled the identification of over 50 positional and cis/trans isomers of fatty acids and phospholipids in selected human gut bacteria. Remarkably high levels of trans-10-octadecenoic acid have been detected in *E. faecalis, Bifidobacterium longum* and *Lactobacillus acidophilus*. $^{13}C$ isotope labeling confirmed that gut bacteria produce trans-10-octadecenoic acid by isomeric biotransformation of oleic acid (Chen et al. 2024).

Numerous studies have focused on lipidomic changes associated with bacterial diseases. For example, bacterial pneumonia caused by *Streptococcus pneumoniae* was successfully distinguished from viral pneumonia using LC–MS-based lipidomic analysis, demonstrating the potential of lipidomics in clinical diagnostics (Rischke et al. 2025).

Comparative lipidomic profiling of the human commensal bacterium *Propionibacterium acnes* and its extracellular vesicles led to the identification of 214 lipids by LC–MS/MS. The extracellular vesicles were enriched in PC, DAG, PA, PE, LPA, LPC and MG, while showing lower levels of PS, sphingosine-1-phosphate, SA1P, LPG, LPI and LPS compared to the parent cells (Jeon et al. 2018).

## Gram-negative pathogens

*Pseudomonas aeruginosa* bacterial cells in biofilms exhibit physiological properties distinct from planktonic cells. MS–ESI was used to compare the lipidomes of the inner and outer membranes during biofilm formation and revealed age-dependent lipidomic changes in both membranes (Benamara et al. 2014).

Phospholipids from a pathogenic strain of *Pseudomonas fluorescens* were visualized and identified using

HPTLC-MALDI-TOF MS, a simple and rapid screening method for bacterial phospholipid classes. This study was the first to identify phosphatidylcholine in *P. fluorescens*, a lipid previously thought to be exclusively eukaryotic (Kondakova et al. 2015). The presence of phospholipids PC, PE, and PG in airborne *P. fluorescens* was also confirmed using HPTLC-MALDI-TOF MS (Kondakova et al. 2015).

Metabolic profiles of *Pseudomonas aeruginosa*, along with *Bacillus subtilis, Streptomyces coelicolor*, and *Mycobacterium smegmatis*, were determined directly using nanospray desorption/electrospray ionization mass spectrometry, without prior lipid extraction from colonies grown in Petri dishes. This approach allowed the spatiotemporal dynamics of metabolite production in living microbial colonies to be monitored in real time (Watrous et al. 2012).

In *Acinetobacter baumannii*, colistin resistance is primarily mediated by the addition of phosphoethanolamine to lipid A, catalyzed by phosphoethanolamine transferase. Although rapid detection of resistance is crucial for effective clinical treatment, current diagnostic methods still rely on the determination of the minimum inhibitory concentration, which requires 16–24 h. A recently developed MALDI-TOF MS-based assay enabled the rapid detection of lipid A modifications and the identification of colistin-resistant isolates in less than 15 min directly from intact bacterial cells (Dortet et al. 2018).

Recent lipidomic studies have broadened our understanding of membrane adaptation and resistance in this pathogen. Dessenne et al. (2024) used LC-HRMS$^2$ to show that clinical strains of *A. baumannii* remodel their glycerophospholipid composition strain-specifically in response to temperature, with most strains accumulating palmitoleic acid (C16:1) at 18° C to maintain membrane fluidity. At the resistance level, Hao et al. (2026) applied integrated proteomics and untargeted metabolomics to a clinical XDR-CRAB isolate and identified a reduced abundance alongside PmrCAB-mediated lipid A and broad metabolic reprogramming as concerted resistance mechanisms.

## Oral microbiome bacteria

Recent studies have identified novel lipid species in oral bacteria, particularly *Porphyromonas gingivalis*. Dihydroceramides containing isobranched fatty acids, serine lipids, and modified glycosyldiacylglycerols with a phosphoethanolamine headgroup have been described. These structures show similarities to lipids described in clostridia. At the same time, antigenic lipids have been identified in *Salmonella* (Garrett 2017).

Comparative lipidomic analysis of oral commensal and opportunistic microorganisms included *Streptococcus oralis, S. intermedius, S. sanguinis, S. gordonii, Porphyromonas gingivalis, Proteus vulgaris, Fusobacterium nucleatum, Veillonella parvula, Treponema denticola, Akkermansia muciniphila* and the yeast *Candida albicans*. LC–MS/MS identified a wide range of lipid compounds, including glycine lipids (Gly) containing fatty acyl esters of hydroxyl fatty acids (FAHFA), Gly-Ser-FAHFA and Gly-Ser-FAHFA-phosphodiacylglycerols, as well as other complex lipid structures (Wood et al. 2024).

## Gut and anaerobic bacteria

*Bacteroides thetaiotaomicron* have been shown to contain ethanolamine and inositol phosphoceramides (Sartorio et al. 2022; Ryan et al. 2023). Using LC–MS/MS, 130 lipids produced by this gut symbiont were identified. MALDI-MS imaging was subsequently used to spatially map these bacterial lipids in the mouse colon. Unlabeled bacterial lipids have been visualized in colon sections of germ-free, specific pathogen-free, and monocolonized mice, both in wild-type and sphingolipid-deficient strains (Ryan et al. 2023; Mirretta Barone et al. 2024).

Anaerobic bacteria from the *Bacteroides fragilis* group, including *B. thetaiotaomicron, B. fragilis, B. vulgatus* and *B. ovatus*, were analyzed using high-resolution multi-stage mass spectrometry. Fifteen lipid classes and subclasses were identified, comprising more than 100 molecular species. These lipids included rare sphingolipids such as dihydroceramides, glycylseryl-dihydroceramides, dihydroceramide-phosphoinositolphosphoryl-dihydroceramides and phosphorylceramides with ethanolamine, inositol and serine heads, as well as PI, PS and PE (Frankfater et al. 2023).

Identification of bacterial lipids, particularly in anaerobic species of the genus *Clostridium*, was described by Goldfine and Guan (2015). Changes in the lipidome of the membrane plasmalogen *Clostridium pasteurianum* during butanol fermentation provided detailed insight into metabolic remodeling under fermentation conditions (Kolek et al. 2015).

Environmental factors such as salinity and hydraulic retention time significantly influence the composition of intact polar lipids in *Halanaerobium congolense* and mixed microbial consortia. 194 molecular species in 13 lipid subclasses were identified using UPLC-MS/MS (Ugwuodo et al. 2024).

Among mesophilic members of the phylum Bacillota, *Desulfosporosinus orientis*, a spore-forming sulfate-reducing bacterium, has been shown to contain *N*-glyceroylalkylaminephosphoglycolipids (NGAPs). These structurally unusual membrane lipids likely contribute to membrane stability under anaerobic conditions. More than 50 intact polar NGAPs were identified using UHPLC-HRMS/MS,

including structures containing iso-C17-type isobranched fatty acids (Bale et al. 2025).

The presence of plasmalogens in anaerobic bacteria has also been the subject of several review studies, which emphasized their analysis together with other lipids containing fatty acid esters (Goldfine 2020; Guan and Goldfine 2021; Vítová et al. 2021b).

The lipidome of the mesophilic and anaerobic sulfate-reducing bacterium *Desulfatibacillum alkenivorans*, which is characterized by a high content of alkylglycerol ether lipids, was analyzed under different temperatures, pH values, salinity, and nutritional conditions, especially with variable availability of $NH_4^+$ and $PO_3^-$. Almost 400 lipid molecules were identified, covering a wide range of ether and ester glycerolipids with different polar heads. These included PG, CL, DAG, acyl/ether glycerols, dietherglycerols, tetraether, triether/monoester, diether/diester, monoether/triester, and tetraester glycerols (Ding et al. 2024).

## Thermophilic bacteria

Thermophilic bacteria represent a specific group of microorganisms adapted to growth at elevated temperatures, which is strongly reflected in the composition of their cell membranes. An extraordinarily diverse group of (NGAPs) has been described in thermophilic members of the phylum Bacillota (formerly Firmicutes), namely *Caldanaerobacter subterraneus* and *Thermosediminibacter oceani* (Bale et al. 2025). These lipids represent structurally unusual membrane components that contribute to the stability of cell membranes under extreme temperature conditions.

Using ultra-performance liquid chromatography coupled with high-resolution tandem mass spectrometry (UHPLC-HRMS/MS), more than 50 intact polar NGAPs were identified. Among them, dialkyl-1,2-diol structures containing iso-C17-type isobranched fatty acids, which are typical of thermophilic bacteria, dominated. The polar head groups of these lipids often contained *N*-acetylglucosamine, which further increases the structural complexity and suggests specific biosynthetic pathways adapted to extreme environments (Bale et al. 2025).

The thermophilic genus *Anoxybacillus* was analyzed in detail by LC–MS/MS with electrospray ionization (ESI), with attention paid to the differences between facultative anaerobic and strictly aerobic species. Lipid extracts from the facultative anaerobic species *Anoxybacillus bogrovensis*, separated by hydrophilic interaction chromatography (HILIC), revealed the predominance of diacyl phospholipids and the presence of plasmalogens, which are typical of anaerobic and microaerophilic bacteria. In contrast, the lipidome of the strictly aerobic species *Anoxybacillus rupiensis* was significantly different and included several unique polar lipids. Alanyl-, lysyl-, and glucosylphosphatidylglycerols were identified, as well as various forms of cardiolipins. These differences point to the fundamental influence of the oxygen regime on the biosynthesis of membrane lipids and on the adaptation of the membrane architecture of thermophilic bacteria to specific environmental conditions (Řezanka et al. 2012b).

Different strains of thermophilic bacteria, namely *Alicyclobacillus acidoterrestris, Geobacillus stearothermophilus, Geobacillus kaustophilus, Meiothermus ruber,* and *Thermus aquaticus*, were analyzed for the production of menaquinones, which play a key role in the bacterial electron transport chain. The analyses were performed using off-line two-dimensional liquid chromatography coupled to tandem mass spectrometry, using a combination of RP18 and COSMOSIL Cholesterol columns.

The results showed that thermophilic bacteria grown at different temperatures produce exclusively all-trans isomers of menaquinones ranging from MK-5 (menaquinone with five isoprenyl units) to MK-15 (fifteen isoprenyl units). The absence of cis-isomers suggests a high stereochemical control of isoprenoid side chain biosynthesis, which may contribute to the increased stability of membranes and respiratory complexes at high temperatures (Timkina et al. 2024).

In the genera *Geobacillus, Meiothermus,* and *Thermus*, lipids contain more than one glycosidically linked glucose molecule attached to the hydroxyl group of the central glycerol of cardiolipin. The number of glucose residues could be as high as five, representing a previously unseen level of glycosylation for this lipid class. The structures of these highly glycosylated cardiolipins were determined using high-resolution electrospray ionization mass spectrometry. The presence of such modified cardiolipins is likely related to the adaptation of thermophilic bacteria to extreme temperatures, as increased hydration and a bulky polar head may affect membrane curvature, stability of protein complexes, and function of respiratory chains (Kyselová and Řezanka 2024).

## Other bacteria

Numerous publications have focused on lipidomic characterization of novel or biologically significant bacterial species. An example is the genomic and lipidomic analysis of *Leeuwenhoekiella parthenopeia*, a rare bacterium of the marine biosphere that has been shown to have antitumor activity. The study combined genomic data with detailed lipidomic characterization, providing new insights into the metabolic potential of this microorganism (Gattoni et al. 2022).

## Yeasts (Fungi)

Yeasts are among the most important microorganisms used in biotechnology. They are unicellular fungi that typically reproduce by budding or fission and have traditionally been used in the production of beer, wine, and bread. Some yeast species, such as *Candida albicans*, are pathogenic. Yeast lipidomics has been the subject of numerous significant studies, primarily focused on the model organism *Saccharomyces cerevisiae*.

### Saccharomyces cerevisiae and related species

One of the earliest systematic studies was a book chapter in Methods in Cell Biology addressing the analysis of the proteome and lipidome of yeast lipid droplets (Schmidt et al. 2013). Using basic analytical techniques such as TLC, GC, MS, and GC–MS, the lipidomes of three yeast species (*S. cerevisiae*, *Yarrowia lipolytica*, and *Pichia pastoris*) were analyzed. The emergence and development of yeast lipidomics were summarized in a review by Gaspar et al. (2007).

A significant methodological milestone was the publication of the updated classification, nomenclature, and shorthand notation for MS-derived lipid structures within the LIPID MAPS framework (Liebisch et al. 2020), which also includes lipids originating from yeasts.

Shotgun lipidomics analysis of two million *S. cerevisiae* cells enabled the identification of 21 lipid classes and more than 250 molecular species. Pronounced changes in lipid content were observed in yeasts cultivated at 24 °C and 37 °C (Ejsing et al. 2009).

Studies employing UHPLC-MS/MS on wild-type and recombinant strains of *S. cerevisiae* demonstrated a correlation between xylose and glucose metabolism, particularly involving phosphatidylinositols (Xia et al. 2011). The dependence of 21 lipid classes in *S. cerevisiae* on cultivation time revealed changes in the abundance of individual molecular species, such as shifts between 34:2-PC and 32:2-PC or between 34:2-PA and 32:2-PA (Casanovas et al. 2015).

Lipidomic analysis of a wild-type *S. cerevisiae* strain and its mutants cultivated at four different temperatures (15 °C, 24 °C, 30 °C, and 37 °C) was conducted to investigate changes in membrane phospholipid composition (Klose et al. 2012). The absence of genes YBR141C and YJR015W, whose functions remain unknown, was also examined in *S. cerevisiae* mutants (Tarasov et al. 2014).

A detailed lipidomic analysis of *S. cerevisiae* using nano-LC–MS/MS–ESI revealed nearly 900 lipid species belonging to 26 lipid classes, including glycerophospholipids, sphingolipids, glycerolipids, and sterols. Odd-chain fatty acids and dienoic fatty acids were found to be commonly incorporated into multiple lipid classes, for example, into monomethylphosphatidylserine (Danne-Rasche et al. 2020).

The lipidome of *S. cerevisiae* in two growth phases, logarithmic and stationary, was investigated by Reinhard et al. (2023). During cultivation, changes were observed in the abundance of monounsaturated acyl chains of phosphatidylcholine as well as in fatty acid chain length, resulting in differences in molecular species such as 16:1/16:1 versus 16:1/16:0.

Practical approaches to the quantification of membrane lipid composition in *S. cerevisiae* were summarized by de Kroon (2017). An untargeted lipidomic analysis of ten *S. cerevisiae* strains, including laboratory, baker's, wine, and sake yeasts with distinct fermentation phenotypes, was performed using LC–MS/QTOF. A total of 352 molecular species were identified, and statistical analysis enabled clear discrimination among strain groups (Komori et al. 2023).

Meyer et al. (2024) compared HPTLC-based lipid quantification with shotgun MS approaches across different *S. cerevisiae* strains. Commonly occurring lipids were identified, including steryl esters, TAG, DAG, ergosterol, PE, PA, PC, PG, PI, and cardiolipin, although the study lacked a thorough statistical evaluation.

### Other non-oleaginous and oleaginous yeasts

The lipidomic profiles of *S. cerevisiae*, *S. bayanus*, *Kluyveromyces thermotolerans*, *Pichia angusta*, and *Yarrowia lipolytica* revealed the presence of nine phospholipid classes, predominantly CL, PE, PI, PC, PS, and PG, comprising more than 100 molecular species (Hein and Hayen 2012).

Lipidomic analysis of *S. cerevisiae* and *Zygosaccharomyces bailii* cultivated on an atypical carbon source (acetic acid) showed that acetic acid tolerance was associated with increased sphingolipid content (Lindberg et al. 2013).

Comparison of lipidomic profiles of homogenates and microsomes from the methylotrophic yeast *Pichia pastoris* revealed changes in TAG, PC, and PI content. Elevated cultivation temperature increased PI levels while decreasing TAG and PE content (Klug et al. 2014).

The oleaginous red yeast *Rhodotorula glutinis* was analyzed using shotgun lipidomics UHPLC-MS/MS, identifying 982 molecular species across dozens of lipid classes, including less common lipids such as DGTS, SQDG, glucuronosyldiacylglycerols, and hexosylceramides (Li et al. 2020). A subsequent study by Li et al. (2023) described dynamic changes in lipid metabolism during different growth phases of *R. glutinis* and outlined strategies to enhance lipid productivity through metabolic or genetic engineering.

Lipid synthesis in the oleaginous red yeast *Sporobolomyces pararoseus* was described by Xie et al. (2024). Using UPLC-MS/MS, nearly 1000 molecular species were

identified, and hydrogen peroxide treatment significantly increased lipid production, particularly triacylglycerols. Joshi et al. (2024) reported on the lipidome of oleaginous yeasts of the genus *Yarrowia*.

## Pathogenic yeasts and microbiome-associated yeasts

A comprehensive lipidomic study of the human pathogenic yeast *Candida auris* compared a drug-sensitive strain (CBS10913T) with a drug-resistant hospital isolate (NCCPF 470033). Major classes of phosphoglycerides, sphingolipids, sterols, DAG, and TAG were quantified at the molecular species level, revealing pronounced differences between the isolates (Shahi et al. 2020).

Yeasts of the genus *Malassezia* (*M. furfur*, *M. pachydermatis*, *M. restricta*, and *M. sympodialis*), which are part of the human and animal skin microbiome, were analyzed using UHPLC-MS/QTOF. Eighteen lipid classes and 428 molecular species were identified, with the most abundant lipids including TAG, sterols, DAG, fatty acids, PC, PE, ceramides, cholesteryl esters, sphingomyelin, and lysophospholipids (Celis Ramírez et al. 2020). The results enabled discrimination among *Malassezia* species.

Sphingolipids from 11 yeast strains representing the genera *Cryptococcus*, *Saccharomyces*, *Schizosaccharomyces*, and *Wickerhamomyces* were analyzed by Řezanka et al. (2018). Nearly 150 molecular species belonging to three classes of complex sphingolipids were identified, and cultivation temperature was shown to affect both the relative abundance of sphingolipid classes and the chain length of long-chain bases.

## Yeasts in trophic interactions

Various yeast species, including *Hanseniaspora uvarum*, *Candida* sp., *Issatchenkia terricola*, *Metschnikowia pulcherrima*, *Saccharomycopsis vini*, and *S. cerevisiae*, serve as food sources for *Drosophila suzukii*. Lipidomic analysis identified 171 molecular species, including DAG, TAG, PS, PC, PE, PG, PI, LPE, and LPC (Bianchi et al. 2020).

## Less studied and extremophilic yeasts

Yeast lipidomics is increasingly expanding to difficult-to-cultivate species, such as psychrophilic species (Řezanka et al. 2016). Eight psychrophilic yeasts (*Cryptococcus victoriae*, *Cystofilobasidium capitatum*, *Holtermaniella wattica*, *Mrakiella aquatica*, *M. cryoconiti*, *Rhodotorula lignophila*, *Kondoa malvinella,* and *Trichosporon aggtelekiense*) grown at 4–28 °C by hydrophilic interaction liquid chromatography/high resolution ESI–MS determined 17 classes of lipids and identified dozens of molecular species of phospholipids including their regioisomers. With few exceptions, most studies to date have focused primarily on *S. cerevisiae*.

## Filamentous fungi (molds)

In contrast to yeasts, comprehensive lipidomic analyses of filamentous fungi have not yet been conducted. Most studies have addressed specific biological questions rather than whole-lipidome characterization.

The symbiosis between *Rhizopus microsporus* and *Burkholderia* bacteria was investigated with respect to the effect of diacylglycerol kinase on the relative abundance of phospholipids and neutral lipids in the hardened host grown with and without the bacterium (Lastovetsky et al. 2016).

The effect of fermentation conditions on *Cephalosporium acremonium* in industrial and pilot-scale fermentations was studied using LC–MS/MS–ESI lipidomics. A total of 77 phospholipids were detected, and 65 were quantified, with significant differences observed mainly for PI, PS, and PA (Xu et al. 2012).

The lipidomic profile of *Penicillium chrysogenum* in industrial fermentations was determined by LC–MS/MS–ESI (Qiao et al. 2013). Cells were shown to absorb significant amounts of exogenous saturated and polyunsaturated fatty acids and incorporate them into cellular membranes, markedly affecting membrane fluidity and enabling optimization of fermentation processes.

Cell wall lipids of *Paracoccidioides brasiliensis* grown in the presence and absence of human plasma were analyzed by Longo et al. (2013). Phospholipids, fatty acids, sterols, and glycolipids were identified, including less common molecular species such as 19:1/19:2-PC and 16:0/19:1-PA.

The lipid composition of the genera *Aspergillus*, *Wallemia*, and *Fusarium* in stored rice was examined using LC–MS. A total of 927 lipid species were identified, and key markers of rice quality deterioration, such as sulfoquinovosyl ceramide and phosphatidylmethanol, were proposed (Wang et al. 2024).

The lipidomic response of the entomopathogenic fungus *Beauveria bassiana* to pyrethroids was described by Litwin et al. (2021), demonstrating increased membrane permeability and changes in phospholipid profiles.

Lipidomic analysis of fungi, particularly filamentous molds, remains in an early stage of development. However, a rapid increase in publications can be expected, especially for species of industrial relevance, such as producers of organic acids (*Aspergillus*), pharmaceuticals, or mycotoxins. Methodological approaches such as two-dimensional developmental HPTLC-MS/ESI are emerging as universal tools applicable not only to yeasts but also to a broader range of fungi (Cebolla et al. 2022).

## Cyanobacteria

Although algae and cyanobacteria are taxonomically very distant, they biosynthesize essentially similar lipids. Their occurrence and cultivation conditions are also largely comparable. Cyanobacteria contain glycolipids (MGDG, DGDG, and SQDG) as well as phospholipids, with PG being the dominant species. In this respect, cyanobacterial lipids resemble those of algae and differ markedly from most bacteria, even though cyanobacteria belong to the bacterial domain.

Marques et al. (2016) investigated the effect of As(III) on the lipidomic profiles of two cyanobacterial species (*Anabaena* and *Planktothrix agardhii*) using LC–MS combined with least-squares fitting. They demonstrated that As(III) induces significant changes in the lipid composition of cyanobacteria. The most pronounced alterations were observed in pigment content, particularly chlorophyll a and its degradation product pheophytin a, as well as carotenoids such as 3-hydroxycarotene and 3-carotene-3,3′-dione, and within the MGDG fraction.

Sterol profiles were characterized in heterotrophically cultivated cyanobacteria *Phormidium autumnale* using three different carbon sources: glucose, sucrose, and slaughterhouse wastewater from the agro-industrial sector (Fagundes et al. 2019). A total of 24 compounds were detected in the biomass, including hop-22,29-en-3-one, squalene, and 22 sterols (e.g., cycloartenol, avenasterol, brassicasterol, sitosterol, stigmasterol, and ergosterol), all identified by GC–MS.

Untargeted lipidomic analysis of *Synechocystis* sp. demonstrated the influence of cultivation conditions on lipid composition (Hewelt-Belka et al. 2020). Cyanobacteria were cultivated photoautotrophically under conditions of either rapid or slow growth, and the effects on the molecular species of MGDG, DGDG, and SQDG were examined.

The lipidome of the marine cyanobacterium *Synechocystis* sp. cultivated at different NaCl concentrations was analyzed using GC–MS and direct-infusion MS (Lee et al. 2021). Pigments such as chlorophyll a, allophycocyanin, and phycoerythrin were identified together with polar lipids including glucosylglycerol, DGTS, MGDG, and PG.

Lipidomic profiling and fatty acid characterization were also applied in the bioprospecting of one cyanobacterium (*Synechococcus* sp.) and two microalgae (*Chlorella vulgaris* and *Scenedesmus* sp.) for biodiesel production (Shanmugam et al. 2020).

Despite relatively limited lipidomic research on cyanobacteria compared to other microbial groups, current studies demonstrate significant advances in understanding stress responses, metabolic plasticity, and biotechnological potential, warranting further investigation of this ecologically important group.

## Algae – general characteristics and reviews

Algae constitute a highly diverse group of photosynthetic organisms, ranging from unicellular to multicellular forms. They inhabit aquatic (freshwater and marine) as well as terrestrial environments and may also exist in symbiosis with lichens. Although algae are primarily photosynthetic, some species can also be cultivated heterotrophically, a property widely exploited in various biotechnological applications.

Algae produce a broad spectrum of lipids, including less common classes such as betaine lipids and sulfolipids. Typical examples include DGTS, DGTA, and DGCC (Fig. 5).

Unlike bacteria and yeasts, algae often contain more than 50% polyunsaturated fatty acids (PUFAs), such as 18:5, 20:5, and 22:6 fatty acids, which are also found in vascular plants. For PUFA production, algae are typically cultivated in fermenters with volumes of tens of thousands of liters, for example, in the large-scale production of docosahexaenoic acid from various algal strains. Lipidomic analysis is frequently employed to study algal responses to stress or non-standard cultivation conditions, such as exposure to elevated salinity. In freshwater algae, this may include cultivation in seawater.

A comprehensive review describing the lipidomes of algae and plants was recently published (Jouhet et al. 2024).

Another review by Bisht et al. (2021) highlights a less commonly used technique-the application of nuclear magnetic resonance spectroscopy in microalgal metabolism and lipidomics. Algae from different taxonomic groups, such as *Chaetoceros calcitrans* (diatom), *Scenedesmus regularis* (green alga), and *Isochrysis galbana* (haptophyte), were used as examples, and both fatty acids and pigments (fucoxanthin and astaxanthin) were identified.

In their comprehensive review, da Costa et al. (2016) summarized insights gained from lipidomic analyses of glycolipids in dozens of microalgal species.

A review describing applications of lipidomics in marine organisms, including algae, has also been published (Rey et al. 2022). This article addresses the use of LC–MS and MS/MS and covers aspects such as sampling and sample preparation, interpretation of MS/MS fragmentation patterns, and data analysis and processing.

A book chapter devoted to the lipidomics of arsenic-containing compounds in algae has also been published (Freitas and Gomes 2019). It provides a detailed description of sample preparation and extraction methods for isolating arsenolipids from macroalgae and microalgae, as well as cyanobacteria. Using advanced techniques, including HPLC-ICP-MS/MS–ESI and HPLC-HRMS/MS–ESI, more than 70 arsenolipids of different structural types were identified.

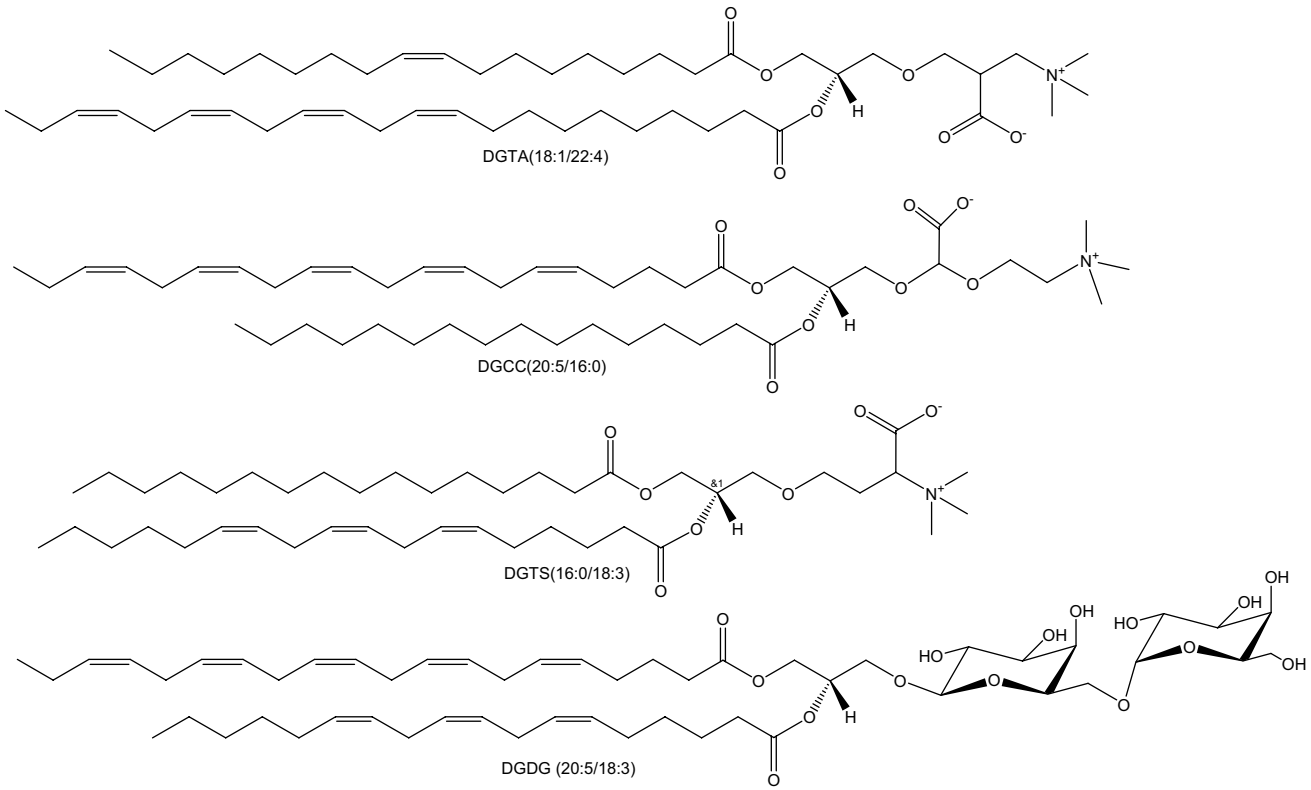


**Fig. 5** Betaine lipids characteristic of algae: diacylglycerylcarboxyhydroxymethylcholine (DGCC), diglycosyldiacylglycerol (DGDG), diacylglyceryl hydroxymethyl trimethylalanine (DGTA), and diacylglyceryltrimethylhomoserine (DGTS). Betaine lipids (DGTS, DGTA, DGCC) are zwitterionic non-phosphorus glycerolipids that structurally resemble phosphatidylcholine in their charge properties and are abundant in algae, particularly under phosphate-limiting conditions where they replace phospholipids to conserve cellular phosphorus. DGDG is a glycolipid characteristic of photosynthetic membranes, where it plays a structural role in the thylakoid membrane. All four lipid classes are widely used as chemotaxonomic markers in algal lipidomics. DGCC: diacylglycerylcarboxyhydroxymethylcholine; DGDG: diglycosyldiacylglycerol; DGTA: diacylglyceryl hydroxymethyl trimethylalanine; DGTS: diacylglyceryltrimethylhomoserine

The review by Kehelpannala et al. (2021) also presents lipidomic data of algae in tabular form, together with lipidomic profiles of various plant species.

## Microalgae—experimental studies

The biotechnologically important unicellular green alga *Haematococcus pluvialis*, cultivated under different light spectra, was subjected to qualitative and quantitative lipidomic analysis using LC–MS (Zhao et al. 2022). The results showed that exposure to red or white light increased cell size, pigment accumulation, starch and lipid content, and overall biomass production.

Analysis of the mesophilic alga *Chlamydomonas reinhardtii* (Yang et al. 2015) identified several polar lipids and their molecular species using $ESI^+$ and $ESI^-$, including 16:0/18:4-DGTS, 16:0/18:3-SQDG, and 16:1/18:3-PG.

In green algae of the genus *Coccomyxa* cultivated in media containing 10 g $L^{-1}$ arsenic, LC-ICP-MS and NAR-PLC-MS with $ESI^+$ and $ESI^-$ were used to identify, among others, 39 molecular species of arsenic-containing TAGs, 15 arsenic-containing PCs, 8 arsenic-containing PEs, 6 arsenic-containing PIs, and 2 arsenic-containing PGs (Fig. 6) (Řezanka et al. 2019a).

The polar lipidome comprising 16 classes of polar lipids together with pigment profiles (cis-neoxanthin, violaxanthin, lutein, and β,β-carotene) of the giant unicellular green alga *Acetabularia acetabulum* was investigated using HILIC-HRMS/MS (Rey et al. 2023). More than 190 molecular species were identified, including common polar lipids such as MGDG, MGMG, DGDG, DGTS, MGTS, DGTA, PC, LPC, PE, HexCer, SQDG, PG, PS, PI, and PA.

Lu et al. (2012, 2013) investigated lipid biomarkers (DGTS, MGDG, DGDG, and SQDG) in a green algal strain isolated from snow, i.e., thriving in highly dilute meltwater (claimed to be *Chlamydomonas nivalis*), using ESI in both positive and negative ion modes. They identified an unusually high abundance of 16:4 fatty acids and characterized lipid profiles of algae grown under different conditions using multivariate statistical analysis.

Geographical variants of the snow alga *Chloromonas pichinchae* were analyzed using silver-ion LC–MS/APCI

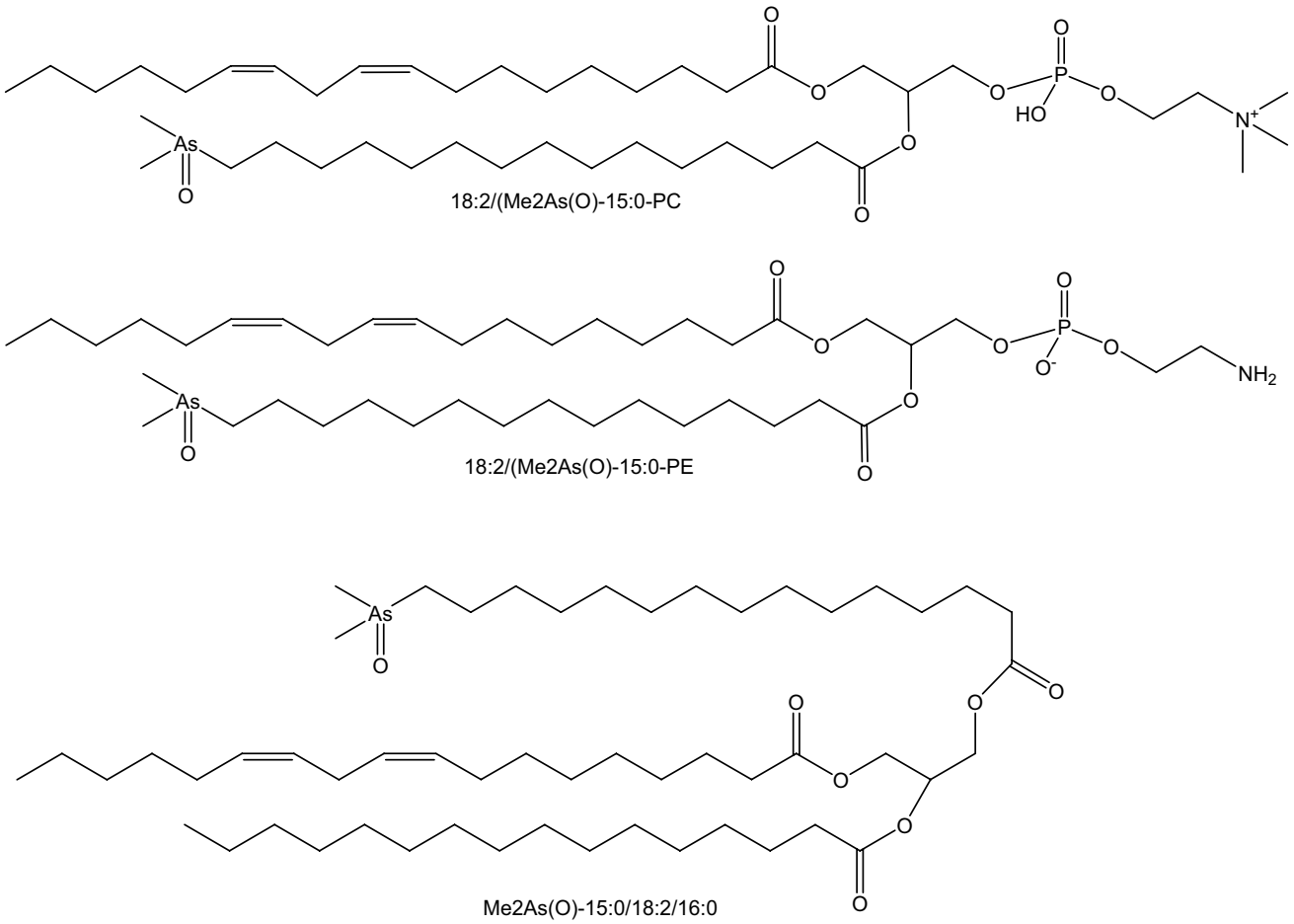


**Fig. 6** Representative arsenolipid structures identified in the green alga *Coccomyxa* sp. Arsenolipids are a chemically diverse group of organoarsenic compounds in which arsenic replaces phosphorus or is incorporated into the acyl chain of conventional lipid classes. They have been identified in algae cultivated under arsenic-rich conditions and include arsenic-containing triacylglycerols (TAGs), phosphatidylcholines (PCs), phosphatidylethanolamines (PEs), phosphatidylinositols (PIs), and phosphatidylglycerols (PGs). The biological function of arsenolipids remains incompletely understood, but they are thought to arise from arsenic detoxification pathways. Their structural characterization requires specialized hyphenated techniques combining liquid chromatography with inductively coupled plasma MS (ICP-MS) and high-resolution ESI–MS/MS. PC: phosphatidylcholine; PE: phosphatidylethanolamine; PG: phosphatidylglycerol; PI: phosphatidylinositol; TAG: triacylglycerol.

and NARPLC-MS/APCI (Řezanka et al. 2014), revealing unusual molecular species such as 16:4/16:4/18:4-TAG, 16:3/16:3/18:4-TAG, and 18:4/18:4-SQDG (Fig. 7).

Using shotgun lipidomics, 303 lipid species were identified in field samples of snow-algal blooms collected from 14 sites across a broad altitudinal gradient in the mountains of Central Europe (Nedbalová et al. 2025). Red, orange, and green snow-algal blooms are formed by vegetative cells or cysts of species belonging to the genera *Sanguina*, *Chloromonas*, and *Chlainomonas* (Chlamydomonadales, Chlorophyta). The higher degree of phospholipid unsaturation observed in algae responsible for red blooms suggests enhanced membrane adaptation to low temperatures compared with cells forming green and orange blooms.

Two geographical variants of *Nannochloropsis oceanica*, which are morphologically and taxonomically indistinguishable based on 18S rRNA, exhibited markedly different and taxonomically relevant lipid profiles when analyzed using UHPLC-MS/Q-TOF (Li et al. 2015). Lipid biomarkers included 20:4/20:5-DGTS, 20:5/14:0-MGDG, 20:5/16:1-DGDG, and 16:1/20:5/20:5-TAG.

The dependence of lipid profiles on cultivation conditions in the red alga *Galdieria sulphuraria* grown at low pH was determined using LC–MS (Vítová et al. 2016). Cultivation was carried out at pH 1–4, and 14 lipid classes comprising dozens of molecular species, including regioisomers, were identified. Growth at low pH promoted the biosynthesis of betaine lipids and altered regioisomer ratios.

For the analysis of highly glycosylated glycosylinositol-phosphorylceramides (GIPCs) from *G. sulphuraria*, a shotgun precursor-ion scan (PIS) at *m/z* 373.0540, corresponding to the [$C_3PO_3$-$C_1$-$CO_2$] ion, was performed (Vítová et al.

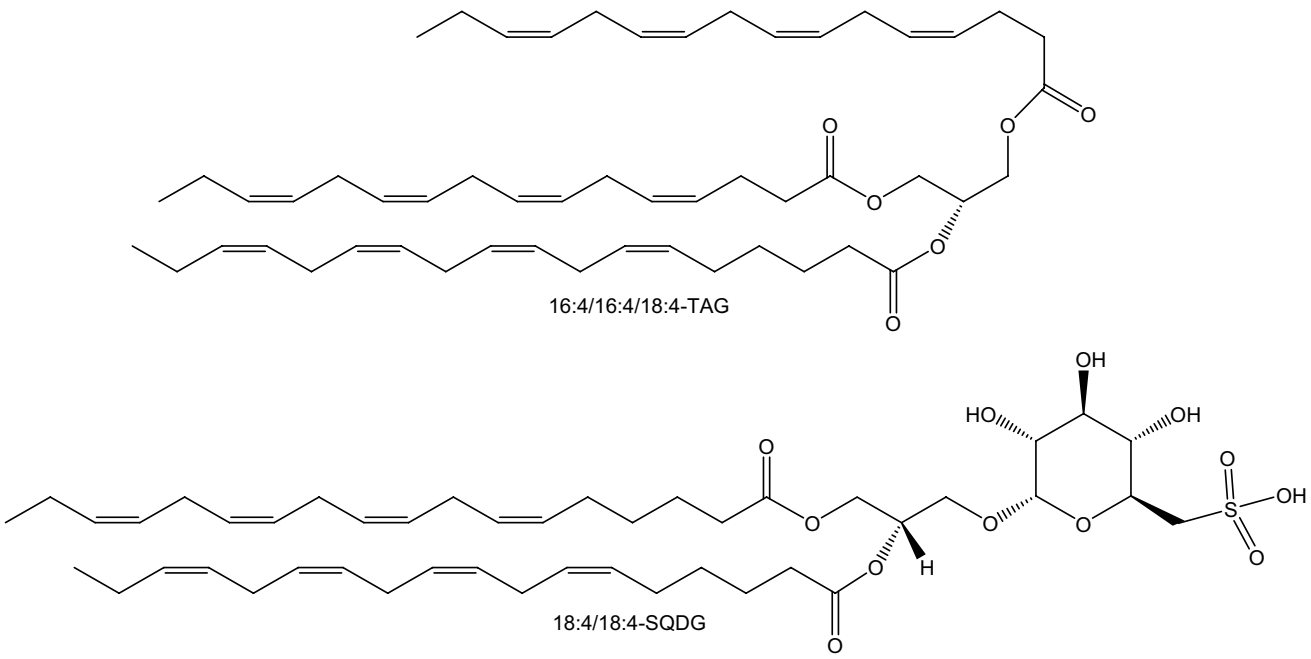


**Fig. 7** Highly polyunsaturated lipid molecular species from a *Chloromonas* snow alga. Snow algae are extremophilic microorganisms adapted to growth at near-freezing temperatures and high UV irradiance. To maintain membrane fluidity under these conditions, they accumulate exceptionally high levels of polyunsaturated fatty acids (PUFAs), including the unusual 16:4 fatty acid rarely found in other organisms. Shown are representative molecular species characteristic of this organism: 16:4/16:4/18:4-TAG, 16:3/16:3/18:4-TAG, and 18:4/18:4-SQDG. The high degree of unsaturation in these lipids lowers the membrane phase transition temperature, providing structural flexibility at low temperatures. SQDG: sulfoquinovosyldiacylglycerol; TAG: triacylglycerol

2022). The GIPC content was found to vary depending on the specific phase of the cell cycle.

Danielewicz et al. (2011) investigated the potential of lipidomic analysis of oleaginous halophilic microalgae such as *Phaeodactylum tricornutum*, *Nannochloropsis salina*, *Nannochloropsis oculata*, and *Tetraselmis suecica*. Using MALDI and ESI-TOF, dozens of TAGs were detected, including 20:5/20:5/20:4-TAG and 16:1/16:3/20:5-TAG. This approach proved highly effective for the rapid screening of algae for biofuel production.

*N. salina* was further analyzed using various ionization techniques (ESI, APCI, APPI, and MALDI), revealing differences in the representation of individual lipid classes (Lee et al. 2013). The study emphasized the importance of internal standards for accurate quantification, although not all required standards are commercially available.

MacDougall et al. (2011) used UHPLC-MS to identify and quantify TAGs in six common algal genera (*Botryococcus*, *Nannochloropsis*, *Neochloris*, *Phaeodactylum*, *Porphyridium*, and *Scenedesmus*). TAGs with extraordinarily long acyl chains were detected, such as 28:1/28:2/18:1-TAG and 28:2/28:2/18:1-TAG-the most extended chains known in nature. *Scenedesmus obliquus* additionally contained polyunsaturated TAGs such as 20:5/18:3/16:3-TAG. Although the study is several years old, it highlights the potential of lipidomic analysis to expand our understanding of lipid diversity and algal metabolism.

Shotgun lipidomics was used to identify very-long-chain fatty acids (VLCFAs) and very-long-chain polyunsaturated fatty acids (VLCPUFAs) in the microalgae *Desmodesmus quadricauda* and *Tetraedron minimum* (Řezanka et al. 2019b). TAGs and PCs, identified by monitoring selected ions corresponding to the two most important carboxylate ions ($R_1COO^-$ and $R_2COO^-$), contained fatty acids such as 24:0, 24:1ω9, 24:6ω3, 26:0, 26:1ω9, 28:0, 28:1ω9, 28:2ω6, and 28:8ω3.

## Macroalgae and related studies

In addition to microalgae, many lipidomic studies focus on macroalgae, which are beyond the scope of this chapter. Nevertheless, several examples are worth mentioning. A study investigating the effect of temperature changes on the lipidome of the red alga *Pyropia haitanensis* showed that this alga contains 39 lipids that may serve as lipid biomarkers (Chen et al. 2016).

Lipidomic analysis of the brown alga *Lobophora* sp. was performed using HPLC-HRMS (Pham et al. 2020), leading to the identification of dozens of molecular species of PG, PI, PC, MGDG, DGDG, SQDG, and DGTA, including PUFAs such as 20:4ω6, 20:5ω3, and 22:6ω3.

The brown macroalga *Fucus vesiculosus* was analyzed using HILIC-HRMS/MS, resulting in the identification of more than 180 molecular species (da Costa et al. 2019). Statistical analyses, including PCA, multivariate, and cluster analysis, revealed significant seasonal differences (winter versus spring) in the composition of PUFA-containing glycolipids and phospholipids such as those containing 18:3, 18:4, 20:4, and 20:5 fatty acids.

Another brown alga, *Undaria pinnatifida*, was analyzed using HILIC and RP-HPLC–MS with ESI (Coniglio et al. 2021). More than 200 molecular species of phospholipids and glycolipids (e.g., SQDG, SQMG, DGDG, DGMG, PG, LPG, PI, PA, PE, PC, and LPC) were identified, containing even-chain PUFAs as well as odd-chain fatty acids (15:0, 17:0, 19:0, and 19:1).

The effects of temperature and light intensity on the polar lipidome of endophytic brown algae *Streblonema corymbiferum* and *Streblonema* sp. were analyzed using RP–HPLC–MS/MS (Chadova et al. 2022). More than 460 molecular species of polar lipids were identified, including MGDG, DGDG, SQDG, PG, PE, PC, and DGTS. Both light and temperature significantly affected lipid class distribution and fatty acid composition.

The lipidome atlas implemented in MS-DIAL 4 was used for comprehensive data analysis across various organisms, including algae (Tsugawa et al. 2020). The authors established MS fragmentation patterns for more than 100 lipid subclasses, incorporating tandem MS with ion-mobility spectrometry. Using MS-DIAL 4, more than 8,000 lipids were annotated and semi-quantified with an estimated false discovery rate of 1–2%.

Finally, the effect of diet on PUFA content in PC and PE of eggs laid by hens fed a combination of flaxseed oil and marine algal biomass was investigated (Neijat et al. 2020). Tandem MS was used, specifically PIS at *m/z* 184 for PC and a neutral-loss scan at *m/z* 141 for PE.

## Viral lipids

Although viruses are not cellular organisms, they are widely considered microbial entities and occupy a central position in microbial ecology, evolution, and pathogenesis. A defining feature of enveloped viruses is the presence of a bilayer lipid membrane, the viral envelope, which is acquired from host cell membranes during the growth process. Lipids constitute approximately 20–35% of the total dry weight of most enveloped viruses, making the lipid component quantitatively significant and functionally indispensable (Ivanova et al. 2015; Lorizate and Kräusslich 2011).

Viral envelopes are not passive structural elements; they play essential roles throughout the viral life cycle, including cell attachment and receptor binding, membrane fusion during entry, assembly, and budding of progeny virions, and egress from the host cell (Lorizate and Kräusslich 2011). The lipid composition of the envelope directly influences the curvature and fluidity of the viral membrane, the lateral organization of viral glycoproteins, and the fusogenic capacity required for cell entry. Consequently, the lipidome of the viral envelope is a key determinant of infectivity and host tropism.

Unlike cellular microorganisms, enveloped viruses do not possess the biosynthetic machinery to produce their own lipids de novo. Therefore, almost all lipids incorporated into the viral envelope are derived from host cell membranes. However, the lipid composition of the viral envelope is not simply a random reflection of the host membrane; rather, viruses exploit specific intracellular membrane compartments and selectively enrich different lipid species during assembly and growth. In particular, viral envelopes are consistently enriched in specific cholesterol, sphingomyelin, and phosphatidylserine species relative to the bulk plasma membrane, a composition reminiscent of lipid raft microdomains (Lorizate and Kräusslich 2011; Saud et al. 2022). This selective lipid sorting is driven both by the intrinsic physicochemical properties of viral structural proteins and by the active exploitation of host lipid trafficking pathways.

Lipidomic studies of purified viral particles have revealed that the envelope lipidomes of different viruses, despite their dependence on host lipids, display characteristic and reproducible compositions. Mass spectrometry-based lipidomics has been applied to characterize the lipidomes of several enveloped viruses, including human immunodeficiency virus (HIV), influenza A virus, herpes simplex virus, severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) and various bacteriophages (Lorizate et al. 2013; Ivanova et al. 2015; Abdel-Megied et al. 2023; Saud et al. 2022). These studies have demonstrated that viral envelopes are markedly enriched in saturated and monounsaturated phospholipids relative to host membranes and that specific lipid species play non-redundant roles in supporting viral glycoprotein function and membrane curvature.

Beyond structural roles, viral manipulation of host lipid metabolism has emerged as an important aspect of viral pathogenesis. Many viruses actively reprogram host lipid biosynthesis, including fatty acid synthesis, cholesterol metabolism, and phosphoinositide signaling, to create membrane environments conducive to replication complex formation, organelle remodeling, and virion production (Heaton and Randall 2011). In this regard, the study of viral lipids is not limited to the characterization of envelope composition, but it extends to the broader perturbation of the host cell lipidome during infection. Therefore, the integration of viral lipidomics within the broader framework of

comparative microbial lipidomics provides a more complete picture of how lipid metabolism is exploited and remodeled across the entire spectrum of microbial life.

## Conclusion – perspectives of microbial lipidomics

This review has documented the remarkable structural diversity of lipids across the major microbial groups – from the unique ether-linked tetraether lipids of archaea adapted to extreme environments, to the complex betaine lipid and arsenolipid repertoires of algae, to the pathogen-specific lipid A modifications of Gram-negative bacteria. Across this diversity, a unifying theme emerges: Lipid composition is not static but is continuously remodeled in response to environmental challenges, and mass spectrometry-based lipidomics has become the essential tool for documenting these adaptations at molecular resolution.

Looking ahead, several developments will reshape the field. Spatial lipidomics and single-cell MS approaches now promise to resolve lipid distributions within microbial communities and individual cells, moving beyond bulk population averages. Spectral annotation is beginning to address the persistent bottleneck of unknown lipid identification. Integration of lipidomics with transcriptomics and metabolomics will allow lipid structural data with regulatory and biosynthetic mechanisms.

Significant gaps remain. Lipidomic data for many environmentally and biotechnologically important microbial groups—including most anaerobic bacteria, deep-sea archaea, and complex soil microbial communities — remain sparse. Viral lipidomics is still in its infancy. The functional significance of most of the identified lipid molecular species remains unknown. Bridging the descriptive power of comparative lipidomics with mechanistic and functional understanding represents the central challenge and opportunity for the field in the next decade.

**Author contributions** L.N.: writing, review and editing, illustrating, and searching. A.P.: writing, review, editing, searching, and figure preparation. B.Š: searching and figure preparation. M.K.: review and editing. T.Ř.: idea, conceptualization, writing, review, editing, revision, and supervising the manuscript. All the authors have reviewed and approved the final version of the manuscript.

**Funding** This work was supported by the Czech Science Foundation project no. GA24-10019S, by the Institutional Research Concept RVO 61388971 (Institute of Microbiology, Prague, Czech Republic), and the Ministry of Education, Youth and Sports of the Czech Republic grant Microorganisms in Ecological Remediation—Bacteria as Cell Factories for Controlled Bioremediation of Ecosystems (CZ.02.01.01/00/23_020/0008502).

**Data availability** Data sharing does not apply to this article as no new data were created or analyzed in this study. The authors confirm that the data supporting the findings of this study are available within the article.

**Declarations** Ethical approval Not applicable.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Conflict of interest** The authors declare no competing interests.



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