



In situ production of branched glycerol dialkyl glycerol tetraethers in anoxic marine water columns



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ABSTRACT

Glycerol dialkyl glycerol tetraether (GDGT) compositions of suspended particulate matter in the water columns of two anoxic marine settings, the Black Sea and Cariaco Basin, were analyzed to better define the sources of GDGTs in marine environments. In deep anoxic waters the enhanced abundance of the conventional branched GDGTs (B-GDGTs) and recently introduced overly- and sparsely branched GDGTs (OB- and SB-GDGTs, respectively) indicated their in situ production by presently unidentified planktonic microorganisms favoring anoxic environment. The elevated concentrations of these branched GDGTs in anoxic waters were accompanied by an increase in their degree of methylation. Such a change in lipid composition may reflect either a microbial community shift or a physiological response of the source organism(s) to redox conditions, but nonetheless, confirms the in situ production of branched GDGTs in anoxic marine settings. In contrast to the B-GDGTs, which have originally been assumed to be of terrestrial origin, OB- and SB-GDGTs in marine sediments are more likely of anoxic marine origin. This notion is supported by a shelf-to-basin transect of surface sediments in the Black Sea, in which OB- and SB-GDGTs were restricted to distal sediments in the central anoxic basin. Even though the OB-, B- and SB-GDGTs are presumed to have related molecular structures, B-GDGTs were the only group that contained cyclopentane rings. The distribution of cycloalkylated vs. non-cycloalkylated B-GDGTs in the water columns of both the Black Sea and Cariaco Basin and surface sediments of the Black Sea suggests a primarily terrestrial origin for the cycloalkylated B-GDGTs but a mixed contribution from both terrestrial and marine sources for non-cycloalkylated B-GDGTs.

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1. Introduction

Glycerol dialkyl glycerol tetraethers (GDGTs) are widely distributed biomarkers in marine and terrestrial settings. There are generally two distinct groups of GDGTs, isoprenoidal (isoGDGTs; see Fig. 1 for molecular structures) and non-isoprenoidal, branched GDGTs, which represent diverse molecular structures and presumably have generally different biological sources. IsoGDGTs were first described as key membrane lipids of the Archaea (Langworthy, 1977; Koga and Morii, 2005, 2007). The presence of isoGDGTs, in particular of crenarchaeol, in marine surface sediments is mainly attributed to planktonic Thaumarchaeota that are now recognized as major players in the marine nitrogen cycle (e.g., Wakeham et al., 2003; Wuchter et al., 2005; Huguet et al., 2006a; Berg et al., 2010; Pitcher et al., 2011; Pearson and Ingalls, 2013; Hernández-Sánchez et al., 2014). However, other planktonic archaea, for example those inhabiting deep waters in oxygen minimum zones and anoxic basins and involved in nitrogen cycling,

methane cycling, or not yet identified processes, also biosynthesize GDGTs and are likely to contribute to the GDGT inventory in marine sediments (e.g. Huguet et al., 2007; Wakeham et al., 2007, 2009; Lam and Kuypers, 2011; Lengger et al., 2012; Schouten et al., 2012; Hernández-Sánchez et al., 2014; Lincoln et al., 2014; Xie et al., 2014).

Non-isoprenoidal branched GDGTs containing 13,16-dimethyl or 5,13,16-trimethyl octacosanyl moieties (B-GDGTs) have been widely identified in peats, coastal marine and lake sediments (Sinninghe Damsté et al., 2000; Schouten et al., 2000; Hopmans et al., 2004; Weijers et al., 2006a; Peterse et al., 2009; Tierney and Russell, 2009). The 1,2-di-O-alkyl-sn-glycerol configuration of B-GDGTs differs from the 2,3-di-O-alkyl-sn-glycerol configuration of isoprenoidal GDGTs that is considered a unique archaeal feature (Koga and Morii, 2005, 2007) and is interpreted as evidence for a bacterial rather than an archaeal origin for B-GDGTs (Sinninghe Damsté et al., 2000; Weijers et al., 2006b). A recent study showed the presence of one branched GDGT with two 13,16-dimethyl octacosanyl moieties and related fatty acid derivatives in hydrolyzed cell material of certain acidobacterial species (Sinninghe Damsté et al., 2011). However, B-GDGTs in natural settings usually consist of a complex series of analogues with four to six methyl groups and up to two cyclopentane rings (Weijers et al., 2006b, 2007). Additionally, B-GDGTs with 6,13,16-trimethyloctacosanyl

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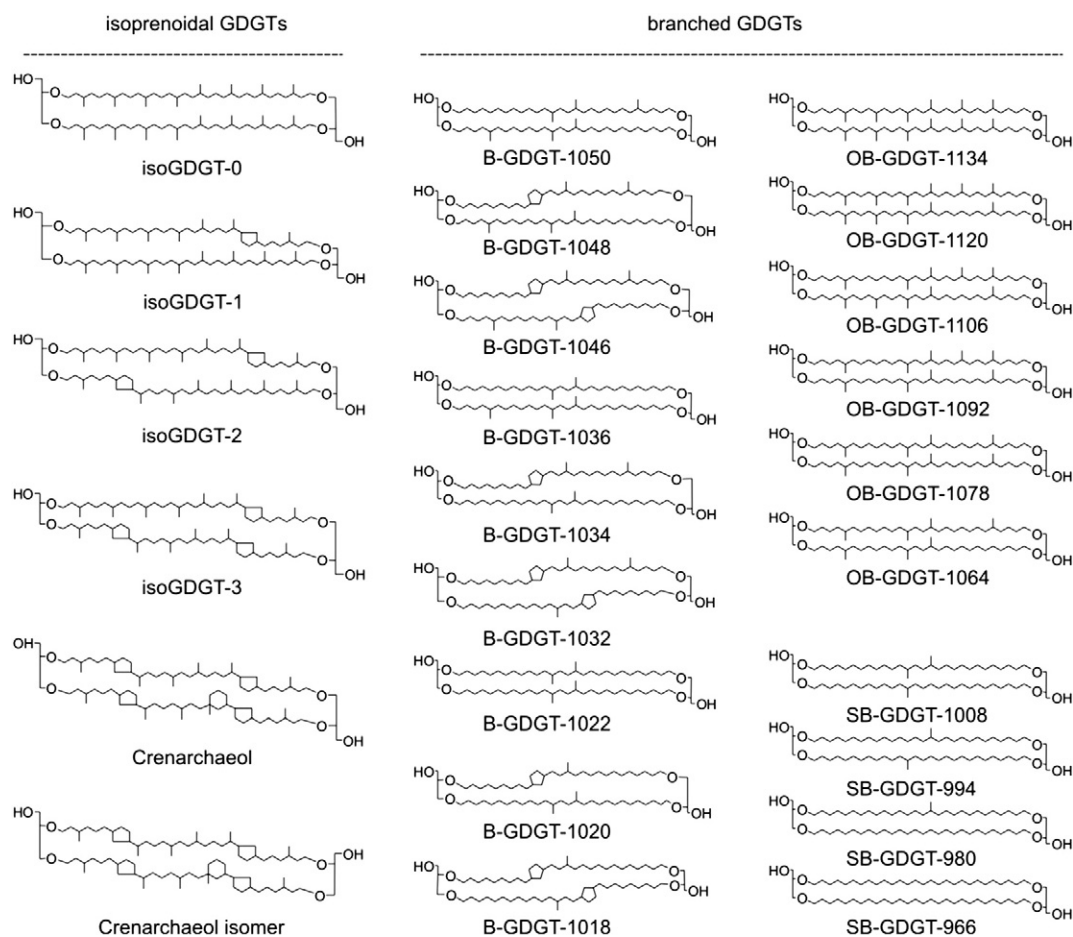


Fig. 1. Molecular structures of studied compounds in this work.

moieties were recently identified and have probably escaped prior identification due to their coelution with the 5,13,16-trimethyl derivatives using established HPLC protocols (De Jonge et al., 2013).

The distribution of B-GDGTs in marine sediments shares many features with that in soils. The abundance of B-GDGTs relative to that of crenarchaeol, a predominantly marine-derived archaeal lipid, has therefore been proposed as a gauge for estimating the relative input of terrestrial organic matter (Hopmans et al., 2004). However, several studies have recently reported that the distinct composition of B-GDGTs, such as their degree of methylation and cyclization, in lake water and sediments implies *in situ* production in addition to inputs from surrounding soils (e.g. Sinninghe Damsté et al., 2009, 2012; Tierney and Russell, 2009; Zink et al., 2010; Sun et al., 2011; Buckles et al., 2014). A few studies have suggested both *in situ* water column and sediment contributions to B-GDGTs in marine sediments, analogous to lacustrine settings (e.g. Peterse et al., 2009; Zhu et al., 2011; Zell et al., 2014; Weijers et al., 2014). Studies focused on marine and continental hydrothermal sites have also reported production of B-GDGTs by potential thermophilic microbes living in the vent systems (Hu et al., 2012; Lincoln et al., 2013; Zhang et al., 2013). Although eolian transport (Fietz et al., 2013; Weijers et al., 2014) into the ocean and fluvial input in coastal areas have been considered to be the most common sources, marine production probably contributes to the ubiquitous occurrence of B-GDGT in diverse marine sediments. If this is true, then the source organisms of B-GDGTs must have been overlooked within the marine microbial community, even though they could play an important role in marine biogeochemical cycles. Investigating the distribution of B-GDGT in marine environments, such as anoxic marine settings in this study, will provide ecological or metabolic information that will inform future studies aimed at constraining their microbial sources.

In addition to the commonly described B-GDGTs (consisting of 13,16-dimethyl or 5,13,16-trimethyl octacosanyl groups) in sediments, the molecular structures of non-isoprenoidal GDGTs have turned out to be more diverse than originally reported. As putative derivatives of B-GDGTs, other recently identified non-isoprenoidal GDGTs with both higher and lower degrees of methylation relative to the initially identified “parent” compounds, the so-called overly branched (OB-GDGTs) and sparsely branched GDGTs (SB-GDGTs), respectively, have been detected in various marine subsurface sediments (Liu et al., 2012) and the oxygen minimum zone of the Eastern Tropical North Pacific Ocean (Xie et al., 2014). During this study, we examined not only the conventional isoprenoidal and branched GDGTs but also targeted the broader group of methyl-branched GDGTs, including OB- and SB-GDGTs, in anoxic marine settings. We analyzed the GDGT composition of the suspended particulate matter (SPM) collected from two marine anoxic basins, the Black Sea and the Cariaco Basin, and of 12 surface sediments along a shelf-to-basin transect across the western region in the Black Sea.

2. Experiments

2.1. Samples and sampling set description

2.1.1. Black Sea

Water column SPM samples were collected in the central Black Sea (43° 06.33'N, 34° 00.6'E; water depth 2200 m) on cruise 178 leg 2 of R/V *Knorr* in 2003. McLane Research WTS-142 *in situ* pumps were used to filter 100–900 L of SPM onto double 142-mm diameter glass fiber filters (GFF) of nominal 0.7- μ m pore size. For investigations of water column archaeal lipids, filtration with GFFs likely under-samples free-living microbial cells of <0.7 μ m that are an important

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