



Differential temperature and pH controls on the abundance and composition of H-GDGTs in terrestrial hot springs



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ABSTRACT

H-shaped glycerol dialkyl glycerol tetraethers (H-GDGTs), also called glycerol monoalkyl glycerol tetraethers (GMGTs), are a unique group of membrane lipids found in several lineages of *Euryarchaeota* and *Crenarchaeota*. Their function in these taxa is, however, not well understood. Here we show their presence in both core lipid and polar lipid fractions from microbial biomass sampled from hot springs in Tibet, China (21.9–80.0 °C; pH 7.0–9.1), Tengchong, China (55.1–93.6 °C; pH 2.5–9.4) and Yellowstone National Park (YNP), USA (16.3–86.7 °C; pH 2.1–9.6) using high performance liquid chromatography–mass spectrometry. The number of cyclopentyl rings ranged from zero (H-GDGT-0) to six (H-GDGT-6) in lipid fractions in Tengchong and YNP and from zero to four (H-GDGT-4) in those from Tibet. While H-GDGT-0 was the most abundant H-GDGT in Tibetan springs, H-GDGT-4 predominated in Tengchong and H-GDGT-6 predominant in YNP, resulting in higher ring indices in the latter springs. While pH appeared to be the most important factor affecting the variation in the relative abundance and average number of cyclopentane rings in H-GDGTs from YNP communities, both temperature and pH appeared to be important controls on the abundance of H-GDGT lipids in Tengchong communities, whereas neither pH nor temperature appeared to influence the abundance or average number of cyclopentane rings in H-GDGTs from Tibetan spring communities. Furthermore, the relative abundance of H-GDGTs to total iGDGTs was greater in hot springs with acidic pH, particularly those from YNP. This finding, coupled with taxonomic profiling of archaeal 16S rRNA genes recovered from the same YNP springs, indicates that H-GDGTs in acidic springs may be synthesized by members of the archaeal order *Thermoplasmatales*, which are adapted to acidic pH.

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1. Introduction

The lipid membrane plays a fundamental role in energy conservation and the maintenance of intercellular homeostasis. Microorganisms synthesize diverse lipid structures with widely varying biophysical properties (Koga and Morii, 2007; Chong et al., 2012) that have facilitated their diversification into environments with wide ranging conditions, including extremes of temperature and

pH (Macalady et al., 2004; Pearson et al., 2008; Boyd et al., 2013). The predominant membrane lipids of Archaea are isoprenoid glycerol dialkyl glycerol tetraethers (iGDGTs), which occur ubiquitously in the natural environment (Schouten et al., 2000, 2013). They consist of two ether-linked C₄₀ polyisoprenoid (i.e. biphytanyl) chains with zero to as many as eight cyclopentyl rings and up to one cyclohexyl ring (i.e. crenarchaeol; Fig. 1; Sinninghe Damsté et al., 2002; Schouten et al., 2000, 2003; Pearson et al., 2004; Zhang et al., 2006; de la Torre et al., 2008). The cyclopentyl rings are thought to increase the packing density of the membrane and thereby enhance its thermal stability (Gliozzi et al., 1983; Gabriel and Chong, 2000) and decrease its permeability to ions (Elferink et al., 1994). Indeed, both pure culture (Macalady et al., 2004; Boyd et al., 2011) and environmental surveys (Pearson et al., 2008; Boyd et al., 2013; Li et al., 2013) indicate that the

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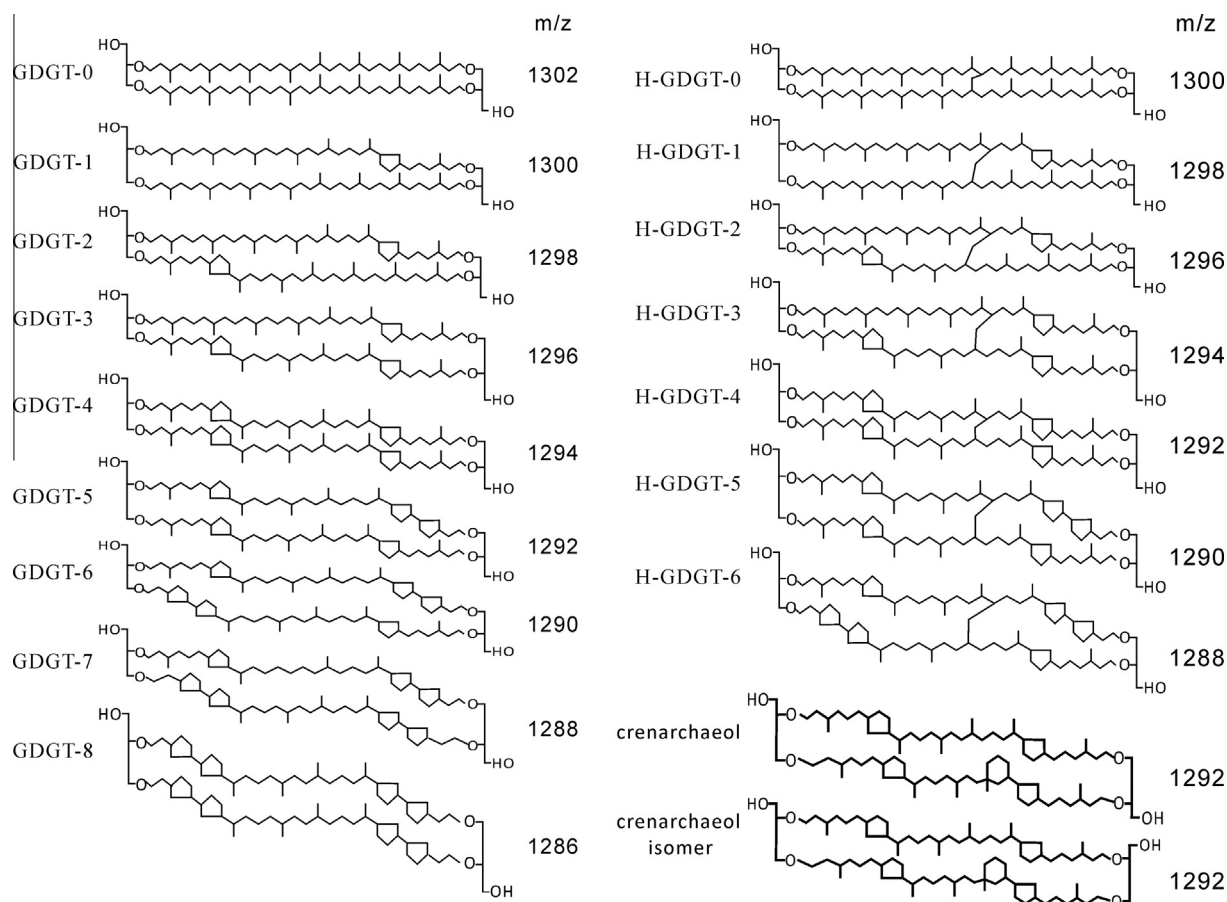


Fig. 1. Structures of isoprenoid GDGTs and H-GDGTs in hot springs.

number of cyclopentyl rings per iGDGT correlates with the temperature and acidity of the system.

H-shaped GDGTs (H-GDGTs), also known as glycerol monoalkyl glycerol tetraethers (GMGTs; Knappy et al., 2011; Schouten et al., 2013), are a unique group of lipids that contain a C–C bond between the two C₄₀ biphytanyl chains (Fig. 1). They were originally found in membrane lipid extracts from the hyperthermophilic methanogen *Methanothermobacter feravidus* (Morii et al., 1998) and have since been found in extracts from other Euryarchaea, including *Aciduliprofundum boonei* and several members of the *Thermococcales* (Sugai et al., 2000, 2004; Schouten et al., 2008b; Knappy et al., 2011). In addition, they have been detected in the crenarchaeon *Ignisphaera aggregans* (Knappy et al., 2011). The number of cyclopentyl rings in H-GDGTs in cultures of *I. aggregans* was similar to that of the iGDGT lipids, a finding interpreted to indicate that these two lipid classes might be synthesized via the same enzymatic pathway or shared components of the same pathway (Schouten et al., 2008a; Knappy et al., 2011). Intriguingly, the maximum number of cyclopentyl rings per H-GDGT in all the cultures is four (Knappy et al., 2011), whereas the maximum per iGDGT in cultures is eight (Schouten et al., 2008a and references cited therein). Furthermore, no H-GDGT counterpart has been reported for crenarchaeol, which has four cyclopentyl rings and one cyclohexyl ring (Sinninghe Damsté et al., 2002). These observations may suggest either a different biosynthetic pathway for H-GDGTs from iGDGTs or that the synthesis of H-GDGTs and iGDGTs is under different regulatory control.

Surveys of environments such as marine hydrothermal systems also reveal a widespread distribution of H-GDGTs. For example,

core H-GDGTs with 0–4 cyclopentyl rings were found in a black smoker field at the Arctic Mid-Ocean Ridge (Jaeschke et al., 2012). Likewise, those with zero cyclopentyl rings (H-GDGT-0) occurred in the core lipid fraction (Lincoln et al., 2013) and the intact polar lipid fraction (Gibson et al., 2013) in different hydrothermal vents at the Mid-Atlantic Ridge. In the latter study, H-GDGTs comprised 5.9–11.5% of total intact polar iGDGTs (Gibson et al., 2013). They have also been reported in low temperature marine or lacustrine environments (Schouten et al., 2008a) where they represent <6% of the total iGDGTs. This suggests that H-GDGTs may be synthesized by mesophilic Archaea. Alternatively, it is possible that the H-GDGTs in low temperature marine or lacustrine environments are allochthonous, originating from hydrothermal vents that are co-located in the sedimentary basin (Lincoln et al., 2013).

Despite the widespread distribution of H-GDGTs in cultivated organisms, as well as those in the natural environment, their function in archaeal physiology is enigmatic. It has been hypothesized that they represent an added feature of archaeal membrane lipids that function to maintain cell membrane fluidity as a protective mechanism against temperature stress or that function to limit pH-induced membrane over-protonation (Knappy et al., 2011). Here, in an effort to elucidate the role of H-GDGTs in archaeal physiology, we report the abundance of and average internal ring distribution in H-GDGTs from biomass from hot springs in Tibet and Tengchong, China and Yellowstone National Park (YNP), USA, for which the iGDGTs have been reported (He et al., 2012; Boyd et al., 2013; Li et al., 2013; Wu et al., 2013). These springs span a gradient in temperature from 16.3 °C to 93.6 °C and pH from 2.1

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