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# UNCOMMON GLYCEROL MONOALKYL GLYCEROL TETRAETHERS (GMGT) SUPPORT MEMBRANE ADAPTION IN THE ARCHAEON *PYROCOCCUS FURIOSUS*

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## Introduction

Microbes preserve membrane functionality and cellular integrity under fluctuating environmental conditions by modulating their membrane lipid composition, a strategy termed homeoviscous adaptation. Archaea harbor membrane lipids distinct from those typically found in Bacteria and Eukarya<sup>1</sup>, and thus implement specific homeoviscous strategies: 1) species generating mixtures of monolayer-forming tetraether and bilayer-forming diether lipids regulate the ratio between the two, whereas 2) species exclusively with monolayer membranes alter the number of cyclopentane-rings from their tetraether lipids<sup>2</sup>. Based on these observations, molecular proxies using archaeal lipids were developed to reconstruct past and present environmental conditions from sedimentary records, e.g., the TEX<sub>86</sub> uses the abundance of ring-containing tetraether lipids to infer past sea surface temperatures<sup>3</sup>. However, although such structural membrane modifications do allow the adaptation of some species to some stresses, the influence of most biotic and abiotic factors on archaeal lipid compositions and the adaptive strategies of archaea with peculiar lipid compositions remain largely uncharted, thus impeding the rationalization and the development of environmental proxies.

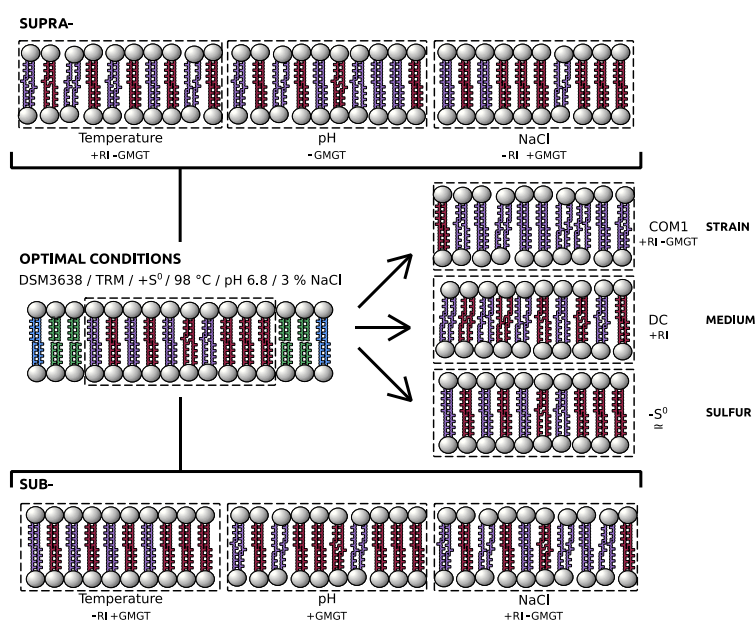
The hyperthermophilic and neutrophilic marine archaeon *Pyrococcus furiosus* is a prime model for membrane homeoviscous adaptive studies, as it is naturally subjected to contrasted environmental conditions and synthesizes remarkable membrane lipids<sup>4,5</sup>. In an effort to better constrain its homeoviscous adaptation strategies, we studied here the influence of temperature, pH, salinity, presence/ absence of elemental sulfur, carbon source, and genetic background on the core lipid composition of this species.

## Results

Most growth parameters tested in the present study affected *P. furiosus*' core lipid composition to some extent: while elemental sulfur did not trigger substantial modifications, the nature of the carbon source and the genetic background exerted the greatest influences. Surprisingly, we observed no significant changes in the relative proportion of bilayer-forming diether lipids (between 20 and 30 % under all conditions) and only limited variations of the number of cyclopentane-rings, which remained too low (maximum value < 0.6 cycle per compound) to really alter membrane properties. *P. furiosus*' membrane adaptation thus appeared to only marginally rely on the two major homeoviscous responses documented so far in Archaea (Figure 1). Instead, *P. furiosus* modulated its proportions of glycerol monoalkyl glycerol tetraethers (GMGT) over glycerol dialkyl glycerol tetraethers (GDGT). For instance, while increasing the pH resulted in a significant decrease of the GMGT/GDGT ratio (from 2.30 at pH 5.5 to 0.43 at pH 6.6), *P. furiosus* responded to increased salinity by substantially increasing this ratio (from 0.83 at 1 % to 3.30 at 4 % (w/v) NaCl; Figure 1).

## Conclusions

We report here an unprecedented strategy for membrane homeoviscous adaptation in the hyperthermophilic and neutrophilic marine archaeon *Pyrococcus furiosus*, i.e., the alteration of the ratio between uncommon monoalkyl and typical dialkyl glycerol tetraether lipids. While previous studies reported no correlation between temperature or pH and the GMGT content of different types of sediments<sup>6</sup>, we highlighted for the first time the adaptive functions of these peculiar lipids towards low temperature, low pH, and high salinity. Besides *P. furiosus*, numerous other species were found to synthesize important proportions of GMGT, which indicates that this original homeoviscous strategy might be common in Archaea. Altogether, our findings pave the way for developing novel, GMGT-based environmental proxies.



**Figure 1** *Pyrococcus furiosus* membrane homeoviscous adaptation to various conditions relies primarily on the alteration of the GMGT(red)/GDGT(purple) ratio and marginally on the modulation of the number of cyclopentane-rings per lipid (Ring Index, RI).

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