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► **To cite this version:**

Maxime Tourte, P. Schaeffer, Vincent Grossi, Philippe Oger. ACYCLIC POLYISOPRENOID HYDROCARBONS: FUNDAMENTAL REGULATORS OF THE ARCHAEAL MEMBRANE?. 30th International Meeting on Organic Geochemistry (IMOG), Sep 2021, Montpellier, France. hal-04895716

HAL Id: hal-04895716

<https://hal.science/hal-04895716v1>

Submitted on 18 Jan 2025

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ACYCLIC POLYISOPRENOID HYDROCARBONS: FUNDAMENTAL REGULATORS OF THE ARCHAEAL MEMBRANE?

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Introduction

Membranes provide dynamic physical boundaries between the inside and the outside of all cells. Membrane regulators have recently gained much attention, as they allow to expand the functional state of the membrane to broader environmental conditions, favour lipid phase separation, and trigger membrane lateral organization and differential functionalization^{1,2}. Sterols found in eukaryotic membranes are currently the best characterized membrane regulators^{2,3}. Although rare exceptions exist, Bacteria are deprived of sterols, but instead use hopanoids as membrane regulators⁴. Although the nature of the archaeal membrane regulators remain speculative due to the absence of both sterols and hopanoids in Archaea, they generate a large diversity of polyterpenes structurally analogous to these two groups of compounds⁵. In particular, acyclic polyisoprenoid hydrocarbons (APH) insert in the midplane of archaeal bilayers, thus increasing membrane impermeability and stability under extreme conditions, and trigger lipid phase separation and microdomain formation^{6,7}. *Thermococcus barophilus*, a hyperthermophilic and piezophilic archaeon, was even shown to modulate the unsaturation level of its APH in response to varying conditions⁸. Building on these observations, APH were proposed as membrane regulator surrogates in Archaea⁵. However, the unresolved APH biosynthetic pathway and distribution within Archaea prevented the generalization of their role as archaeal membrane regulators.

In an effort to further support the importance of APH in the membrane structuration of Archaea, we investigated here the composition of 65 halo-, alkalo-, acido-, or (hyper)thermo-philic strains homogeneously distributed within the archaeal domain, including all the Thermococcales, and conducted an extensive literature survey in all Archaea.

Results

APH with 20, 25, 30, 35, and 40 carbons and unsaturation degrees ranging from full saturation to one unsaturation per isoprene unit were identified in almost all archaea investigated so far, notable exceptions being the acidophilic *Aciduliprofundum boonei* and the alkalophilic *Aeropyrum pernix* (Figure 1). In the particular case of Thermococcales, i.e., a group of hyperthermophilic archaea which *T. barophilus* belongs to, C₃₀ to C₄₀ APH were only detected in 17 out of the 53 strains analysed, and neither APH presence nor composition correlated with either phylogenetic relationships, lipid compositions, optimal growth conditions, or genetic content. The absence of genes exclusive to species synthesizing APH as well as the minute amounts of compounds that are produced (i.e., 1-2 % of the membrane content) suggested that technical issues might have prevented their detection in some, if not all, species investigated.

Conclusions

We describe here the archaeal APH diversity, which includes C₂₀ to C₄₀ isomers, C₃₀ being present in all APH-producing strains, and show that the majority of archaea do synthesize APH, regardless of their phylogenetic position, preferential environmental conditions, and core lipid composition. Such a wide occurrence of APH throughout the archaeal phylogenetic tree and ecological niches indicates that members of all archaeal lineages might be capable of their biosynthesis. These findings further support the potential role of APH as archaeal membrane regulators and pave the way to decipher their adaptive functions and biosynthetic routes in the third domain of life.

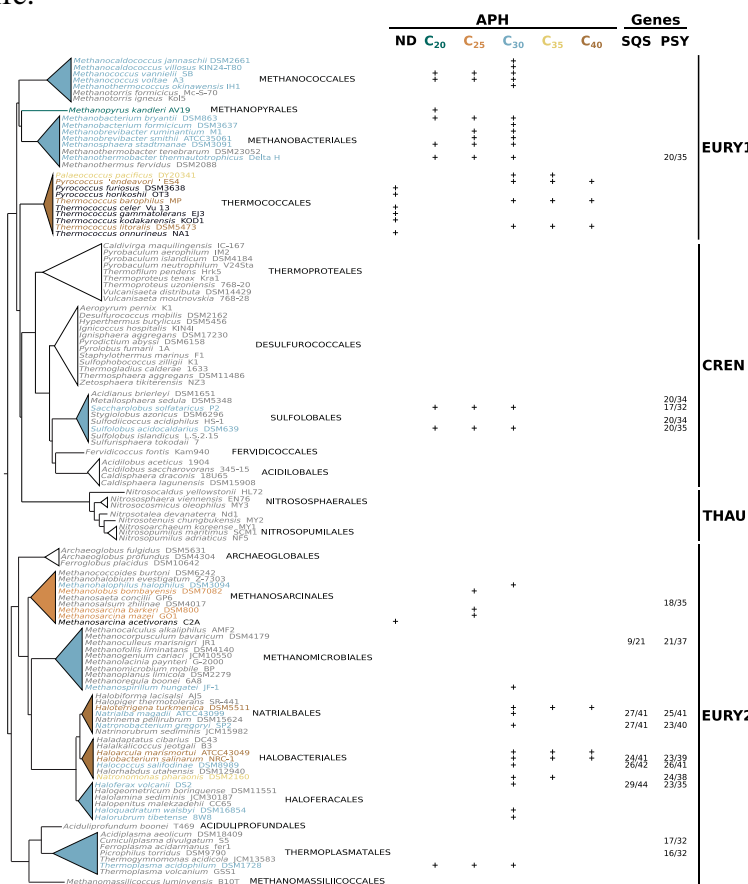


Figure 1 Distribution of acyclic polyisoprenoid hydrocarbons and of eukaryotic and bacterial homologues of genes for their synthesis in Archaea. Species were coloured depending on the longest APH that were detected: green, C₂₀; orange, C₂₅; blue, C₃₀; yellow, C₃₅; brown, C₄₀.

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