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► **To cite this version:**

Vincent Grossi, C Thomas, D Sala, Ingrid Antheaume, D. Ariztegui, et al.. New Insights Into Bacterial Wax Ester Biosynthesis, Natural Occurrence And Adaptive Role In Anaerobic Environments. 29th International Meeting on Organic Geochemistry, Sep 2019, Göteborg, Sweden. hal-02340717

**HAL Id: hal-02340717**

**<https://hal.science/hal-02340717>**

Submitted on 31 Oct 2019

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## NEW INSIGHTS INTO BACTERIAL WAX ESTER BIOSYNTHESIS, NATURAL OCCURRENCE AND ADAPTIVE ROLE IN ANAEROBIC ENVIRONMENTS

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### Introduction

Some bacteria accumulate lipophilic compounds as intracellular inclusions in response to environmental stress or growth under imbalanced conditions. The accumulation of storage lipids is advantageous for cell survival in natural habitats and the capability for their synthesis may provide a strong advantage during evolution. Wax esters (WE) are a major class of storage compounds synthesized by bacteria in which they can have different physiological functions such as energy and carbon storage, deposit for toxic or useless cellular metabolites and resistance towards desiccation (Wältermann and Steinbüchel, 2005).

So far, the potential of WE biosynthesis by prokaryotes has been mostly investigated in aerobic bacteria, and the use of WE in geochemical and environmental studies has been overlooked due to their apparent rapid hydrolysis during early diagenesis. However, some reports have documented a possible formation of WE by facultative (Rontani et al., 1999) or phototrophic (van der Meer et al., 2010) anaerobic bacteria, and WE have been reported in up to 40,000 years old lacustrine sediments (Cranwell, 1986), suggesting their possible formation in anoxic environments and their preservation in the geological record under adequate conditions.

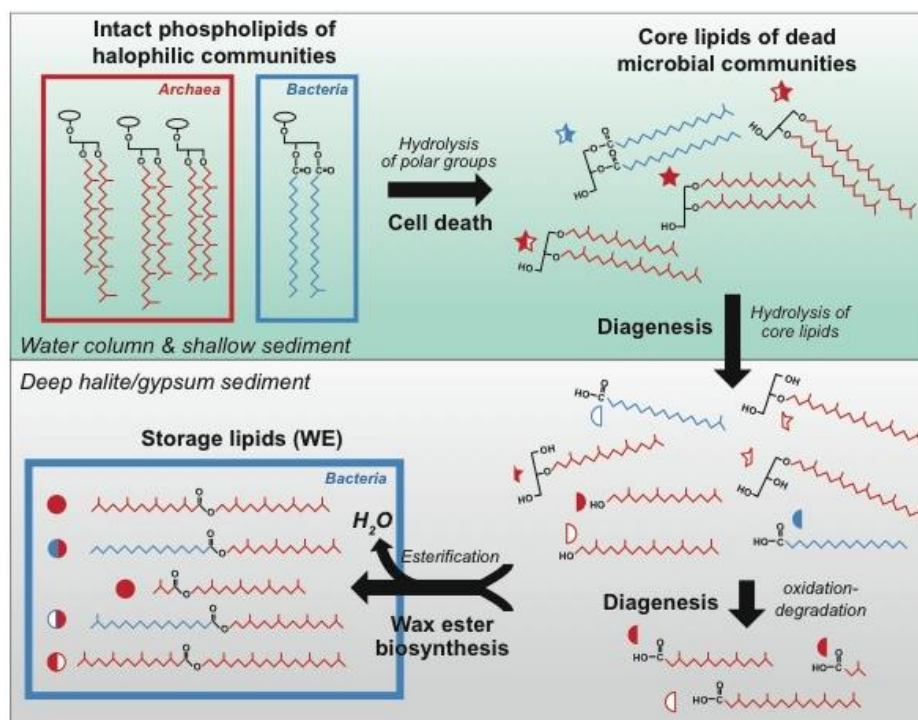
Here, we present a combination of recent data giving new insights into 1) the biosynthesis of WE by strict anaerobic bacteria, 2) the production of specific WE in different extreme anoxic environments and, 3) the potential role of bacterial WE formed by recycling of dead biomass as a strategy to survive in the deep biosphere.

### Results

The study of the anaerobic biodegradation of different types of *n*-alkyl substrates by pure strains of sulfate-reducing bacteria (SRB) grown under laboratory conditions showed the formation, among different metabolites, of series of long-chain WE whose distributions strongly depend on the substrate used for growth (Grossi et al., in prep.). Thiowax esters (TWE) were also observed along with WE during growth on unsaturated hydrocarbons (*n*-alkenes), indicating that, in addition to being used as carbon and energy sources, part of such substrates can be sulfurized (by reaction with biotically-produced sulfides) and serve as building block for TWE biosynthesis. This is the first report of the biosynthesis of WE in strict anaerobic non-phototrophic bacteria and of the bacterial formation of TWE from non-sulfur substrates. Our results further demonstrate that abiotic and biotic sulfurization processes can concomitantly occur during the degradation of organic matter (OM) by SRB, and that sulfurization of OM can lead to the formation of organosulfur compounds that, in return, can potentially fuel microbial communities.

In parallel to laboratory experiments, WE were observed to be specifically produced below the aphotic and euxinic chemocline of a contemporaneous stratified haloalkaline tropical lake (Sala et al., in prep.). Lipid depth profiles combined with phylogenetic analyses of the microbial diversity suggest that other types of non-phototrophic anaerobic bacteria belonging to the Firmicutes and/or Bacteroidetes phyla can also biosynthesize WE, thus expanding this metabolic capacity among anaerobic Bacteria. Another biogeochemical investigation of

unconventional sedimentary ecosystems showed the presence of isoprenoid WE in extreme evaporitic facies of the Dead Sea deep sediments. These WE were mostly derived from the recombination of hydrolyzed moieties of archaeal membrane lipids and were retrieved in gypsum and/or halite sedimentary deposits down to 243 meters below the lake floor (Thomas et al., 2018). Since Archaea do not synthesize WE, these isoprenoid WE attest for the recycling of archaeal cell wall constituents by deep subsurface bacteria, which can thus build up intracellular carbon stocks and gain access to free water in this deprived environment (Fig. 1).



**Figure 1** Schematic pathway for the formation of isoprenoid WE by bacteria recycling membrane lipids of dead biomass in deep Dead Sea sediments (from Thomas et al., 2018).

## Conclusions

Our laboratory and field studies demonstrate that WE can be biosynthesized in various anoxic environments by several families of anaerobic bacteria and, that WE biosynthesis may be specifically important for some bacteria to survive in environments experiencing harsh environmental conditions. Our studies also describe original interactions between abiotic and biotic processes that can occur during OM diagenesis and show that WE can constitute an interesting molecular tool to decipher carbon transformation pathways in the geosphere.

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