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Are Marine Group II Euryarchaeota significant contributors to tetraether lipids in the ocean?

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Lincoln et al. (1) claim that Marine Group II Euryarchaeota (MGII) are significant contributors to glycerol dibiphytanyl glycerol tetraether (GDGT) lipids in the ocean and biosynthesize crenarchaeol, a membrane lipid generally attributed to Thaumarchaeota (MGI). They present two lines of convergent evidence for their far-reaching claim.

The first line of evidence is the presence of GDGTs, including crenarchaeol, in suspended particulate matter (SPM) at 83m, which archaeal community is nearly exclusively composed of MGII (>94% of archaeal reads; Table 1) as determined by pyrosequencing. However, according to the authors' definition, all SPM samples <100 m do not contain sufficient archaeal reads (i.e. <1000; Table S2; Fig. S6) to draw any conclusion. This low abundance of archaeal DNA is also evident from the absence of detectable MGI 16S rRNA gene copies (Fig. 2). It is, however, not surprising that GDGTs were detected in the 83m SPM sample since the lipid tracers used are core lipids. Core lipids do not occur as such in living cells, where they contain polar sugar and phospho head groups (e.g. 2). Thus, by definition core lipid GDGTs are derived from dead material. The second line of evidence is based upon relating the presence of monohexose GDGTs in two SPM samples (although not the crucial 83 m sample) with archaeal diversity data. Although this approach uses intact polar lipids, it has been shown that monohexose GDGTs are also poor tracers of living archaeal cells (3) since they have a turnover time in the order of thousands of years (4), *de facto* also representing dead material.

This dominance of dead lipid material readily explains the absence of any correlation of total MGI+MGII DNA abundance with total GDGT abundance ($r^2 = 0.06$ and 0.04 for 0.3-3 µm and 3-57 µm fractions, respectively). Furthermore, it explains the much higher abundance of GDGTs in the large particle fraction (16-490 versus 1-20 pg L⁻¹), contrasting its lower total archaeal abundance (0.3-1.8 x10⁵ versus 1-7 x10⁵ cells L⁻¹; Fig. 2). We conclude that both lines of evidence are based on a comparison of minute amounts of archaeal DNA (often below detection limit) with unsuitable lipid tracers.

The dominance of dead material and low abundance of archaeal cells make it impossible to infer the lipid composition of uncultivated MGII from these samples, let alone to extrapolate this to the global ocean. In contrast, other studies, using abundant archaeal DNA and more suitable phospholipid GDGTs, do show a good match between MGI DNA abundance and crenarchaeol concentration and not with MGII (3,5). Nevertheless, members of the Marine Group III Euryarchaeota have been suggested to contribute to GDGTs 0-3 (3), so members of the MGII may potentially contribute to this pool of GDGTs as well. However, based on the data and arguments of Lincoln et al. (1) this is impossible to infer. The jury is, therefore, still out.

References

- Lincoln S.A., Wai B., Eppley J.M., Church M.J., Summons R.E., DeLong E.F. (2014) Planktonic Euryarchaeota are a significant source of archaeal tetraether lipids in the ocean. *Proc. Nat. Acad. Sci. USA111*, 9858-9863.
- Pitcher A., Hopmans E. C., Mosier A. C., Park S.-J., Rhee S.-K., Francis C. A., Schouten S., and Sinninghe Damsté J. S. (2011) Core and intact polar glycerol dibiphytanyl glycerol tetraether lipids of ammonia-oxidizing Archaea enriched from marine and estuarine sediments. *Appl. Environ. Microbiol.* 77, 3468-3477.
- Schouten S., Pitcher A., Hopmans E. C., Villanueva L., van Bleijswijk J., and Sinninghe Damsté J.
 S. (2012) Intact polar and core glycerol dibiphytanyl glycerol tetraether lipids in the Arabian

Sea oxygen minimum zone: I. Selective preservation and degradation in the water column and consequences for the TEX₈₆. *Geochim. Cosmochim. Acta* 98, 228-243.

- Xie S., Lipp J. S., Wegener G., Ferdelman T. G., and Hinrichs K.-U. (2013) Turnover of microbial lipids in the deep biosphere and growth of benthic archaeal populations. *Proc. Natl. Acad. Sci.* USA, 110, 6010-6014.
- Pitcher A., Wuchter C., Siedenberg K., Schouten S. and Sinninghe Damsté J.S. (2011) Crenarchaeol tracks winter blooms of planktonic, ammonia-oxidizing Thaumarchaeota in the coastal North Sea. *Limnol. Oceanogr.* 56, 2308–2318.