

The relative high level of HGT found in Thaumarchaeota and GII/III-Euryarchaeota genomes supports the idea that shared HGT events can be used as support for the monophyly of prokaryotic lineages (Abby et al. 2012) and suggests that HGT from bacteria has been an important determinant in the evolution of those two archaeal lineages. In recent comparisons of COGs in archaeal genomes, Wolf et al. (2012) inferred a gain of 494 genes at the base of the Thaumarchaeota while asserting that most gene gain should be derived from HGT. Our direct observations confirm that prediction to a large extent, since we observed 290 cases of early HGTs to the ancestor of marine and soil Thaumarchaeota. Although slightly inferior, gene gain can also occur from gene duplication and de novo formation. In addition, some of the late HT-genes that we observe may be early HT-genes followed by losses in some specific lineages. Such losses would be indeed consistent with the expected streamlined nature of deep-sea archaea living in oligotrophic conditions. They might also explain the ongoing nature of HGT in these archaea, in eventual agreement with the hypothesis that HGT is a need in lineages under genome size constraint (Isambert and Stein 2009).

HGT in deep-sea Thaumarchaeota and GII/III-Euryarchaeota is not only extensive and ongoing but also directional, with most HT-genes having been imported from bacteria. This confirms a trend already observed in cases of interdomain HGT, which mostly occur from bacteria to archaea and not the opposite (Kanhere and Vingron 2009; Nelson-Sathi et al. 2012). The high level of bacteria-to-archaea HGT might lead to several, nonmutually exclusive, hypothetical explanations. First, because bacteria dominate in terms of both diversity and relative abundance in most environments, including oceans, preferential bacteria-to-archaea HGT might be simply a statistical outcome. Second, archaea might have a higher capacity to incorporate foreign genes, for instance, through facilitated gene import and genome incorporation via known and/or yet-to-be discovered mechanisms and keep them if these are of adaptive value. Third, archaea might experience a lower cost of HGT in terms of fitness, implying an easier fixation of HT-genes. Lower fitness costs would depend on how the genomic environment accommodates foreign DNA (Baltrus 2013) and on the “friendliness” of HT-gene products (Gophna and Ofra 2011). Finally, an additional explanation might be related to the adaptive benefits that the newly acquired genes provide. In this sense, genes related to metabolism and providing new functions should be enriched in HT-genes. Exploring the potential contribution of these different factors should help to understand the underlying mechanisms of genome evolution in archaea.

From a functional point of view, our pangenome results reinforce the idea that deep-sea Thaumarchaeota are ammonia oxidizers able to metabolize urea with a potential for chemolithoautotrophic growth. Deep-sea GII/III-Euryarchaeota seems to be heterotrophic organisms lacking the photoheterotrophic ability of their proteorhodopsin-containing surface

relatives. Many of the genes involved in the metabolic function of these lineages may be genuinely archaeal. Indeed, one striking observation corresponds to the high level of lineage-specific core genes of unknown function, which contrasts to HT-genes and highlights how little is known about the function of lineage-specific core genes in these archaea (fig. 7). Nevertheless, metabolism-related genes are the most abundantly acquired by HGT in Thaumarchaeota and GII/III-Euryarchaeota (fig. 7). In particular, the large proportion of HT-genes related to membrane biogenesis in our thaumarchaeal and GII/III-euryarchaeal pangenomes (supplementary figs. S8–S10, Supplementary Material online) suggests that at least an important fraction of functions related to membrane activity and recognition, which are of uttermost importance in cold, oligotrophic oceans, have been imported from bacteria.

Supplementary Material

Supplementary files S1 and S2, table S1, and figures S1–S10 are available at *Genome Biology and Evolution* online (<http://gbe.oxfordjournals.org/>).

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