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Review

The Elusive Boreal Forest Thaumarchaeota

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Abstract: In recent years, Archaea have, with increasing frequency, been found to colonize both agricultural and forest soils in temperate and boreal regions. The as yet uncultured group I.1c of the Thaumarchaeota has been of special interest. These Archaea are widely distributed in mature vegetated acidic soils, but little has been revealed of their physiological and biological characteristics. The I.1c Thaumarchaeota have been recognized as a microbial group influenced by plant roots and mycorrhizal fungi, but appear to have distinct features from their more common soil dwelling counterparts, such as the *Nitrosotalea* or *Nitrososphaera*. They appear to be highly dependent on soil pH, thriving in undisturbed vegetated soils with a pH of 5 or below. Research indicate that these Archaea require organic carbon and nitrogen sources for growth and that they may live both aerobically and anaerobically. Nevertheless, pure cultures of these microorganisms have not yet been obtained. This review will focus on what is known to date about the uncultured group I.1c Thaumarchaeota formerly known as the "Finnish Forest Soil" (FFS) Archaea.

Keywords: I.1c Thaumarchaeota; mycorrhiza; boreal forest soil; humus; uncultured Archaea; Crenarchaeota

1. Introduction

In 1992, when the first findings on non-extreme Crenarchaeota were reported from coastal waters of the Western Atlantic Ocean [1] and the deep waters of the Pacific Ocean [2], they were thought to be a non-thermophilic lineage of the thermophilic Crenarchaeota. Over the years, more and more of these non-extreme, non-thermophilic crenarchaeotal lineages have been found in different lacustrine [3–5] and soil environments [6–9]. The crenarchaeotal groups that were most frequently detected in soils belonged to the Group I Crenarchaeota (according to the division by DeLong *et al.* [10]). Several specific phylogenetic sub groups were recognized, of which the most common were the I.1a, I.1a associated, I.1b, and I.1c lineages (e.g., [11–13]) (Figure 1). However, after phylogenetic examination of large genome fragments of uncultured I.1b Crenarchaeota [14] and the almost whole genome sequences of the I.1a crenarchaeote *Cenarchaeum symbiosum* [15], it was proposed that the Group I Crenarchaeota indeed defined a novel Phylum of the archaeal domain. This new Phylum was given the name Thaumarchaeota [16]. After this, many more non-thermophilic Group I.1a and I.1b Thaumarchaeota have been isolated in pure cultures and sequenced, such as the Group I.1a *Nitrosopumilus maritimus* [17], *Candidatus Nitrosopumilus salaria* [18], *Candidatus Nitrosopumilus sediminis* [19], and *Candidatus Nitrosopumilus koreensis* [20], the Group I.1a-associated *Nitrosotalea devanaterra* [21], and the Group I.1b *Nitrososphaera viennensis* [22], *Nitrososphaera gargensis* [23], and *Nitrososphaera evergladensis* [24]. The characterization of all these strains supports the division of the non-thermophilic Crenarchaeota into the novel phylum Thaumarchaeota. Nevertheless, Guy and Ettema [25] proposed that the phylum Thaumarchaeota is part of the superphylum TACK, containing, in addition to Thaumarchaeota, the Aigarchaeota, Crenarchaeota, Korarchaeota, and Euryarchaeota.

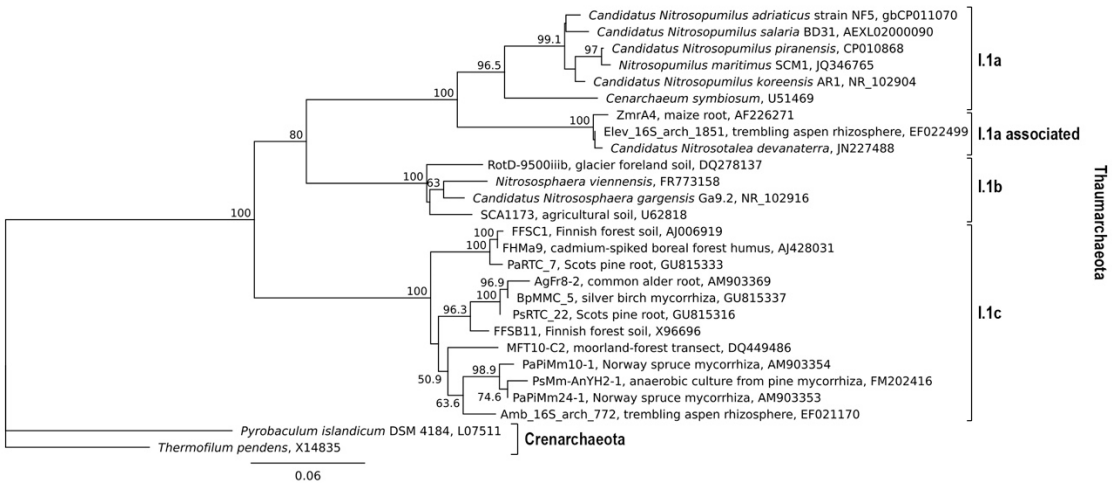

Figure 1. Phylogenetic maximum likelihood tree representing Thaumarchaeota of the groups I.1a, I.1a-associated, I.1b, and I.1c. The taxa presented in italics are pure cultured strains. The sequences were trimmed to similar lengths of 400 nucleotides covering the V1 to V3 variable regions of the 16S rRNA gene. The tree was calculated based on a MAFFT alignment in Geneuous Pro (version 6.1.6, Biomatters Inc., Auckland, New Zeeland) using the Jukes and Cantor substitution model. Bootstrap support values were calculated based on 1000 random repeats and are shown for nodes with over 50% support. The scale bar indicates number of substitutions. The tree is rooted by thermophilic Crenarchaeota.

Despite the obvious success in cultivating, isolating, and genome sequencing novel thaumarchaeotal species, no representative of the Group I.1c has yet been obtained in pure culture, nor have their sequences appeared in metagenomic libraries in sufficient amounts for genomes to be identified. This makes them one of the least studied groups of Archaea thus far. The I.1c group has been found in many environments, but have been considered boreal Archaea due to the initial discovery of this group in acidic (pH 3.5–5) boreal forest soil [9], the so-called Finnish Forest Soil, or FFS, group. Later this group has been detected with increasing frequency and found in many acidic soil (reviewed in [26]) and aquatic environments [27], as well as from deep peat (280 cm) from boreal fens [28], shallow peat from elevated oligotrophic subtropical bogs [29], and even tropical peat swamp forest soils [30], where they have been found to represent up to almost 50% of the archaeal community.

2. Factors Affecting the Distribution of the I.1c Thaumarchaeota

2.1. The Influence of the Season on the Abundance of Thaumarchaeota in Soil

It has been estimated that Archaea constitute up to 6% of the microbial cells in different soil environments [31]. In boreal forest soil, however, archaeal numbers are much lower. First of all, Archaea are rarely detected in end point PCR applications without the use of nested PCR. Based on detection frequency of archaeal 16S rRNA gene fragments in end point PCR from different mycorrhizospheric, rhizospheric, and soil compartments, a cautious estimate was proposed that the mycorrhizal Scots pine roots harbored at least 10^4 archaeal cells g^{-1} (fresh weight, fw) mycorrhiza. Non-mycorrhizal short roots were estimated to have harbored one order of magnitude less Archaea [32]. There were also differences between tree species, as alder roots had at least 10^4 archaeal cells g^{-1}, while Norway spruce roots harbored significantly lower amounts of Archaea compared to what was detected on Scots pine roots. Enrichment cultures of microbial communities in boreal forest tree mycorrhizas, however, point to an archaeal cell number of more than 10^5 per g mycorrhiza [32,33]. The boreal forest humus devoid of mycorrhizospheric root systems was estimated to contain only around 10^2 archaeal cells g^{-1}. These are, however, only estimates.

Fritze *et al.* [34] attempted to determine the archaeal biomass by detection of the Archaea-specific lipid archaeol in pristine coniferous forest humus. However, the detection limit of the assay was 10^8 archaeal cells g^{-1} dry weight (dw) soil, and no archaeol was detected. It has been estimated by phospholipid fatty acid (PFLA) analysis of humus from a Norway spruce stand in Norway that the number of bacterial cells g^{-1} fresh weight humus is between 0.6 and 7.9 $\times$ 10^{10} [35]. This leads to the assumption that the Archaea represent only approximately 0.1% of the microbial communities in boreal forest humus.

Long *et al.* [36] reported an archaeal 16S rRNA gene abundance of 0.18 $\times$ 10^2 to 1.91 $\times$ 10^7 copies g^{-1} dry soil in a Swedish Norway spruce stand constituting around 10% of the total prokaryotic 16S rRNA gene pool in the forest soil. Unfortunately, the archaeal gene sequences were not determined. Nevertheless, archaeal *amo*A gene abundances were measured and the number of *amo*A genes was only about 0.1% of the archaeal 16S rRNA gene abundance. Since the *amo*A genes in soil generally belong to the I.1b Thaumarchaeota, the result by Long *et al.* [36] indicates that most of the Swedish Norway spruce forest soil Archaea were not the typical soil I.1b Thaumarchaeota. The soil used for the study was collected in August, which may influence the number of Archaea present in the soil due to high plant productivity. Kemnitz *et al.* [37] showed that Archaea constituted a considerable part of the prokaryotic community (12%–38%) in a temperate mixed deciduous forest soil in Germany. In this study, the phylogenetic affiliation of the archaeal 16S rRNA gene sequences was determined, and it was shown that the majority (85%) of the detected Archaea belonged to the I.1c cluster. The authors estimated, by quantitative PCR (qPCR), the number of archaeal 16S rRNA genes in the upper layers of the forest soil to be as high as 0.5 to 3.9 $\times$ 10^8 g^{-1} dw soil. The soil was sampled in June and July. Karlsson *et al.* [38] reported around 2 $\times$ 10^6 archaeal 16S rRNA genes g^{-1} dw soil in temperate coniferous forest soil from British Columbia, harvested in late July, during the peak of the growth season. Rasche *et al.* [39] showed an increase in archaeal abundance in alpine coniferous forest soil during the late winter and spring months, at the beginning of the growth season (up to 3 $\times$ 10^7 archaeal 16S rRNA genes g^{-1}), with a dramatic drop in archaeal abundance in summer. Unfortunately, in both the above-mentioned temperate forest studies, the archaeal types were not determined. Nevertheless, Juottonen and co-workers [40] showed that Archaea are also active in boreal fen peat in winter when the peat is frozen and that I.1c Thaumarchaeota are active throughout the year. The archaeal community profile of the peat was investigated using Terminal restriction fragment length polymorphism (T-RFLP) analysis. In this analysis, the authors showed that the Terminal restriction fragment (T-RF) peak representing the I.1c Thaumarchaeota was highest (indicating high abundance) in the sample in February and lowest in August. Unfortunately, the length of the T-RF of the I.1c Thaumarchaeota was identical to that of the Methanosarcina, which were also abundant in the peat. This makes drawing exclusive conclusions about which archaeal group was more abundant at which time point difficult. Nevertheless, the authors identified I.1c Thaumarchaeota from clone libraries produced from the rRNA fractions of samples harvested in February when the peat was frozen. Furthermore, it has been reported that the community richness of the I.1c Thaumarchaeota was higher in tree roots and mycorrhizas grown at 7 °C than at 20 °C [41], and, in accordance with the study by Juottonen *et al.* [40], the community richness of methanogens increased at higher temperature.

2.2. pH

The distribution of the I.1c Thaumarchaeota has been shown to be affected by the soil pH. In a few studies, both group I.1b and I.1c Thaumarchaeota have been reported simultaneously (e.g., [37,42,43]), but I.1c Thaumarchaeota have most frequently been found in acidic soils with pH below 5. This approaches the pH minimum in which I.1b Thaumarchaeota have usually been detected [44–46]. Nevertheless, an extensive study on the distribution of Thaumarchaeota in temperate soils (covering forest, agricultural, moorland and grassland soils) showed that this division is not absolute [43]. However, the most frequently encountered I.1c thaumarchaeotal representatives had higher relative abundances in acidic soils with a pH less than 5, while the most frequently encountered I.1b clusters

were most abundant at pH above 6. Putkinen *et al.* [28] showed a correlation between the abundance of I.1c Thaumarchaeota and decreasing pH in deep boreal peat. pH may be "the" driver, or one of the most important ones, in addition to organic carbon substrates, determining the distribution of the I.1c Thaumarchaeota. Thus, the I.1c cluster is not restricted to only boreal forest soils, but have also been detected in various mature and unmanaged grassland soils, where the soil pH has been maintained below 5 [27,44,46–48] and even in acidic subtropical and tropical peatland soils [29,30].

2.3. Association of Thaumarchaeota with Plants

Thaumarchaeota have been shown to be associated with many different plants, both mycorrhizal and non-mycorrhizal. Simon *et al.* [49,50] demonstrated the presence of I.1b Thaumarchaeota on the roots of tomato plants grown in agricultural soil. Chelius and Triplett [51] detected I.1a Thaumarchaeota on the roots of maize grown in agricultural field soil. The rhizospheres of environmental (non-agricultural) plants growing in undisturbed soils were also inhabited by I.1b Thaumarchaeota [48,52]. Generally, the types of I.1b Thaumarchaeota did not appear to be plant species or genus-specific, but their distribution was more dependent on the sampling location.

The I.1c type, on the other hand, have specifically been associated with boreal forest scrub and tree roots and mycorrhizospheres and to be differently distributed in different compartments of the (mycor)rhizosphere [12,51–55]. Nicol *et al.* [48,56] showed that the I.1c Thaumarchaeota could not be detected in recently exposed glacier foreland soil. However, when the soil was inhabited by mycotrophic plant species, I.1c Thaumarchaeota also appeared. In addition, without an ectomycorrhizal fungus, Archaea were less frequently detected on Scots pine fine roots [41,54,55]. However, when the Scots pine rhizosphere was colonized by ectomycorrhizal fungi, the detection rate of Archaea increased. This is interesting, since, in contrast to the Archaea, fine roots of Scots pine growing in humus generally harbor extensive populations of bacteria [57,58].

Nicol *et al.* [12] showed that specific groups of I.1c Thaumarchaeota correlated strongly with *Vaccinium* spp. and denseness of forest, while other I.1c groups correlated with the *Calluna vulgaris* of the treeless moor. In Finnish forest soil microcosms, Norway spruce was shown to collect the least variety of I.1c Thaumarchaeota, while deciduous boreal forest trees and Scots pine were considerably better preferred by these microorganisms [41,55]. The colonization of the tree roots by mycorrhizal fungi increased the colonization of the root systems by I.1c Thaumarchaeota [53–55], and it was seen that the archaeal community composition was dissimilar between the different species of mycorrhizal fungi [55].

Karlsson *et al.* [38] showed that the abundance of Archaea was highest in soil receiving only fungal exudates diffused into the soil, while the Archaea decreased when the fungal and root exudate levels increased. There were considerable differences between tree species in this study; however, in general, growing mycorrhizal tree seedlings did not increase the abundance of Archaea detected in the soil. Rasche *et al.* [39] detected a similar pattern in the abundance of the Archaea in an Austrian alpine coniferous forest. The archaeal abundance was greatest during the cold months when the tree productivity and exudation rates were the lowest. They also detected an increase in archaeal abundance over the year when the root exudation had been hampered by girdling the trees. Both studies suggest that the Archaea have not benefitted from the high concentration of organic carbon provided by forest trees and mycorrhizas. However, the effect may be due to the quality and quantity of specific exudates. For example, the secretion of methanol from plant tissues is highest in the beginning of the growth season and decreases over the summer and is also released from the decomposition of pectin-containing plant tissues [59,60]. Methanol was shown to induce growth of I.1c Thaumarchaeota in enrichment cultures from mycorrhizal root tips of boreal forest trees [33]. Karlson *et al.* [38] and Rasche *et al.* [39] studied temperate forests, and the Archaea detected were not identified, and it is possible that they were I.1b rather than I.1c Thaumarchaeota, which have been detected in similar forest environments before.

Elevated atmospheric CO_2 levels are thought to increase plant productivity and thus to have an impact on the rhizospheric microbial community. Lesauliner *et al.* [61] studied the rhizosphere soil of trembling aspen in Wisconsin, USA, in an ambient and elevated CO_2 atmosphere. Interestingly, and in accordance with Karlson *et al.* [38] and Rasche *et al.* [39], in an elevated CO_2 atmosphere, the richness and diversity of Archaea decreased significantly in comparison to ambient conditions. However, the abundance of mycorrhizal fungi increased. The majority of the Archaea detected by Lesauliner *et al.* [61] belonged to the Thaumarchaeota, and the I.1c group was found both in the ambient and elevated CO_2 treated plots. This result again contradicts the theory that the I.1c Thaumaarchaeota would specifically benefit from root exudates.

Lanzén *et al.* [62] found Group I.1c Thaumarchaeota in Spanish mountain pasture soil, and, in agreement with previous studies, showed that the I.1c Thaumarchaeota were more abundant in soils with dense vegetation in comparison with soils that had recently been cleared of vegetation. I.1c Thaumarchaeota may also prefer more undisturbed soils as shown by Chronáková *et al.* [63], where the impact of all-year cattle grazing on the soil microbiota was investigated. I.1c Thaumarchaeota were only found in control soils unaffected by cattle, or in pasture soils that were regenerating from a moderate impact of cattle, but not from soils with a heavy impact of cattle. The soils preferred by the I.1c Thaumarchaeota had the lowest pH (5.2–6.05), lowest P (50–250 mg$\cdot$ kg^{-1} soil), lowest N (3–7.1 mgN$\cdot$ g^{-1}), and lowest organic C (19–45 mgC$\cdot$ g^{-1}) contents of the tested soils. Oton *et al.* [43] showed a similar correlation between the I.1c Thaumarchaeota and low pH; however, in contrast to Chronáková *et al.* [63], they also showed a strong correlation between the I.1c Thaumarchaeota and high organic carbon content of the soil. Different forestry practices, such as clear-cutting and prescribed burning, also affect the distribution of lineages of the I.1c Thaumarchaeota [64]. Although the thaumarchaeotal communities appeared more diverse in the clear-cut and burned forest soils compared to the control forest soil, specific 16S rRNA gene types were only detected in the control forest soil.

2.4. Growth Requirements by the I.1c ThaumarChaeota?

No pure cultured representatives of the I.1c Thaumarchaeota have been reported yet. However, some parameters affecting the abundance on this group in enrichment cultures have been identified. Certain types of the I.1c Thaumarchaeota have been shown to increase when cultured in broths amended with methane and methanol, and to grow on yeast extract [33]. They have also been shown to grow both in oxic and anoxic conditions [33]. However, the I.1c Thaumarchaeota did not grow well on CO_2 as sole carbon source.

The I.1a and I.1b Thaumarchaeota are involved in ammonia oxidation in both aquatic and terrestrial habitats [31]. However, such traits have not yet been shown for the I.1c group. Stopnisek *et al.* [65] studied the abundance of Thaumarchaeota and *amo*A genes/transcripts in microcosms containing ammonia amended temperate forest soil from Slovenia. The most abundant Thaumarchaeota in the ammonia amended forest soil were I.1c and I.3 Thaumarchaeota, but the *amo*A gene transcripts obtained belonged to the Group I.1b. Weber *et al.* [66] also showed that ammonia oxidation was not necessary for growth of the I.1c Thaumarchaeota, but they prefer organic nitrogen compounds as N source. In fact, they showed that the community size of I.1c Thaumarchaeota increased in soil microcosms most at over 30 °C when organic nitrogen compounds were provided, but inorganic carbon alone did not promote growth of this group of Archaea. It has also recently been shown that I.1c Thaumarchaeota are abundant in highly decayed wood of logs in natural boreal forests and that the abundance correlates strongly with the availability of nitrogen in the decayed wood [67].

3. Conclusions

What, then, are the main ecological roles for the I.1c Thaumarchaeota? They appear not to perform ammonia oxidation, nor do they appear to be inclined to autotrophic growth. Instead, this group of Archaea commonly resides in soils, which are rich in organic carbon and have a dense plant

cover. They may utilize plant root exudates to some extent; however, when the carbon allocation rate to the rhizophere is at its most intense, the I.1c thaumarchaeotal numbers decrease. It is possible that these Archaea are involved in the decomposition of organic material rather than benefitting directly from easily degradable carbon compounds allocated below ground by the plants. The plant cover is still an important factor for the I.1c Thaumarchaeota, because the roots and litter provide decomposing organic material for the I.1c Thaumarchaeota. These Archaea may be slow-growing organotrophs that are outcompeted by the faster growing microorganisms when root exudation rates are high. However, when the easily degradable carbon compounds have been exhausted, the I.1c Thaumarchaeota may have a competitive edge over the fast growing microorganisms in conditions where only more recalcitrant organic matter is available.

Conflicts of Interest: The author declares no conflict of interest.

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