

The Cooccurrence of Archaea and Bacteria Among Diverse Globally Distributed Ecosystems

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1 Introduction: Historical Perspective on Archaeal Ecology

Though the discovery of Archaea is commonly attributed to Carl Woese and colleagues, it is important to note that Woese's greatest contribution (and arguably the most important contribution to the study of Archaea so far) was not his culturing of a novel third domain of life, but rather his ability to synthesize available ideas, information and techniques to ultimately discover that the Archaea are a separate biological entity from the Eukaryotes and the Bacteria. Archaea have been isolated and described as early as the late 1800s, when halophilic Archaea (then presumed to be bacteria) were isolated as a means to understand the preservation of salt-packed fish (Kocur and Hodgkiss 1973). Additionally, archaeal methanogens (then also considered a curious type of bacteria) had been commonly isolated from the 1930s onwards. Both of these organismal groups were thought of as strange prokaryotes—methanogens because of their unique biochemistry and the halophiles because of their salinity tolerance. It, however, was not until the efforts in understanding these odd microbial organisms' place in evolutionary trees by Carl Woese et al., that it became clear that methanogenic, halophilic and thermoacidophilic Bacteria actually belonged to a domain of life that was entirely distinct from both Bacteria and eukaryotes (Woese and Fox 1977; Woese et al. 1990).

Following the seminal late 1970s work by Woese and colleagues, members of his collaborative group and his academic progeny advanced the study of Archaea through two different methodological trajectories: culture-based methods and molecular, cultivation-independent techniques. Of equal importance to

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understanding the phylogenetic relations and diversity of the Archaea is understanding their physiological characteristics in order to inform phylogenetic studies. In this regard, some of the most important early researchers to characterize Archaea, Karl Stetter, and Wolfram Zillig, were both also involved in the initial discovery of the archaeal domain. While Stetter's work has focused on hyperthermophiles, which he was first to discover, his additions to culture collections have helped fill in information gaps concerning the physiological characteristics of Archaea that would be otherwise weighted heavily towards the readily cultured halophiles and mesophilic methanogens. Stetter followed earlier culturing precedents set by Ralph Wolfe (Stetter et al. 1981), who was also influential in the third domain discovery. Using culture conditions that mimic the anoxic, volcanic gas-rich environments of hyperthermophiles, they were able to recover a far greater archaeal diversity from these environments than was previously thought to exist. As of current, the vast majority of isolates within the Thermoprotei, and a significant portion of the hyperthermophilic Euryarchaeota were first cultured and discovered by Stetter, Zillig and their colleagues.

While Stetter, Zillig and others were making great advancements towards elucidating the known diversity of Archaea and providing cultures for physiological study, the molecular biology offshoot of Woese's idealogical descendents were also beginning to develop research programs that would greatly influence the study of Archaea as well as Bacteria. In particular, Norman Pace, a post-doctoral researcher at the University of Illinois at the time of Woese's discovery, began to develop a method incorporating Woese's comparative phylogenetics techniques with environmental microbial communities. As a logical extension to the phylogenetic analysis of strains based on ssu rRNA identities, Pace's group developed a method for fingerprinting natural microbial communities based on the 16S ssu rRNA gene (Olsen et al. 1986). The process relied on extracting environmental DNA, shotgun cloning the DNA to create a vector library, amplifying the library and probing for the presence of 16S rRNA gene sequences. Making use of the newly described dideoxy termination sequencing method developed by Fred Sanger et al., the sequences could be compared against a reference database and the in situ microbial communities could then be inferred based on the database query results. While Pace's approach to ecological analyses did not directly concern the Archaea initially, members of his lab group, as well as those influenced by his methods, quickly began to advance the discovery and study of Archaea without the hindrance of culturing.

In one of the early archaeal studies to use Pace's approach, Edward Delong, a post-doc of Norman Pace's, used archaeal-specific probes to detect archaeal 16S rRNA genes in surface coastal waters off of North America. Surprisingly, he found a particularly abundant ribotype that was highly divergent from other Archaea, but most closely affiliated with the Crenarchaeota (DeLong 1992). Given that the Crenarchaeota were only known to be extreme hyperthermophiles at the time, and other Archaea (aside from the methanogens) were only known to be extremophiles, the finding was surprising and provocative. The discovery of this ribotype was certainly curious and at the time suggested that the previous understanding of

Archaea as strictly extremophilic was not entirely accurate. Importantly, this study marked the beginning of research into what we now know are members of the Thaumarchaeota phylum, which has gained a considerable amount of attention in recent years (discussed later). Importantly, this study also marked the beginning of a more accurate understanding of archaeal diversity outside of the realm of extreme environments.

Throughout the 1990s and 2000s, myriad studies of uncultured ‘ribotypes’ via environmental 16S rRNA gene surveys led to a surprisingly large amount of known archaeal phylogenetic diversity in a wide variety of ecosystems. In particular, known archaeal diversity was no longer restricted to just extreme environments, but also most environments where Bacteria had been thought to be dominant. More recently, the advent and application of environmental genomics (Tyson et al. 2004) has led to a number of new insights into the functional potential of many of these uncultured archaeal lineages and has been highlighted by expanding roles of Archaea in global carbon, nitrogen and sulfur cycling.

Following from the traditional perspective that Archaea dominate extreme environments to the exclusion of Bacteria, Archaea were largely thought to not significantly overlap ecologically with Bacteria (Valentine 2007). It was not until the seminal environmental studies by Ed Delong et al. which indicated that Archaea were particularly numerous in more mesic environments. The widespread use of cultivation-independent techniques has significantly changed our view of archaeal ecology and, in particular, their ecological co-occurrence with bacterial populations across globally distributed systems. Below, I describe advances in our understanding in the overlap between archaeal and bacterial taxa in numerous environments, highlighting some seminal finds.

2 Methane Oxidizing Archaeal and Bacterial Consortia

One of the most integral discoveries that have been made regarding the interactions between Archaea and Bacteria has been that of anaerobic oxidizing methane (AOM) consortia. AOM are widespread among oceanic environments and comprise diverse groups of euryarchaeal organisms that often cohabit with bacterial consortia to couple oxidation of methane (CH_4) with the reduction of several oxidants including SO_4^{2-} , NO_3^- and multiple metal oxidants (Knittel and Boetius 2009; Scheller et al. 2010a, b). While the anaerobic oxidation of methane has long been known, the precise microbial mechanisms of this process were only recently discovered. These inter-domain consortia potentially leverage electron transfer conduits in order to surmount energetic barriers to the anaerobic oxidation of methane, which can occur via coupling to a variety of oxidants, including sulfate and nitrate, among others (Beal et al. 2009; Ettwig et al. 2010; Scheller et al. 2010a, b; Lai et al. 2016). A number of anaerobic methane oxidizing euryarchaeotal groups (ANME) are known, which are thought to mediate the anaerobic oxidation of methane in association with bacteria. ANME are affiliated with methanogens in the

taxonomic groups of Methanosarcinales, Methanobacteriales, and the Methanococcoides which all belong to the Euryarchaeota phylum. Recently, the isolation of the first anaerobic alkane oxidizing Archaea, *Candidatus* Syntrophobacterium spp. provided important insights into the physiological nature of these organisms (Laso-Perez et al. 2016). Although, somewhat surprisingly, *Candidatus* Syntrophobacterium spp. were responsible for longer chain alkane degradation (butane) via butane activation with the key enzyme in methanogenesis/reverse methanogenesis (McrA).

Of particular global importance, these archaeal and bacterial consortia are responsible for a significant amount of mitigation of global methane flux from the open ocean environments into the atmosphere. For example, 7–25% of the total global methane flux is consumed by AOM, which also nearly for the near total oceanic methane fluxes (Knittel and Boetius 2009). Methane is a potent greenhouse gas, with an order of magnitude greater global warming potential compared to carbon dioxide. Thus, these anaerobic methane oxidizing consortia play a critical role in the biogeochemical cycling of carbon, in addition to the regulation of earth's climatic variations. However, there is still a considerable amount of physiological information that is unknown due to the recalcitrance of these organisms and consortia to cultivation.

3 Ammonia Oxidizing Archaea in Open Oceans and Soils

Perhaps no greater contribution to our current understanding of archaeal ecology was made than by early efforts to understand the role of 'cold Crenarchaeota' that were first discovered by DeLong et al. in the early 1990s in cold Antarctic ocean waters (DeLong 1992). These so called 'cold Crenarchaeota' are now known to belong to an entirely distinct phylum of Archaea known as the Thaumarchaeota (Brochier-Armanet et al. 2008), which comprise a diverse group of ammonium oxidizers that are distributed globally in fresh waters, soils, oceans and many other environments where they compete with bacterial assemblages. Early estimates indicated the Thaumarchaeota represented significant fractions of oligotrophic open ocean waters, which implicated them as potentially significant biogeochemical players (DeLong 1992). Interestingly, the first evidence for the physiology of the Thaumarchaeota arose not from free-living planktonic populations, as were discovered by DeLong et al., but rather from a metagenomic analysis from a marine sponge which housed a different genus compared to open ocean phylotypes, *Candidatus* Cenarchaeum symbiosum (Preston et al. 1996). Sequencing of the sponge symbiont's genome indicated the capacity for ammonia oxidation, which was then later confirmed in free-living Thaumarchaeota. Considering the ubiquity of free-living thaumarchaeotes among water columns and sediments from globally distributed environments (Francis et al. 2005), their role in global nitrogen cycling is certainly appreciable. Although Ammonia Oxidizing Bacteria (AOB) were thought to be the predominant nitrifiers until the discovery of Ammonia Oxidizing

Archaea (AOA), quantitative cultivation-independent studies (assessing abundance of the key ammonia oxidation gene—ammonia monooxygenase—*amo*) have indicated that AOA are significantly more abundant than AOB in many environments, suggesting they likely play a larger biogeochemical role (Wuchter et al. 2006; Mincer et al. 2007).

Studies of the distribution of AOA and AOB via *amo* gene abundance distributions indicated discrete distributions of the two types of microorganisms along gradients in NH_4^+ availability (Wuchter et al. 2006; Agogue et al. 2008). Later, physiological studies of the first free-living thaumarchaeote isolate, *Candidatus Nitrosopumilus maritimus* (Konneke et al. 2005) provided context for these ecological distributions. In particular, *Ca. N. maritimus* exhibits NH_4^+ affinities that are over two orders of magnitude greater than that of AOB (Martens-Habbenha et al. 2009). These data suggests that AOA outcompete AOB at low concentrations of NH_4^+ and thus occupy different ecological niches with regards to NH_4^+ availability. Intriguingly, although AOB were long considered the primary nitrifiers in most environments, the abundance and activity of AOA in oligotrophic environments indicates that AOA may be more globally important, as environments, and particularly the open ocean, tend to be considerably more oligotrophic. In addition to the dominance of AOA in ocean settings, they are also dominant in soil communities (Leininger et al. 2006), where they further contribute to global nitrogen cycling.

As in open oceans, AOA appear to occupy different ecological niches than AOB in other environments, including soils, as the former are generally more prevalent in low NH_4^+ -availability environments and also exhibit similar adaptations to low NH_4^+ availabilities. Terrestrial cultivars of the Thaumarchaeota that were recovered after the initial thaumarchaeote isolate (*Ca. N. maritimus*) also exhibit high NH_4^+ affinities (Lehtovirta-Morley et al. 2011), suggesting that they are particularly adapted to natural environments with low nutrient fluxes. Perhaps most conspicuously, the AOA tend to dominate AOB in acidic soils (Nicol et al. 2008) and have provided the missing link to ammonium oxidation in acidic soils, where AOB were not known to be present.

4 Hydrothermal and Acidic Environments

Since the discovery of Archaea as a separate domain, the extreme environments of hydrothermal systems were thought to be mostly dominated by archaeal taxa. Indeed, the prevailing thought was that Archaea predominate in the hottest and most acidic of hydrothermal environments (Reysenbach and Shock 2002). While there is evidence to support their dominance in hydrothermal systems with the highest temperatures and lowest pH (Colman et al. 2017), they also comprise highly diverse and abundant populations in more ‘mesic’ hydrothermal systems (Bowen De Leon et al. 2013; Boyd et al. 2013; Inskeep et al. 2013; Colman 2015). Indeed,

Archaea may contribute significantly to community function within these environments. While less acidic systems have traditionally been squarely in the realm of bacterial dominance, recent cultivation-independent approaches have highlighted a growing role for Archaea in circumneutral hydrothermal environments alongside major bacterial community members (Bowen De Leon et al. 2013; Inskeep et al. 2013; Colman 2015). For instance, numerous uncultured divisions of Archaea have representative genomes that have been reconstructed from circumneutral hydrothermal environments, including members of the candidate divisions 'Bathyarchaeota', 'Hadesarchaea', and the 'Asgard Archaea' (Saw et al. 2015; Baker et al. 2016; Zaremba-Niedzwiedzka et al. 2017). While bacterial divisions in these environments are most likely to be the primary producers (Takacs-Vesbach et al. 2013), it is likely that many of these candidate divisions contribute to carbon cycling within these largely bacterial-dominated environments. For instance, the 'Bathyarchaeota' are thought to be potentially involved in C1 carbon compound cycling (i.e. through methanogenesis or methanotrophy; (Evans et al. 2015)) or potentially acetogenesis (He et al. 2016), although a role in heavier chain alkane degradation may be more likely (Laso-Perez et al. 2016). Regardless, it is clear that these uncultured, recently genomically analyzed, microbial taxa have clear interactions with their bacterial community members in what were once thought to be traditionally bacterially dominated environments.

Perhaps more intriguingly, are the geochemical environments where the shift from bacterial to archaeal dominance occurs within hydrothermal environments. Archaea can be found across the span of major geochemical gradients (i.e. temperature and pH) in hydrothermal systems (Boyd et al. 2013; Inskeep et al. 2013; Xie et al. 2014; Colman 2015). However, Archaea are particularly dominant in hot springs with the lowest pH and the highest temperatures, suggesting that they are uniquely adapted to these extremely stressful environments (Colman et al. 2017). Indeed, others have suggested that Archaea, as a whole, are especially adapted to energetically expensive environments and that energetic limitation is a defining feature of the archaeal domain (Valentine 2007). Though Archaea dominate the highest temperature acidic environments, Bacteria dominate some of the most acidic habitats known, albeit at lower temperatures (Tyson et al. 2004). The observation that the dominance between Archaea and Bacteria shifts along temperature gradients in low pH environments suggests that physical interactions may permit the exchange of genetic information via horizontal gene transfer (HGT) within and among the two domains where their ecological niches overlap at moderate temperatures. Some evidence from comparative genomics exists that genetic transfer has occurred down temperature gradients within acidic habitats within the archaeal domain from the Sulfolobales order taxa that are adapted to higher temperatures to Thermoplasmatales which are adapted to lower temperatures (Ruepp et al. 2000; Futterer et al. 2004; Colman et al. 2017), which may have contributed to the adaptation to acidophily by one or the other of the orders (Colman et al. 2017). However, future research may elucidate whether inter-domain HGT has occurred between Bacteria and Archaea in acidic environments, and whether this HGT has resulted in adaptation to these particularly extreme environments.

5 Ocean Sediment Environments

In addition to the discovery of Archaea as abundant members of open ocean waters, Archaea have long been known to be significant populations of open ocean sediments (Teske and Sorensen 2008; Lloyd et al. 2013). However, it was not until the recent application of environmental metagenomics that their physiologic function has come into focus. In particular, members of the ‘Bathyarchaeota’ are abundant in open ocean sediments where they cohabit with organic carbon degrading Bacteria. In one of the first published reports regarding the potential function of ‘Bathyarchaeota’, it was suggested that they were predominantly responsible for degradation of proteins and other organic carbon metabolites (Lloyd et al. 2013). Later reports have indicated a role in other carbon metabolic pathways including methanogenesis and acetogenesis (discussed above). Regardless, as in other systems, it is becoming increasingly clear that Archaea in these environments, which were once thought to be predominantly bacterial, are important contributors to organic carbon degradation along with their co-occurring bacterial community consortia.

A recent study highlighted the potential function and interaction of thermophilic sediment Archaea with sulfate reducing bacterial consortia at the level of reducing equivalent transfers. As mentioned above, the *Candidatus* genus *Syntrophoarchaeum* was recently demonstrated to active butane using McrA, the key protein that is involved in activating methane during methanogenesis (Laso-Perez et al. 2016). *Syntrophoarchaeum* spp. are related to the ANME-1 group of Archaea that carry out methanotrophy via a near reversal of the methanogenesis pathway in concert with bacterial members of the Deltaproteobacteria class that perform sulfate reduction. However, these organisms oxidized butane in concert with co-habitated Deltaproteobacterial organisms in the ‘HotSeep-1’ clade. A particularly complicated problem for methane (or butane) oxidizing Archaea is that they must get rid of ‘reducing equivalents’ or excess reductant, which is typically performed in methanogens via the production of methane. Since AOM and butane-oxidizing Archaea run a near reversal of the methanogenesis pathway, an important physiological problem is passing electrons on elsewhere. In AOM consortia, and in *Syntrophoarchaeum* spp.-bacterial consortia, this problem is solved via passing the reducing equivalents (essentially electrons) through ‘nanowires’ or pilus-like structures that allow the hydrocarbon degrading Archaea to remove excess reductant, which is then provided to the bacterial partners for SO_4^{2-} , or other oxidant, reduction (Wegener et al. 2015; Laso-Perez et al. 2016). Though these recent analyses have provided much insight into the functioning of sediment and AOM Archaea, they also highlight that much more information is needed regarding the physiological nature and consequent ecological importance of many of these organisms, especially in hydrocarbon degradation, which is of central importance to our understanding of global carbon cycling.

One of the most intriguing questions that remains about the nature of archaeal and bacterial interactions are the nature of these interactions at the level of reductant

and/or oxidant transfer. As the above studies highlight, consortia have co-evolved to mitigate the problem of removing reducing equivalents (from the AOM) and providing it to co-occurring partners (i.e. the sulfate reducing bacteria). In many cases, reducing equivalents can be transferred via H_2 , which is produced by many organisms as a way to dispose of excess electrons. One of the core observations of archaeal ecology is that sulfate reducing bacteria generally outcompete Archaea for H_2 , thus excluding methanogens from environments where these bacteria are present. That consortia have co-evolved around a mechanism of inter-domain electron transfer suggests that many more interactions that await to be discovered may also revolve around syntrophic interactions that rely on shuttling reductants or oxidants among partners in order to increase environmental habitability and/or lower thermodynamic barriers to certain metabolic processes, such as AOM. The recent documentation of ‘Cable Bacteria’ provides one such example that may be ripe for further understanding inter-domain interactions at the level of direct energy transfer.

6 Conclusions

Though Archaea were once thought to be relegated to only the most extreme environments and were generally presumed to be ecologically distinct from Bacteria, the application of increasingly insightful cultivation-independent analyses have shown otherwise. In particular, Archaea are now known to co-occur and interact with Bacteria in complex, global biogeochemical cycles in a variety of environments in addition to the most extreme environments. It may not be likely that additional microbial diversity will be discovered after the exhaustive efforts of the previous several decades. However, the functional role of most of the recently documented, uncultured Archaea has yet to be fully realized and holds much promise for future insights into their global role. Moreover, the mechanistic functional interactions between many of these Archaea and their co-occurring archaeal and bacterial community members at the intra- and inter-domain level remain to be elucidated and are an important target for future research concerning the interactions between Archaea and Bacteria, and in particular, understanding how these interactions lead to more emergent properties that influence evolutionary trajectories for lineages and global biogeochemical cycles.

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