

Table 1. Deep branching lineages in a sample of prokaryote phylogenies

Study	Earliest archaea	Ae/An/M	Earliest bacteria	Ae/An/M
Woese (1987)	Mixed assemblage	M	Thermotogae	An
Gupta (2001)			Firmicutes	M
Daubin et al. (2002)			Chlamydia, Spirochaetes	M
Rappe and Giovannoni (2003)			Aquifaeceae	M
Battistuzzi et al. (2004)	C/E split	M	Aquifex, Thermotogae	M
Brochier et al. (2004)	C/E split	M		
Brochier et al. (2005a)	C/E/N split	M		
Brochier et al. (2005b)	C + EN split	M		
Baptiste et al. (2005)	C/E/N split	M		
Ciccarelli et al. (2006)	CN + E split	M	Firmicutes (Clostridia)	An
Gribaldo and Brochier-Armanet (2006)	C + EN split	M		
Cox et al. (2008)	Mixed	M		
Boussau et al. (2008)			Aquifaeceae, Thermotogae	An
Yarza et al. (2008)	C/E split	M	Thermotogae, Clostridia ^a	An
Lake et al. (2008)			Firmicutes/ Actinobacteria split	M
Wu et al. (2009)			Deinococcus-Thermus, Thermotogae	M
Kelly et al. (2011)	E + T + CKN or EN + T + KC	M		
Brochier-Armanet et al. (2011)	TAC + KNE	M		
Williams et al. (2012)	E + TACK	An		
Wolf et al. (2012)	E + N + TACK	An		
Rinke et al. (2013)	(E ² + TACK) + DPANN	An	Candidate division SR1	
Raymann et al. (2015)	(E ² + TACK) + E ^b	An	Deinococcus-Thermus, Thermotogae	M
Spang et al. (2015)	E + (DPANN + (E + TACKL))	An		
Zuo et al. (2015)	Halobacteria ^c	Ae		

C, Crenarchaea; E, Euryarchaea; N, Nanoarchaea; K, Korarchaea; T, Thaumarchaea; A, Aigarchaea; DPANN, Diapherotrites, Parvarchaea, Aenigmarchaea, Nanohaloarchaea, and Nanoarchaea; L, Lockiarchaea; Ae, aerobic; An, anaerobic; M, mixed aerobic and anaerobic organisms.

^a*Thermodesulfobiaceae* family, Firmicutes are nonmonophyletic.

^bEuryarchaea separated into two clusters with methanogenic archaea basal.

^cWhole genome comparison.

tosynthesis, on that all biologists agree, but whether the two photosystems of cyanobacteria became divergent in one and the same genome or in different genomes is more debated (Hohmann-Marriott and Blankenship 2011), whereby lack of a deep split in chlorophyll biosynthesis that would mirror the deep split of the photosystems is lacking (Sousa et al. 2013a), suggesting that the two photosystems arose and diverged within the same cell (Allen 2005). The

evolution of photosynthetic electron transport chains (with chlorophylls) requires that basic biochemical components like cytochromes and quinones were in place, meaning that respiratory electron transport chains (with heme) preceded photosynthetic electron transport chains (and O₂) in evolution. That means that anaerobic respiratory chains—of which there are very many forms with many different terminal acceptors (Amend and Shock 1998)—preceded both pho-



tosynthesis and biological production of oxygen. So far so good, but what came before anaerobic respiratory chains?

Anaerobic respiratory chains involve cytochromes and quinones (Schäfer et al. 1996; Berry 2002). Are there simpler forms of microbial physiology that do not require cytochromes and quinones? Yes, but among the autotrophs they are not that numerous. There are acetogens (Schuchmann and Müller 2014) and methanogens (Buckel and Thauer 2013), which are anaerobic autotrophs that lack both cytochromes and quinones (but they have corrins). That would make them arguably the simplest and possibly most primitive forms of microbial physiology known, and indeed they only have one coupling site each: a methyltransferase complex (MtrA-H) in the methanogens (Thauer et al. 2008), and a ferredoxin:NADP⁺ oxidoreductase called Rnf in the clostridial acetogens (Biegel and Müller 2010), whereby there are also cytochrome lacking acetogens that use the energy-converting hydrogenase (Ech) instead of Rnf (Schuchmann and Müller 2014). Our terse physiological inference thus brings us right back to the Decker et al. (1970) scheme from the introduction, the only difference being that the Decker et al. (1970) tree had acetogens and methanogens grouped together as sisters, whereas today we would have to put their split at the very bottom of the tree of life, where bacteria and archaea diverge (Fig. 1). From our point of view, that is not an unreasonable proposition, others would surely disagree.

The idea that acetogens and methanogens are very ancient forms of microbial physiology has been out there for 45 years now, a version of that notion that puts them basal among the bacteria and archaea, respectively, and that links them to hydrothermal vents, which has been out there for ~10 years; is there any evidence to support it? The acetogens and the methanogens are both very strict anaerobes. They both live from the reduction of CO₂ with H₂, they both use the acetyl-CoA pathway at the core of their carbon and energy metabolism, and they both live from very modestly exergonic reactions that are close to the thermodynamic limits of life (Deppenmeier and Müller 2007). The core bio-

energetic reaction of methanogens (reduction of CO₂ to methane) occurs spontaneously at alkaline hydrothermal vents today (Lang et al. 2010; Etiope et al. 2011; McCollom and Seewald 2013; Schrenk et al. 2013). The chemiosmosis dependence of their carbon and energy metabolism when growing on H₂ and CO₂ is readily understood in terms of the geochemical origin of chemiosmotic gradients at alkaline hydrothermal vents (Lane and Martin 2012). Their carbon and energy metabolism is replete with transition metal catalysis (Sousa and Martin 2014). Those are aspects that make sense, but direct experimental support is even better.

In an exciting new work, McDermott et al. (2015) reported accumulation of formate from abiotic CO₂ reduction at the Von Damm hydrothermal field, at rates fast enough to support anaerobic methanogenesis. Such CO₂ reduction is typically attributed to serpentinization, but the details of the underlying geochemical process of rock–water–carbon interactions are still not resolved. Furthermore, the latest laboratory simulations are also of interest in this respect. Roldan et al. (2015) reported the laboratory synthesis of formate, acetate, methanol, and pyruvate from CO₂ using gregite (Fe₃S₄) as a catalyst under simulated alkaline hydrothermal vent conditions; that is exciting because the carbon species obtained very closely resemble the first steps of CO₂ fixation in the acetyl-CoA pathway (Fuchs 2011). Yamaguchi et al. (2014) reported the FeNiS-catalyzed synthesis of CO and methane under simulated alkaline vent conditions, while Herschy et al. (2014) obtained CO and formaldehyde. Simulated hydrothermal vents, while so far falling short of spewing forth vitamins, bases, and proteins, do produce compounds that are central to acetogen and methanogen metabolism, and they produce electrochemical gradients (Barge et al. 2014), which Mike Russell (Russell and Hall 1997) has been saying all along are essential for early life.

AND WHAT ABOUT LUCA?

The concept of LUCA (the last universal common ancestor) means different things to different people. For us, LUCA is the last common

ancestor of archaea and bacteria. Because archaea and bacteria differ in so many aspects, their common ancestor was perhaps not even a free-living cell (Martin and Russell 2003; Koonin 2011; Sojo et al. 2014). Clearly, the inference of the LUCA gene set requires (and is sensitive to) a rooted backbone tree, and strongly depends on the starting data set and method used (Table 1). The new trees that have a two-domain topology, with eukaryote ribosomes branching within the archaea (Williams et al. 2013; Spang et al. 2015), will deliver different estimates of LUCA gene content than the traditional three-domain topology did. Nevertheless, the deep bacterial–archaeal split is one of the few traces of early evolution that is consistently present across the majority of different trees of life.

Comparative genomics and modern phylogenetic approaches to infer the genetic content of LUCA usually estimates LUCA as a small genome-sized organism(s), containing 500 to 1000 genes (Koonin 2003; Kannan et al. 2013). These numbers are in agreement with the computational and experimental determinations of the minimal genome size necessary to sustain a functional cell (Itaya 1995; Mushegian and Koonin 1996; Pál et al. 2006). However, the ancestral reconstruction of a minimal gene set in LUCA approaches are influenced by several factors. Plotting presence and absence of homologous genes across a genome tree does not easily accommodate acquisition of genes by horizontal gene-transfer events. Thus, genes distributed in archaea and bacteria will apparently trace back to LUCA, although they might in fact have been transferred in one direction or another in recent history (Dagan and Martin 2007). This is certainly the case for the haloarchaea, aerobic heterotrophs that arose from methanogenic ancestors via gene acquisition from bacteria (Nelson-Sathi et al. 2012), and for several other groups of archaea, whose origins also correspond to gene acquisitions from bacteria (Nelson-Sathi et al. 2015). It should be possible to exclude LGTs identified by Nelson-Sathi et al. (2015) for the purpose of LUCA gene content inference (Mirkin et al. 2003), but that has not yet been reported.

It is becoming increasingly clear that in the field of early microbial evolution we have to

decouple—to some extent, but to which extent is still not yet known—the evolution of bioenergetic processes from the evolution of ribosomal lineages. Both evolutionary processes drive microbial diversity, but the two do not strictly coevolve over the fullness of geological time. This is seen in the assortment of bacterial photosynthesis with three kinds of CO₂ fixation pathways (Hohmann-Marriott and Blankenship 2011): the variation and the patchy distribution of sulfur reduction across microbial lineages (Pereira et al. 2011), the evolutionary transition from methanogenesis to aerotolerant heterotrophy in the halophiles (Nelson-Sathi et al. 2012), or in the association of archaeal ribosomes with bacterial energy metabolism in eukaryotes (Ku et al. 2015).

CONCLUDING REMARKS

In genome-wide phylogenies for prokaryotes, Nelson-Sathi et al. (2015) found an asymmetry of gene transfers between archaea and bacteria, with bacteria-to-archaea transfers predominating by 5:1 and >80% of all such transfers targeted to methanogenic recipients. That makes good sense in light of the methanogenic ancestry of archaea suggested by comparative physiology (Decker et al. 1970), by geochemistry (Sousa and Martin 2014), and by ribosomal phylogeny (Raymann et al. 2015). Phylogenetic trees, physiology, and geochemistry will continue to enrich our understanding of evolution within archaea, and help to identify the nature of genes acquired in the course of those transitions. This will, however, raise the question of who did most of the biochemical inventing (bacteria we think), and that might send us right back to square one, and Figure 1, a most insightful, intuitively understandable, 45-year-old picture of a very interesting problem.

ACKNOWLEDGMENTS

We thank Frances Westall, Orleans, for very insightful discussions about geochemistry and early life, Sriram Garg, Düsseldorf, for kindly preparing Figures 1 and 2, and the European Research Council (ERC) for financial support.

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Cold Spring Harb Perspect Biol 2016; doi: 10.1101/cshperspect.a018127 originally published online December 18, 2015

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