Mineral facilitated horizontal gene transfer: A new principle for evolution of life?

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A number of studies have highlighted that adsorption to minerals increases DNA longevity in the environment. Such DNA-mineral associations can essentially serve as pools of genes that can be stored across time. Importantly, this DNA is available for incorporation into alien organisms through the process of horizontal gene transfer. Here we argue that minerals hold an unrecognized potential for successfully transferring genetic material across environments and timescales to distant organisms and hypothesize that this process has significantly influenced the evolution of life. Our hypothesis is illustrated in the context of the evolution of early microbial life and the oxygenation of the Earth's atmosphere, and offers an explanation for observed outbursts of evolutionary events caused by horizontal gene transfer.

Traditionally, we think of evolution as following the phylogenetic tree of life, where organisms principally evolve through vertical modification of genetic information by means of sexual reproduction (Fig.1 dark blue lines). However, genes also move between lineages, where DNA from one organism is incorporated into distantly or non-related organism through a horizontal transfer of genetic material. The introduction of foreign DNA into an organism through horizontal gene transfer (HGT) can effectively change the ecological character of the recipient species[1,2] and tangle the traditional evolutionary phylogenetic relationships (Fig. 1). Over the past years, an increasing amount of evidence has solidified that HGT was essential for prokaryotic evolution[3] and played a large role in the evolution of eukaryotes.[4] For prokaryotes, HGT is currently recognized as a key source of innovation and adaptation to new environments and lifestyles[5–9] and Puigbò et al. 2014[10] found that ~ two-thirds of accounted evolutionary events originated from HGT. The impact of HGT on prokaryotic evolution is additionally highlighted by recent evidence showing that the evolution of prokaryotes is not driven by small adaptive variations, but by much more dramatic changes instigated by HGT and gene loss.[10]

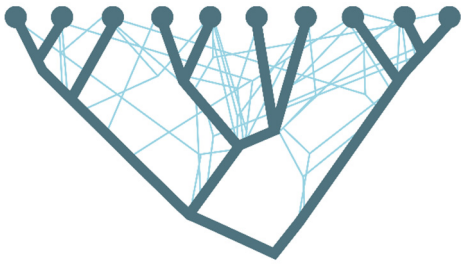

Figure 1. Schematics of the branches of the phylogenetic tree being crossed by the horizontal gene transfer (bright blue lines) Adapted from Puigbo et al. 2013.[11]

In general, the evolution of an organism is tied to its ever-changing habitat and the successful processes of innovation and adaptation in which the geologic environment plays an indirect role by providing the environmental settings. We propose that the distribution and availability of DNA for HGT could be facilitated by sedimentary processes and geologic events and we assign a much more direct role for the geologic environment in the evolution of life. Thus, certain geologic processes and events could explain the dramatic outbursts of prokaryotic innovations caused by HGT.

"Free" or "extracellular" DNA are typically released during cell growth,[12,13] from a biofilm or cell remnants,[12,14] or through lysis of dead bacteria.[12] However, DNA released into the aqueous environment or soil is subjected to degradation by dynamic biological, physical, and chemical factors[15] which are working against the success of HGT. In sea- and freshwater environments, free DNA can only survive for weeks[16–18] but when associated with minerals, experimental work shows that the longevity of the DNA can be significantly prolonged.[19] E.g. Lorenz et al. (1981)[20] showed that DNA adsorbed to a sediment was considerable more resistant to enzymatic digestion than aqueous DNA. Compared to degradation of aqueous DNA, DNA adsorbed to clay minerals was found to be 10 times more resistant[21] and DNA adsorbed to sand grains required 100 times more DNase to be degraded.[22] In addition, ~14-550 thousand years old DNA retrieved from sediments confirm that minerals can protect adsorbed DNA in a natural setting and preserve it for geologically relevant time scales.[23,24] On a global scale, free DNA (not part of a dead biomass) found in the uppermost 10 cm of recent marine sediments corresponds to about 0.30–0.45 Gt of DNA, and might represent the largest reservoir of DNA in the world's oceans.[25] Free DNA is found in the majority of Earth's surface ecosystems such as aqueous environments, soils and sediments.[15,25,26] Up to 95% of this DNA is estimated to be in association with minerals[7] and the prolonged longevity provided by this association significantly contributes to the available pool of evolutionary traits in the aqueous environments. When geologic processes and events start acting on this mineral archive of genes, we have a framework where minerals act as shuttles and facilitate transfer of evolutionary traits through time and across environments, and can directly impact the evolution of life. HGT of DNA can occur though the HGT transformation mechanism where the mineral adsorbed DNA are incorporated into the genome of a recipient organism,[28–32] and even fragmented and damaged DNA are able to transfer the genetic information.[3,33]

In the following, we advocate for the mineral facilitated HGT hypothesis and its impact on life by combining insight from mineral-DNA adsorption studies with metagenomic evidence and reports on early life and associated environmental settings. We summarize the main factors that give rise to our hypothesis and illustrate the potential impact of mineral facilitated HGT for the evolution of life. We describe a scenario that provides an explanation for detected outbursts of HGT[10] that caused dramatic evolutionary changes for prokaryotes[10,34] and link the processes of mineral facilitated HGT to the distribution of microbial metabolic traits 3.1 – 2.85 billion years (Ga) and the subsequent O_2 buildup in the atmosphere.

Factors influencing mineral facilitated HGT

Mineral associated DNA found in the environment does not simply mirror the diversity of the current active biota but represents a mixture of DNA from the overlying waters, surrounding sediments surrounding habitats as well as dead biomass that accumulated over time. During early stages of the evolution of life, this mineral associated archive of genetic information in the water column and the seabed would have been relatively poor compared to present day simply because of less biomass. Regardless, the factors impacting mineral facilitated HGT include a) the longevity of mineral adsorbed DNA as defined by the stability of the mineral-DNA binding, b) the dynamics of geological environment in terms of events and sedimentary processes and c) the Earth's near-surface mineralogy which relates to the abundance of minerals with a high DNA adsorption capacity. a, b, and c are closely interlinked but in contrast to a and b which describe more or less uniform processes in the geologic history, c has significantly changed over time.

a) The longevity of mineral adsorbed DNA depends on a range of factors where in particular minerals species,[35–40] background ions,[19,36,41] salinity, and pH[37,42–45] determine the DNA adsorption capacity of the mineral. Depending on the crystalline structure and composition, the surface charge of most minerals changes as a function of pH. In general, silicates have a low point of zero charge, i.e. they are negatively charged in wide pH range, whereas oxides and hydroxides have high point of zero charge, i.e. positively charged in wide pH range (Fig. SI-1). DNA interacts with minerals through its phosphate backbone, and

the nucleobases (Fig. SI-2) provide only a limited contribution to adsorption.[46] The phosphate moieties of DNA are positively charged below ~pH 2 and can interact directly with negatively charged silicates and basal planes of clay minerals. Above ~pH 2, the deprotonated and hence negatively charged phosphate moieties of the DNA can adsorb to negatively charged mineral surfaces through polyvalent cations (Ca^{2+}, Mg^{2+}, Al^{3+}) which make a "bridge" between two negative charges. These charge relationships between DNA and minerals as a function of pH make adsorption and desorption of DNA very sensitive to the geochemical characteristics of the environment (solution composition, oxygen fugacity, temperature, pH).[37–40,47] In addition, the longevity of DNA is originally assumed to be most efficient in anoxic depositional environments.[48] Yet, the unambiguous finding of ancient DNA within sediments deposited under oxic conditions[49,50] highlight that oxic environments also offers preservation. The experimental aims and setups of reported studies of DNA-mineral interactions varies significantly between studies making it very difficult to quantitatively address the causal effects on longevity from available data. In the following we therefore generalizing trends primarily based on grain sizes and general trends for DNA adsorption capacities.

b) The dynamics of the environment is a result of a variety of geological events such as seawater transgressions and regressions, weathering rates as well as the acting local sedimentation processes. The latter includes distance to shore, climate zone, depth, ocean, currents, energy levels etc. These dynamics can facilitate transport of the DNA-mineral association, i.e. if the association is suspended rather than deposited on the seabed they can be distributed by smaller scale dynamics such as local currents. The rate of deposition is primarily determined by the retention time of the suspended particles. Retention times depends on the particle size and density (and the acting energy levels). The particles with dimensions of a few micrometers or less, i.e. the clay fraction (less than 0.002 mm), have the longest retention times and thus the higher potential to shuttle DNA across environments. The adsorption capacity of DNA depends on the surface area as well as the electrostatic interaction between DNA, the mineral and solution composition (as discussed in a). The clay fraction is enriched in clay minerals and iron oxyhydroxides which, beside their high surface areas, have the highest adsorption capacity for DNA, (tens of micrograms of DNA per gram of mineral).[12] In contrast, silt (0.002-0.05 mm) or sand (above 0.05 mm) sized particles typically have a hundred-fold lower capacity primarily because of a smaller surface area[12] and electrostatic effects (mineral-DNA-solution interaction). The point is, that minerals in the clay fraction such as clay minerals, iron oxides and hydroxides are more likely to meet suspended DNA, adsorb it and transport it to distant sedimentary environments than e.g. sand fraction minerals.

c) In terms of the Earth's near-surface mineralogy clay minerals, oxides, hydroxides and carbonates contribute to a significant fraction to the mineral surfaces of suspended sediments in recent water columns.[51] However, on the early Earth, prior to the GOE, the mineralogy was less varied and marine suspended particles were likely dominated by sand fraction silicates produced by weathering and which have shorter retention time compared to clay fraction. Prior to the buildup of atmospheric oxygen, (2.45 Ga)[52] the occurrence of oxides, hydroxides and clay minerals was restricted to environments where physical erosion and aqueous weathering of (ultra)mafic and granitic rocks operated.[53] The only volumetrically important amounts of clay minerals in the oceans were most likely produced by serpentinization of oceanic crust around hydrothermal vents.[53] However, there would have been some amounts of terigenic clay minerals[54] that were transported to the early oceans by rivers or winds. These would have been suspended in the water column prior to sedimentation and could well have been acting as DNA carriers. Globally, the near-surface mineralogy of the Earth changed after the great oxidation event[53,55] (GOE) some 2.45 Ga ago,[52] where about 2500 new minerals were formed.[53] Iron oxyhydroxides such as ferrihydrite and hematite are particularly important products of the GOE because they precipitated in significant amounts from the upper part of the ocean as a consequence of lower solubility of Fe^{3+} compared to the Fe^{2+} ion. In addition to the higher abundance of clay fraction minerals the proportion of clay minerals increased because of the associated onset of Fe^{3+}-rich clay mineral formation on the continental shelf,[56] combined with increased weathering. We propose that the sudden abundance in numbers of these major DNA carriers following the GOE, added to the success and magnitude of mineral facilitated HGT. During buildup of free O_2, the emergence of new

ecological niches was high and would have boosted the demand for new traits and innovations. In contrast, the emerging oxic conditions most likely decreased the DNA longevity as it has been observed for the recent anoxic lake sediments.[48] Unfortunately, there are major gaps in current knowledge about the longevity of mineral bound DNA and a quantitative assessment of the interplay between these factors is a still-standing frontier.

Genomic evolution and O_2 buildup on early Earth

Genomic research has identified an Archaean expansion (AE) in genetic innovations between 3.3-2.85 Ga that coincides with a rapid diversification of bacterial lineages.[34] David and Alm (2011)[34] generated a detailed evolutionary history for ~4,000 major gene families where they account for events caused by HGT. Specifically they compared individual gene phylogenies with the phylogeny of organisms (the 'tree of life'). They show that gene histories reveal marked changes in the rates of gene birth, gene duplication, gene loss and HGT over geological timescales (Fig. 2). Interestingly, during the decline in the genetic expansion there is an outburst of HGT driven evolution (Fig. 2 arrow), which stabilizes at a maximum ~2.7 Ga and remains relatively constant until present times. Genes born during the AE were found likely to be associated with an expansion in capabilities of microbial respiration and electron transfer capabilities, with an enrichment in oxygen-using genes towards the end of the expansion.[34] In addition, genes arising after the expansion show increasing use of free oxygen.[34]

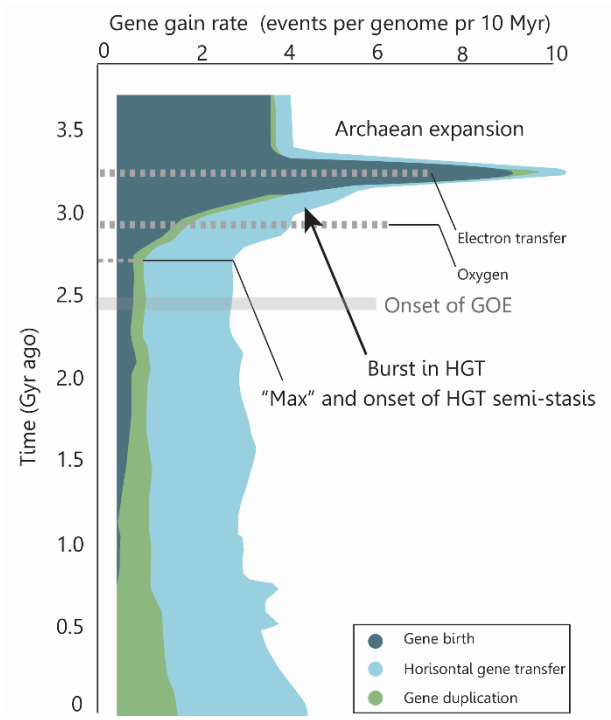

Figure 2. Rate of genomic macroevolutionary events over time. An Archaean expansion mark a rapid diversification of bacterial lineages. During the expansion the metabolic complexities of respiratory pathways evolved to include electron-transfers and after the expansion arising genes showed increasing use of molecular oxygen. At the decline of the expansion a significant amount of gene rates is caused by HGT. This contribution reaches a maximum and remains semi-constant until present time. Adapted from David and Alm (2011).[34]

Oxygenic photosynthesis is the only significant source of free oxygen in the hydrosphere and atmosphere and the dominant metabolic pathway for life on Earth. Before the invention of photosynthesis, life was solely dependent upon chemical sources of reducing power such as hydrothermal activity and weathering.[57] The photosynthesis might have evolved prior to 3.8 Ga[58] and evidence suggest whiffs of atmospheric oxygen[52] occurring as early as 3 Ga.[59] This means that, at least locally, pockets of O_2 were present in the

Earth's near surface environments as a product of sparse photosynthetic life prior to the build-up of appreciable amounts of free atmospheric O_2. At that time, several processes have competed for the free O_2 including oxidation of sulfides, reduced geothermal outflow and oxidation of organic matter as well as limited formation of oxides and hydroxides. We propose that mineral facilitated HGT have had a higher impact in suboxic compared to anoxic conditions, i.e. the combination of i) increased local development of clay fraction minerals with associated high DNA adsorption capacities, ii) the overall anoxic conditions (enhancing longevity) and iii) the local whiffs of O_2 would have been offering compelling sites for archiving DNA on mineral surfaces and a demand for innovations. Despite the steady levels of free atmospheric O_2, recent data imply that for much of the Proterozoic Eon (2.5-0.5 Ga), Earth's oceans were moderately oxic at the surface and still anoxic at depth,[60] which would have favored DNA preservation.

Considering the interdependence of O_2 levels, abundance of minerals with a high DNA adsorption capacity, geological environments, opportune niches for innovations and DNA longevity, we find it plausible that the variation in rates of macroevolutionary events caused by HGT during and post the AE (Fig. 2) are related to all these factors. The initial rise of the of gene transfer events in the AE is dominated by gene births and the emerging role of HGT could well be caused by development of life, a higher frequency of DNA transfer combined with the need for innovation. The subsequent rise and the following stasis of HGT contribution to genomic evolution could represent a balance between the need for innovations, the development of oxic environments (decreasing preservation potential) and the promoted formation of minerals which preserve the DNA (enhancing longevity) as well as abundance and higher adsorption capacities as determined by the local geology and O_2 levels. Although, considering the present-day amount of DNA in sediments, we do not consider oxic conditions as important to the DNA longevity as the increased number of mineral DNA-carriers contribute to its longevity.

In the following, we illustrate the advocated framework for mineral facilitated HGT and our proposed impact on the early life. The timing of events and likely evolutionary order of the metabolic mechanisms are accounted for in Fig. 2, but the distribution of traits and the subsequent evolution as illustrated in Fig. 3 are hypothetic scenarios. The purpose of Fig. 3 is to illustrate likely processes and the proposed significance of mineral facilitated HGT for the evolution of life.

Proposed framework for mineral facilitated HGT and the impact for early life

Likely candidates for the earliest habitable environments are anoxic submarine-hydrothermal vents[61] where heat and chemical gradients in aqueous solutions rich in hydrogen, methane, carbon dioxide and sulfur would have sustained early life with primitive metabolism such as the white smoker and the black smoker habitats in Figure 3. PreGOE white and black smokers had some of the largest deposits of e.g. carbonate and serpentine group clay minerals. The DNA from the microbes dwelling in these habitats was able to adsorb to carbonates through electrostatic interactions and to serpentines through ion bridging (Fig S1-Schindler diagram), which would facilitate transport of DNA to distant environments. In Fig. 3 genes encoding a primitive metabolic pathway are carried from the white smoker to a shallower black smoker habitat, which have a higher content of reduced Fe and S. The "newly"-arrived DNA enables the evolution of electron transfer mechanism (e.g. chemolithotrophs). Minerals with adsorbed DNA from the black smoker is subsequently carrying genes that encode electron transfer metabolism to a locally oxygenated pocket in the subphotic zone, where early photosynthesis is occurring. The suboxic environment and the new traits result in evolution of Fe oxidizers such as microaerophilea *Gallionella* type filamentous bacteria. The bacteria oxidize Fe^{2+} which precipitates iron oxyhydroxides on its filaments causing it to sink to the anoxic zone and cause draw down of carbon (and DNA) which in turn enhances the buildup of free O_2.[62]

DNA from the Fe-oxidizing bacteria is carried toward shallower conditions into the photic zone where cyanobacterial mats, stromatolites, are generating buildup of free O_2. Here, the new environment and the presence of both stromatolitic cyanobacteria and the DNA transported by minerals facilitates the evolution of a new photosynthetic bacteria. At this point in time, the increasing amounts of free O_2 in the upper part of the ocean lead to precipitation of e.g. banded iron formations and an increasing amount of clay minerals, oxides and hydroxides that carry DNA thereby creating opportune conditions for life and innovations. It is noteworthy to emphasize that dynamic geologic processes such as marine regression or sea currents could facilitate the above presented scenario. E.g. currents could bring mineral bound DNA kept in sediments to completely new habitats or a regression could bring previously deep-sea sediments are to shallower waters.

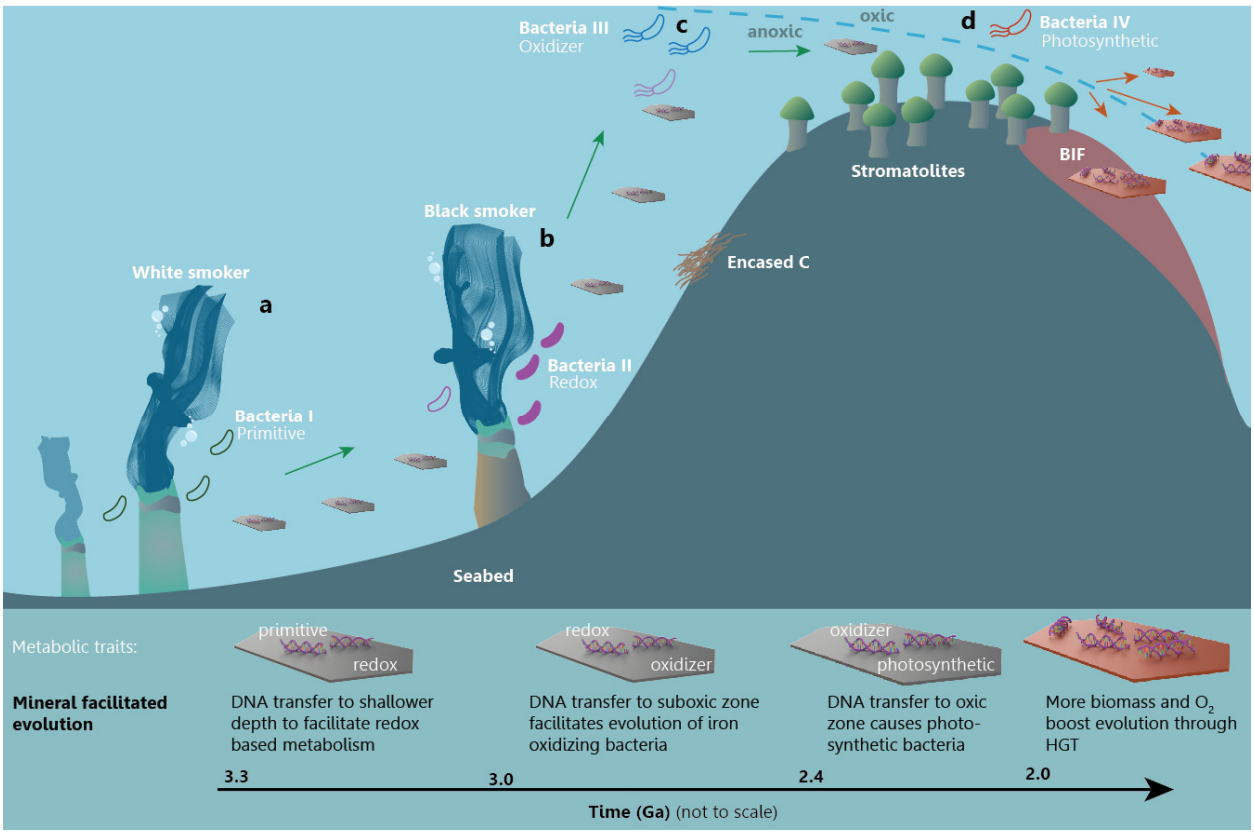

Figure 3. Simplified framework illustrating mineral facilitated HGT and proposed impact for the evolution of early life. Minerals are distributing adsorbed metabolic traits across time and space (from a through to d) facilitating evolution of increasingly advanced metabolic pathways in a marine setting.

There are many imaginable scenarios for the impact and determining processes of mineral facilitated HGT on the evolution of life. Because of the major gaps in our understanding of the interplay between minerals and DNA, we cannot currently quantitatively predict the longevity of mineral associated DNA in various environmental conditions, nor assess the impact on evolutionary events from the acting local sedimentation processes or geologic events (trans/regressions, tectonics etc.). Consequently, we need more information to pinpoint geochemical, phylogenetic, sedimentological or mineralogical signatures that could identify an event of mineral facilitated HGT in the geological record. Regardless, the high rates of HGT over time

since ~3 Ga highlight the significance of HGT on evolutionary innovations and we find it timely to combine geologic and genomic efforts to address the contribution of minerals in the evolution of life. We advocate that the high amount of DNA associated with minerals, can function as an archive for genes and evolutionary innovations, which could be distributed across environments and timescale at a rate that depends on mineral assemblages, sedimentary processes and the geochemical conditions. The subsequent effect in terms of species evolution would depend on the need for innovative adaptions and the availability of recipient organisms. Overall, we would encourage future studies to investigate the correlation between larger and smaller geological events and the prokaryotic evolutionary outbursts. We find that changes in the mineralogy of the geological setting would affect the longevity of mineral bound DNA and it availability for HGT. The mineral facilitated HGT holds a potential for a new principle for the evolution of life that calls for integrated studies of mineralogy, geology and evolutionary biology in a multidisciplinary effort to reassess and combining the historical geology.

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