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Review of the Unique Mode of Evolution of Bacteria: An Opinion

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Received June 5, 1996; Accepted August 25, 1996

Abstract

Bacteria have evolved as a single clone, with collaborating but disjunct cells whose offspring has become increasingly specialized. During their long evolution the ability of different bacteria to associate into cooperating entities has developed so extensively that bacterial communities behave like dispersed-cell multicellular organisms. Their adaptation to change involves continuous local selection of more appropriate strains to replace the temporarily less successful ones. Each bacterial cell furthermore can act as a donor and a recipient of genes. Unique to prokaryotes, mechanisms for frequent DNA exchange allow quick and efficient adjustment to new environmental conditions providing bacteria with a worldwide communication system. Associations and genetic exchange between bacterial cells permit complex functions that would be impossible for tiny unicellular organisms if they were independent of each other. Because different bacteria associate so easily, the opportunity for successful symbioses including those that led to the origin of the eukaryotic ancestor was enhanced. So were the chances of association of bacteria with subsequent progeny of the early eukaryotes and their descendants. Symbioses between bacteria and many different eukaryotes produced major innovative evolutionary events, e.g. the origin of plant cells by association with cyanobacteria. The colonization of the continents by plants followed by other abundant and diversified life ultimately depended on bacterial cell symbiotic associations.

Keywords: Bacterial individuality, bacterial evolution, bacterial communities, bacterial symbioses.

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1. Cellular Solidarity in Local Communities

The unique evolution of bacteria and the decisive role they have played for 3,500 million years in the organization and maintenance of life on Earth are still ignored or severely underestimated by most biologists (Mathieu and Sonea, 1995; Zook, 1995). Prokaryotes, both bacteria and archaea (Woese et al., 1990) were the only form of life on Earth for the first two billion years of its history. Their offspring gradually occupied every available niche on our planet and the ancestral clone slowly diversified by random mutation its ancient genome (Fig. 1). Genes for photosynthesis appeared early in the history of life on the planet. Photosynthetic bacteria increased tremendously the channeling of energy into the synthesis of more living cells. The stock of successful genes was perpetuated in growing progeny. Genes from the beginning were also acquired horizontally by neighbouring bacteria, most likely through an early form of transformation. Complex extant bacterial associations suggest that early and progressively prokaryotes resorted to cooperation.

We explore the question of why bacteria still have not evolved towards larger, more complex multicellular organisms but rather towards structurally simple and increasingly specialized cells that complement each other. Most bacteria live in closely knit, efficient and adaptable communities formed by isolatable and characterizable strains that biochemically and genetically support each other. We suggest that the activities of bacteria in communities that usually produce local homeostases significantly contribute to the environment and together maintain the global milieu (the biosphere). Bacteria as they collaborate practicing an advanced form of division labor, provide many examples of experiments in the multicellular lifestyle (Andrews, 1995). Bacterial life is highly relevant to the interpretation of major ecological and evolutionary trends. Often different bacterial strains cannot be isolated from other members of the communities and cultivated on artificial media. This hampers progress in the study of bacterial diversity. Many bacteria are so specialized in community life that they depend on peculiar, often unknown, nutritional factors provided by companion members of the local interacting populations. The living part of a fertile soil is formed by abundant and interdependent microbial populations that represent roughly a third of the dry weight. Similar abundant microbial communities dwell on the ocean floor. Others, less extensive, exist in the digestive cavities of insects, mammals and other animals, being especially complex in cellulose-ingesting herbivores. As the global bacterial clone complexified, evolutionary pressures apparently favored mutualistic interactions (de Repentigny and Mathieu, 1974) so that the hallmark of evolution of prokaryotes has been division of labor, genetic exchange and strong long-term interaction in adapting communities.

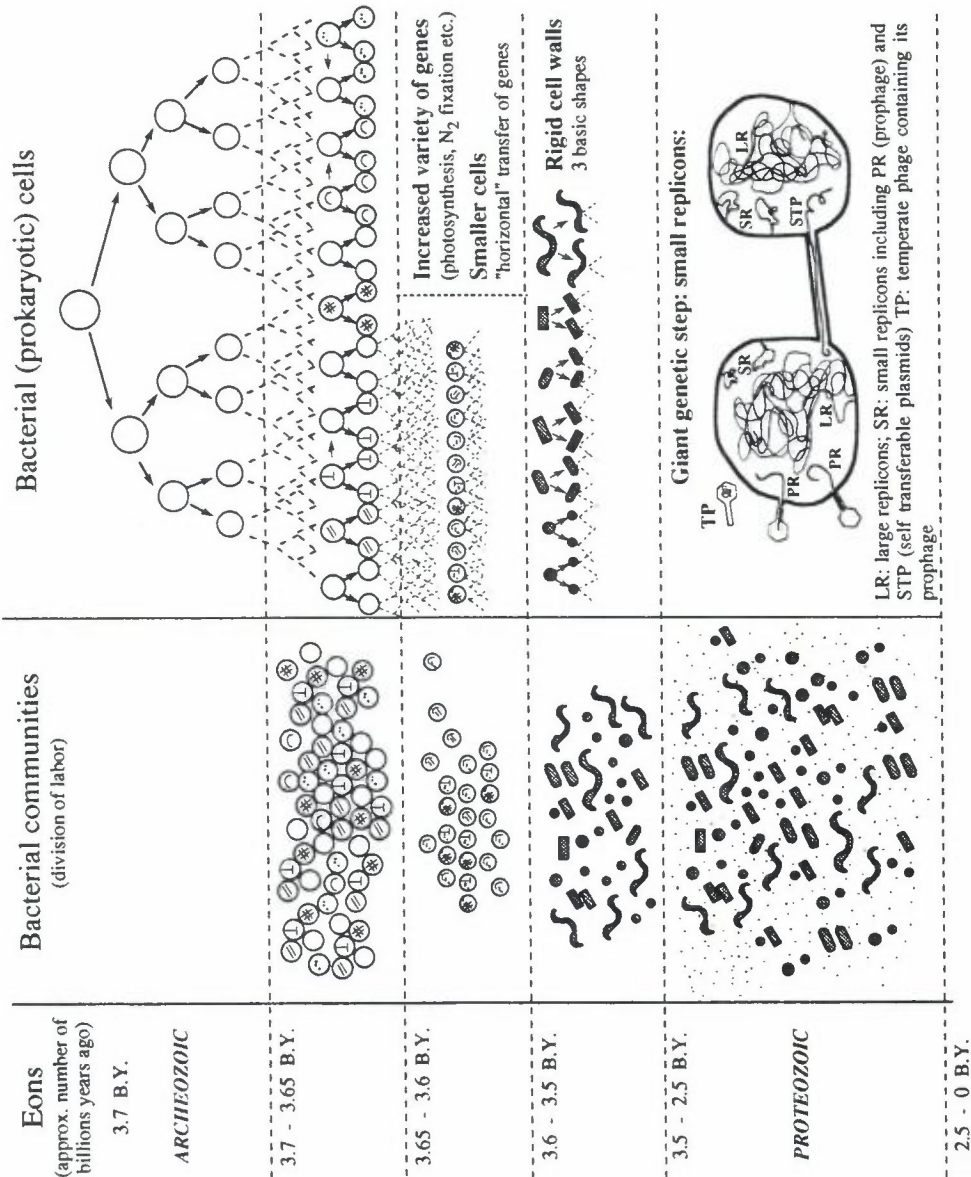


Figure 1. Schematic representation of bacterial evolution from the original progenitor to a unified, global labor-sharing and gene-exchanging entity. Starting as a clone from the ancestral prokaryotic cells, new genes appeared by mutation. If useful in any given environment they were selected for, retained and eventually transferred to offspring, and horizontally. Bacteria with certain metabolic abilities were progressively selected to fit into different communities and to associate easily. Mechanisms for gene exchange, release and transfer also improved. Today members of all bacterial communities contain many small replicons (represented by black dots in the proteozoic era, center column).

2. Exchange of Genetic Material by Bacteria

Exchange of hereditary material among bacteria is highly refined and it has been essential to bacterial evolution. Transformation, most likely the oldest genetic exchange process, is the mechanism by which small "foreign" DNA molecules are bound, actively taken in and integrated by another bacterium (Dreiseilkelmann, 1994). Receptivity (competence) which evolved as an inducible physiological property encoded by specialized genes or parts of operons (Lorenz and Wackernagel, 1994) is present in about half of the existing strains examined. Observations indicate that such "horizontal gene transfer" can occur in natural bacterial, including archaebacterial populations, more frequently than was believed previously (Lorenz and Wackernagel, 1994).

Genome-modifying processes in bacteria are not limited to mutation and transformation. Probably the most innovative process has been the formation of small, movable and interchangeable replicons (plasmids and prophages). These common vehicles for transport of genes apparently evolved long before the origin of the first eukaryotes (Ackermann and DuBow, 1987). They are temporarily shared, "visiting", self-replicating and often self-transmissible DNA molecules which carry genes for their own transfer and also a few potentially useful, ("converting") genes for the different prokaryotic cells they "visit". Small replicons are always present but on a temporary basis in any bacterium. They transfer as genes the information for their integration and often their release and have therefore evolved as a highly efficient general system of prokaryotic communication. This became strikingly evident in the last forty years as drug resistance of pathogenic bacteria appeared worldwide due to resistance genes brought to different strains by plasmids or prophages (Watanabe, 1963; Richmond and John, 1964; Reanney, 1976). Microbial ecologists identified and reported similar situations with the acquired resistance of bacteria exposed to some natural or waste-produced toxic substances (Schütt, 1989).

Prophages also provide an additional gene transmission-amplifying system: the spontaneous induction of lysogenic (prophage-carrying) strains which occurs in one out of a few thousand bacteria of lysogenic strains in each generation. Each lysed bacterium liberates about one hundred temperate phages (the virus-like, transfer forms of prophages) together with its large replicon ("chromosomal" genes). These also become available for exchange. Some 25-30% of all studied bacterial strains are lysogenic (Ackermann and DuBow, 1987), leading us to estimate that billions of temperate phages and copies of other genes are incessantly released, distributed and available in the environment (Prescott et al., 1996). Bacterial genetic global communication is versatile and problem solving (Sonea, 1990). Every type of bacterium can access

the totality of the global prokaryotic genetic information. For the strain confronted with such a stupendous stock of available genes, consecutive mechanisms of choice ensures the best solution for a given set of circumstances. It usually begins with attraction and early selection by bacterial surface receptors. Then, some of the DNA molecules newly arrived in the receptive bacterium may be selectively cut in recombinogenic fragments (Arber, 1993) or diminished in number by restriction-modification systems. The ultimate gene choice is made as selected and integrated genes lead to new successful combinations allowing the host bacterium to outgrow the others. As on the Internet: a giant data bank, all the bacterial genes, exists from which the appropriate, contingent information is selected and used as necessary.

Once a newly-appeared gene proved advantageous for one strain of bacteria and was replicated in its host, it also became available to others. This not only guaranteed dissemination but also assured safekeeping of copies of useful genes. Another consequence of these selection-amplification-dissemination capacities has been the acceleration of the prokaryotic evolution comparable with the increasing pace of the technical and cultural evolution of mankind. Prior to the appearance of the earliest eukaryotes, probably around 1.5 billion years ago, bacteria had already synthesized and shared an immensely rich variety of genes which covered nearly all possible bacterial ways of life. Probably during that time prokaryotic life has branched into different, yet collaborative domains: the bacteria and the archaea. Thereafter, there was little or no need for entirely new genes.

3. The Superorganism Solution

We suggest that the entire prokaryotic world now functions as a global ensemble formed by the dynamic, opportunistic and temporary sharing of immensely abundant and differently materialized basic elements (cells, plasmids and prophages). These provide, on the one hand, their genetic information and, on the other hand, in complex communities, their metabolic know-how (Sonea and Panisset, 1983). Through these schemes of generalized collaboration the prokaryotic world has become an extremely resourceful giant superorganism (Mathieu and Sonea, 1995).

Very little room remains in a bacterial cell for silent (neutral) DNA. The appearance of new, functional genes in today's prokaryotes by series of non-lethal random mutations is unlikely and bacteria had probably completed the essential genetic inventory (every possible useful gene) compatible with life on our planet many million years ago. Existing genes and entire bacterial cells could easily be reshuffled then as they are now (Sonea, 1987). The stable

intracellular bacterial genome, the large replicon, in contrast to the eukaryotic genome, has been reduced to a minimum of essential information. All bacteria freshly isolated from nature in which small replicons have been sought possess such temporary hereditary supplements, between one to ten types of them. Subject to selection pressure any given small replicon is retained only as long as it is useful. Structural and morphological standardization was a natural consequence of the minimal genetic information carried by prokaryotes. After 3.5 billion years of evolution large replicons with minimal information are stored in bacterial cells whose shapes have remained simplified to three major types: spherical, cylindrical or spiral with a rigid, heteropolymer, peptidoglycan-based external envelope (cell wall).

4. Bacterial Cells, Small Replicons and the Origin of Eukaryotes

In the prokaryotes the cell is standardized for rapid proliferation and small replicon transfer permitting little opportunity for other genetic adventures. Only through a series of stable symbioses between interactive bacteria (motile, respiring, fermenting, able of photosynthesis, etc.) did another form of life appear. The ancestor of eukaryotes, perhaps an archaebacterial victim of motile spirochete predator, later acquired an eubacterium capable of aerobic respiration (the ancestor of the mitochondrion) (Margulis, 1993). The prophages and plasmids of these prokaryotes probably entered into this permanent and eventually irreversible endosymbiosis (Sonea, 1972). So equipped with a rich and versatile genome, this ultimate eukaryotic ancestor, according to serial endosymbiosis theory (SET) diverged towards a mitotic and eventually meiotic fertilization, one of the major evolutionary transitions in the history of life. We suppose that in the first millions of years of their existence, the new nucleated cells did not require gene transfer mechanisms for survival and hence lost them. The transfer mechanisms, the most advanced functions of the bacterial world, the global communication system (Sebeok and Umiker-Sebeok, 1992) at this junction was lost to the eukaryotes in which they were probably used to centralize the organelle genes in a nucleus rather than effect the release of small replicons to the environment.

5. Bacterial Symbioses and Evolutionary Innovations in Eukaryotes

Because of their genetic isolation eukaryotic organisms are the only beings to form species on our planet. Sexuality, genetic exchange between parents to form new genetically recombined individuals only partially compensated for the isolation because it requires exclusively mates of the same or of closely related

species. Thus meiotic fertilization sexual systems produce relatively minor variations. One consequence of the bacterial complementary symbioses that lead to eukaryotes (Margulis and Fester, 1991) was the origin of the genetic isolation which had an enormous impact on the subsequent evolution of life.

Photosynthesis, the major contribution of life to planet Earth, evolved only in prokaryotes. Many unicellular eukaryotes established symbioses with photosynthetic bacteria, particularly cyanobacteria. The resulting unicellular algae still populate oceans and lakes. On the continents lichens and complex plants formed by symbiogenesis. Bryophytes and tracheophytes produce branching roots that increase access to water and minerals from below the surface of soils. These are carried through conduits to vertical stems. This plant tissue supports the exposure to sunshine of fronds, leaves or needles containing chloroplasts (descendants of former cyanobacteria). The plants thus expose to sunlight an enormously larger surface than the previous, thin bacterial cover on the soil. The increasingly complex plants prospered and around 450 million years ago they covered much of the continents with abundant growth. Benefiting from this rich new biomass, land-dwelling animal species evolved. So did the soil bacteria. This put an end to the 3 billion years of practically lifeless continents. A most fateful evolutionary innovation on the continents, and a giant evolutionary transition was the extension of photosynthetic cyanobacteria to the third dimension by plant tissue.

Other symbioses between multicellular eukaryotes and bacteria followed, giving rise to, for example, nitrogen fixation in many plants. The ruminants (cattle, sheep, deer, etc.) use assimilable hydrocarbons obtained in their rumen from cellulose by a complex community of bacteria and ciliates. Many insect species depend on their symbiotic bacteria. Some marine animals generate methane and survive by sulfide oxidation because they harbour symbiosis with methanogens and sulfide oxidizers, respectively. Life, as we know it today, is inconceivable without products of symbiosis between prokaryotic and eukaryotic organisms.

6. Conclusion

Bacteria evolved in a unique way based on genetic exchange and release into the environment of exchangeable genes. They benefited from widespread and increasingly complex solidarity. The fate of eukaryotes, which evolved from prokaryotes as a different domain, remains closely associated with that of the bacteria which are still essential stabilizers of the biosphere and safekeepers of an enormous and available pool of genes. Bacteria with their much longer

evolution and history represent "the other" half of the living world. Both solidarity in the promotion of stable communities and competition in their rapid growth rates after reversible acquisition of genes from each other work as constructive and unifying forces. Because of their generalized complex associations prokaryotes should be understood as a single superorganism – a single species – with different components and global functions. This single bacterial entity has, to the present day, adjusted to the pervading presence of their distant offspring, the eukaryotes. It has collaborated in different ways with the sexually isolated eukaryotes, notably through symbioses yielding momentous evolutionary impact.

Human technological excesses could unbalance the present equilibrium simply by ignoring bacterial existence and the role of their superorganism in maintaining the biosphere. We recommend that the lingering eukaryotic-centered "tunnel vision" of some evolutionists and biologists be reconsidered in favor of a broader, more complex and more accurate description of evolution. Consideration needs to be given to the immense and versatile pool of genetic information available to bacteria and the ubiquity and global function of the prokaryotic domain.

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