



SIMPOSIO INTERNACIONAL
INTERNATIONAL SYMPOSIUM



CONTRIBUCIÓN DE LOS MICROBIOS A LA BIOLOGÍA
THE MICROBE'S CONTRIBUTION TO BIOLOGY

Barcelona, 27-28 abril 2006

Institut d'Estudis Catalans
C/ del Carme, 47 – 08001 Barcelona

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Organized by: **Fundación Ramón Areces**, with the collaboration of the **Institute for Catalan Studies**

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Introducción

En el año 2006 se cumple el 50 aniversario de la publicación del libro *The Microbe's Contribution to Biology*, de Albert J. Kluver y Cornelis B. van Niel. Dicho libro está basado en las prestigiosas conferencias "John M. Prather" que impartieron ambos científicos en la Universidad de Harvard en abril de 1954 y que marcaron un hito en la microbiología contemporánea. El libro mostraba la contribución de los microorganismos a los conocimientos generales de la biología y ofrecía una síntesis de los avances en la comprensión del metabolismo y la genética en las bacterias y trataba de la diversidad y la uniformidad bioquímica de los seres vivos. El libro de Kluver y van Niel ofrecía una nueva perspectiva del mundo microbiano que representó un cambio de paradigma en la investigación y en la enseñanza de la microbiología en todo el mundo. Kluver, considerado el padre de la bioquímica comparada, y su discípulo Van Niel abogaban por la unidad metabólica de la vida y proponían la utilización de los microorganismos para dilucidar las vías bioquímicas y las transformaciones de energía de todos los seres vivos. Era un modelo que ponía de manifiesto la relación existente entre todas las formas de vida por medio del reciclado de la materia, y la conexión de todos los organismos entre sí a través de la red de los ecosistemas. Hoy día, otra rama de la biología con una gran componente interdisciplinar, la ecología microbiana, ofrece la perspectiva más aventajada para entender la unidad inherente a la aparente diversidad de la vida.

La microbiología, ciencia todavía joven, se encuentra en un período de gran vitalidad, lo cual se debe, por una parte, a su extraordinaria diversidad y, por otra, a la incorporación de diversos avances tecnológicos. Desde sus comienzos, la investigación microbiológica y sus aplicaciones han

ejercido una gran influencia en la sociedad. Los numerosos avances conceptuales de esta ciencia tienen aplicación práctica en la resolución de problemas de índole muy variada que aquejan a la sociedad contemporánea. Y precisamente estamos ahora en un año especial para la microbiología: el último premio Nobel de Fisiología o Medicina ha sido concedido a dos bacteriólogos australianos, Barry J. Marshall y J. Robin Warren, por su trabajo pionero sobre *Helicobacter pylori*. La microbiología se encuentra, tal como se ha escrito, en su "Tercera Edad de Oro".

El objetivo del Simposio es evaluar el progreso de la microbiología desde la publicación del libro de Kluver y van Niel, y reflexionar sobre los cambios producidos, la situación actual y el futuro que se vislumbra para la microbiología, desde una perspectiva amplia y multidisciplinar. Para ello, un grupo de expertos representantes de las principales áreas de la microbiología expondrán su punto de vista, combinando la perspectiva histórica con sus aportaciones al desarrollo de la microbiología desde su propia experiencia y especialidad.

Introduction

In 2006 we commemorate the 50th anniversary of the publication of *The Microbe's Contribution to Biology*, by Albert J. Kluver and Cornelis B. van Niel. The book is based on the prestigious "John M. Prather" lectures that both scientists gave at Harvard University in 1954 and that were a landmark in contemporary microbiology. The book showed the contribution of microorganisms to the general biological knowledge. In addition, it offered a synthesis of the advances in the understanding of bacterial genetics and metabolism, discussed the biochemical uniformity and diversity of living beings. A new perspective of the microbial world was offered that meant a paradigm shift in microbiological research and teaching of this science worldwide. Kluver, considered the father of compared biochemistry, and his disciple van Niel postulated the metabolic unit of life and proposed the use of microorganisms to elucidate the biochemical pathways and the transformations of energy in all living beings. Their model showed up the relationship existing between all forms of life by means of both matter recycling and the connection of all organisms through the network of ecosystems. Nowadays, another branch of biology with a great interdisciplinary component, microbial ecology, offers the most advantageous perspective to understand the inherent unity in the apparent diversity of life.

Microbiology, still a young science, is currently thriving, mainly due to its extraordinary diversity and to the use of technological advances. From its very beginning, microbiological research and its applications have exerted a great influence on society. The numerous conceptual advances of this science have practical applications in the resolution of a wide range of problems that affect contemporary societies. And this a especial year for microbiology: the latest Nobel prize on Physiology or Medicine has been awarded to two Australian bacteriologists, Barry J. Marshall and J. Robin Warren, for their pioneering work on *Helicobacter pylori*. Microbiology is, as it has been written, in its "Third Golden Age".

The objective of the Symposium is to evaluate the advances of microbiology since the book by Kluver and van Niel was published, by analyzing the changes produced, the current situation and the prospects of microbiology, from a wide multidisciplinary perspective. To achieve this goal, a group of experts representing major fields of microbiology will show their own points of view, offering also a historical perspective, and their own contributions to the development of microbiology from their own experience and field of expertise.

PROGRAMA CIENTIFICO / *SCIENTIFIC PROGRAM*

JUEVES, 27 DE ABRIL / THURSDAY, APRIL 19TH

SESIÓN DE MAÑANA / MORNING SESSION

09:00 h Inauguración del Simposio / *Opening Ceremony*

Julio R. Villanueva

Vice-presidente del Consejo Científico

Fundación Ramón Areces

Stanley Maloy

San Diego State University, CA, USA.

Presidente de la ASM, Washington, DC, USA

Ricardo Guerrero

Departamento de Microbiología, Universidad de Barcelona

Coordinador del Simposio

Presentación de los objetivos del Simposio

Presentation of Symposium objectives

PRIMERA SESIÓN / FIRST SESSION

Moderador / *Chairperson*: Stanley Maloy

09:30 h De la fisiología del crecimiento bacteriano a la biología de sistemas

From bacterial growth physiology to systems biology

Moselio Schaechter

San Diego State University / UC San Diego, CA, USA

10:15 h Las dos caras del concepto de procariota: organizativa y filogenética

Two faces of the prokaryote concept: organizational and phylogenetic

Jan Sapp

York University, Toronto, Ontario, Canada

11:00-11:30 Descanso

SEGUNDA SESIÓN / SECOND SESSION

Moderador / *Chairperson*: Rubén López

11:30 h Evolución del concepto de patogenia bacteriana

Evolution of the concept of bacterial pathogenesis

Fernando Baquero

Hospital Ramón y Cajal, Madrid

12:15 h Patógenos bacterianos que esquivan la inmunidad innata: el vínculo

endosimbótico

Bacterial pathogens that hide from innate immunity: the endosymbiotic link

Ignacio Moriyón

Universidad de Navarra, Pamplona

13:00-16:00 Descanso

SESIÓN DE TARDE / AFTERNOON SESSION

Moderador / *Chairperson*: Thomas M. Schmidt

- 16:00 h Edouard Chatton (1883-1947), vida y obra
Edouard Chatton (1883-1947), life and work
Marie-Odile Soyer-Gobillard
Observatoire Océanologique de Banyuls-sur-Mer, CNRS, France
- 16:45 h Extremófilos, antes y ahora: diversidad y fisiología
Extremophiles, then and now: diversity and physiology
Milton S. da Costa
Universidade de Coimbra, Portugal
- 17:30 h. “La unidad y flexibilidad de la vida”: la conexión ecológica
“Life’s unity and flexibility”: the ecological link
Ricardo Guerrero
- 18:15 h Metales pesados, bacterias y medio ambiente
Heavy metals, bacteria and environment
José Antonio Gil
Universidad de León

VIERNES, 28 DE ABRIL / FRIDAY, APRIL 28

SESIÓN DE MAÑANA / MORNING SESSION

PRIMERA SESIÓN / FIRST SESSION

Moderador / *Chairperson*: Enrique Herrero

- 09:30 h. From pathogenesis to genetics to evolution and back again: *Salmonella*'s contributions to biology
De la patogenicia, a la genética, a la evolución, y vuelta a empezar: contribución de *Salmonella* a la biología
Stanley Maloy
- 10:15 h Biología del neumococo
Pneumococcus biology
Rubén López
Centro de Investigaciones Biológicas, CSIC, Madrid

11:00-11:30 Descanso

SEGUNDA SESIÓN / SECOND SESSION

Moderador / *Chairperson*: Milton S. da Costa

- 11:30 h La contribución de los virus a la biología
Virus contribution to biology
Esteban Domingo
Centro de Biología Molecular, CSIC-UAM, Madrid

12:15 h La contribución de las levaduras a la biología
Yeast contribution to biology
Enrique Herrero
Universidad de Lérida

13:00-16:00 Descanso

SESIÓN DE TARDE / AFTERNOON SESSION

Moderador / *Chairperson*: Marie-Odile Soyer-Gobillard

- 16:00 El ascenso de la ecología microbiana
The rise of microbial ecology
Thomas M. Schmidt
Michigan State University, East Lansing, MI, USA
- 16:45 Genómica del mar
Marine genomics
Carles Pedrós-Alió
Instituto de Ciencias del Mar, CMIMA, CSIC, Barcelona
- 17:30 h Relaciones planta-microbio. Aplicaciones de microorganismos beneficiosos en el control de las enfermedades de plantas
Plant-microbe relationships. Applications of beneficial microorganisms in plant disease control
Emilio Montesinos
Universidad de Gerona
- 18:15 h. Taxonomía de los procariotas: en busca del sistema natural, si es que existe
Prokaryotic taxonomy: in search of a natural system, or does one even exist?
Gary O. Olsen
University of Illinois, Urbana, IL, USA
- 19:00 h Conclusiones y perspectivas
Conclusions and perspectives
Jan Sapp, Ricardo Guerrero
- 19:30 h Clausura del Simposio
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ABSTRACTS

FROM GROWTH PHYSIOLOGY TO SYSTEMS BIOLOGY

Moselio Schaechter

San Diego State University and University of California, San Diego, CA, USA

mschaech@sunstroke.sdsu.edu

As it focuses on the integrated behavior of the entire cell, systems biology is a powerful extension of growth physiology. Here, I briefly trace some of the origins of modern-day bacterial growth physiology and its relevance to systems biology. I describe how growth physiology emerged from the foggy picture of the growth curve as a self-contained entity. We can thank for this the insights shaped by Henrici, Hershey, Monod, Campbell, Maaløe, and others. As a result, the growth rate is understood to be the unitary manifestation of response to nutritional conditions and the control condition for studies on the effect of environmental stresses. For this to be usefully reproducible, cultures must be in the steady state known as balanced growth. I point out that present day experimenters are not always aware of this imperative and do not always use conditions that ensure the balanced growth of their control cultures.

Keywords: bacterial growth · physiology · systems biology

TWO FACES OF THE PROKARYOTE CONCEPT: ORGANIZATIONAL AND PHYLOGENETIC

Jan Sapp

York University, Toronto, Ontario, Canada

jsapp@yorku.ca

Bacteria had remained undefined for century when, in 1962, Roger Stanier and C.B. van Niel published their famed paper “The Concept of a Bacterium”. Their formulation of the prokaryote-eukaryote dichotomy marks a signal moment in the history of biology. This paper aims to provide a brief overview of how the prokaryote concept was constructed and what it implied for bacterial classification and phylogeny. Two concepts intermingled within the prokaryote-eukaryote dichotomy. One was organizational; it referred to comparative cell structure. Based on contemporary data from molecular biology and electron microscopy, the prokaryote concept was designed to close long-simmering issues. It confirmed the similarity between the organization of bacteria and “blue-green” algae, and articulated their differences to viruses and the cells of protists, fungi, plants and animals. The other concept was phylogenetic; it referred to a natural classification. Microbial taxonomy of the first half of the twentieth century had been infused with methodological debates over whether one could have a natural classification of bacteria that reflected evolutionary relationships. Most bacteriologists of the first half of the century agreed that a bacterial phylogeny was speculative and impossible and that the classification of bacteria should be determinative, based solely on utility—like the organization of library books. Van Niel and Stanier had argued for a classification based on genealogies. However, by 1955, they had abandoned that hope. From its very inception, the prokaryote concept was associated their views that a natural system of bacterial classification was a waste of time. The prokaryote-eukaryote dichotomy, as Stanier and van Niel initially formulated it, was an organizational distinction only. During the 1960s, however, the meaning of that dichotomy quickly changed so as to signify phylogenetic taxa. Although the monophyly of the prokaryotes was untested and unproven, the fundamental commonality among bacteria was naturalized within the kingdom Monera or superkingdom, *Prokaryotae*. It might seem paradoxical to maintain that one could not have a genealogical classification of bacteria based on structure, and yet assert that prokaryotes were a natural phylogenetic group on the same basis. But no microbiologists of the 1960s questioned it. The belief in the monophyly of the prokaryote was backed by historical inertia and strengthened by molecular biology’s focus on the model organism, *E. coli* as representative of all prokaryotes. It was not until 15 years after its formulation that the prokaryote-eukaryote dichotomy was challenged with the emergence of the field of molecular evolution and the development of coherent methods for bacterial phylogenetics based on 16S rRNA. Corroborated by certain unusual phenotypic traits including cell membrane and cell wall structure, proteins involved in the translation processes, and a host of other phenotypic differences, the rRNA data indicated fundamental phylogenetic differences among bacteria, as represented in the three domain proposal of Bacteria, Archaea and Eucarya. This trifurcation was based on phylogenetic distance and common ancestry, but, critics argued, it failed to consider the amount and nature of evolutionary change; it obscured the phenomenal morphological differences between prokaryotes and eukaryotes.

Keywords: prokaryote · eukaryote · phylogeny · evolution · taxonomy

EVOLUTION OF THE CONCEPT OF BACTERIAL PATHOGENESIS

Fernando Baquero

Ramón y Cajal University Hospital, Madrid, Spain

baquero@bitmailer.net

I am convinced that least part of the influence of Cornelius van Niel in Spanish microbiologists involved in clinical microbiology and pathogenesis was due to my continued close relation with one of the most prominent pupils of van Niel: my friend Carlos Asensio (1925-1982). Quoting Gad Avigad, and accordingly with my own experience, Carlos never ceased to glorify his experiences in the summer course in microbiology with van Niel (1961). For an analytical biochemist, a wide door for ecological synthesis of natural phenomena was opened, and from this very moment, the Carlos's mind was re-oriented in another way. When he learnt that I had presented a Thesis in clinical microbiology plenty of ecological concepts, he came to my lab and a great collaboration started in the first 70's, leading ultimately to the discovery of microcins as possible ecological effectors of microbial interactions in the gut microbiota (1974). During the next thirty years, the concept that most infectious diseases results from ecopathies, and that bacterial pathogenesis should be understood as an ecological problem, has been progressively imposed in the scientific field. Even though bacterial diseases remain one of the leading causes of human and animal morbidity and mortality, we do not consider bacteria, even pathogenic bacteria, as "our natural enemies" any more. We know now that all bacteria are intrinsically innocent, but—as all of us, in a Franciscan way—compelled to survive and evolve. Unfortunately, the ability of *Homo sapiens (sapiens?)* to produce deep environmental changes in nature, as a catabolic process resulting from our growth, is probably changing our relations with the microbial world. The release of industrial compounds able to damage microbes, including heavy metals and antimicrobial agents, is certainly changing the ecological landscape of the microbial ecosystems that are closer to humans, and that should result in a break of the old-established interactions between our species and the bacterial organisms. For instance, we know now that an important part of the antibiotic resistance determinants creating critical problems of therapy in hospitals had evolved from soil bacteria. It is here appropriate to mention the organism *Kluyvera*, as it honours the name of Kluyver, that we honour here together with van Niel. Gene capturing sequences enriched by antibiotics in hospital-based bacteria had recruited *Kluyvera* genes encoding novel hyper-destructive enzymes inactivating the more advanced antibiotics. Our relation with microbes is a continuing process, and anthropogenic-driven changes in nature might result in re-orientations of the microbial networks, both in the deep machinery of cell function and in bacterial interactions, with unpredictable pathogenic and ecological consequences that we should commit ourselves to predict. Fortunately, in recent years, more powerful tools are available that permits to make progresses in the understanding the population biology of bacteria, to identify, much beyond the "pathogenic species", both in downwards (pathogenic clones, pathogenic genes, pathogenic sequences) and upwards directions (pathogenic communities) the pathogenicity units. Finally, the responsibility of the host in pathogenesis is now recognized as critical, helping to conceive bacterial pathogenesis as a "pathology of interactions".

Keywords: van Niel · Carlos Asensio · pathogenesis

**BACTERIAL PATHOGENS THAT HIDE FROM INNATE IMMUNITY:
THE ENDOSYMBIOTIC LINK****Ignacio Moriyón**

University of Navarra, Pamplona, Spain

imoriyon@unav.es

The ability to distinguish self from non-self is the cornerstone of adaptive and innate immunity. In the last decade, it has become apparent that innate immunity mechanisms are deeply rooted in evolution and that they act by recognizing pathogen associated molecular patterns (PAMPs) absent from self and repeatedly used by microbes. To this end, eukaryotes have developed pathogen recognition receptors (PRR) that detect microbes by their PAMPs. Molecules bearing PAMPs include bacterial lipoproteins, some nucleic acid motifs, flagellin, peptidoglycan, and the outer membrane (OM) proteins and lipopolysaccharide (endotoxin or LPS) of Gram-negative bacteria. Examples of PRRs are the bactericidal peptides and proteins, the mannose binding protein, some complement components and the toll-like and Nod receptors of cells. PRRs often trigger inflammatory responses in vertebrates, thus bolstering the initial steps of the adaptive immune response. Molecules bearing PAMPs admit little change because of functional restrictions. Therefore, most microbial pathogens counteract immunity by means of adhesines, flagella, surface masking capsules, antigenic variation, exotoxins, exoenzymes, and type III and IV secretion systems. Accordingly, horizontal acquisition of a small number of genes, often carried in plasmids, lysogenic phages or assembled in pathogenicity islands, turn attenuated strains into virulent forms. Some intracellular bacteria, however, lack most of such factors. Among these pathogens stand the members of the genus *Brucella*, the agents of brucellosis. In nature, the *Brucellae* do not perpetuate outside their hosts but behave as chronic intracellular parasites. They are thus different from other intracellular gram-negatives like *Salmonella* that cause acute inflammatory syndromes. We have noted that *Brucella* virulence is linked to the toughness and the lack of marked PAMPs of its OM. This OM carries an LPS devoid of a typical PAMP and phosphatidylcholine, a typically eukaryotic phospholipid. A sensory/regulatory system (BvrR/BvrS) controls the expression of OM proteins as well as some structural aspects of the LPS lipid A section. Experimental data show that the *Brucellae* escape innate immunity by virtue of these OM components and the properties linked to them. Although these structural factors are complemented by the activity of cyclic β -glucans (C β Gs), quorum-sensing, flagella-like and VirB elements, the importance of the OM to avoid the rapid adaptive immune response linked to inflammation is critical for *Brucella* to establish a chronic infection. This strategy, and the use of an infectious route devoid of harmful OM permeants, compensate for the loss of those OM functions associated to typical PAMPs. This hypothesis may apply to bacteria with similar OM structures, such as *Legionella*, *Ehrlichia* and *Bartonella*. *Brucella* is placed in the α -2 *Proteobacteria*, along with other gram-negatives that act as intracellular or pericellular parasites of animals and plant endosymbionts. Mitochondria have also been assigned to the α -2 *Proteobacteria* on the basis of rRNA analysis. Whereas the physiological similarities between mitochondria and bacteria have drawn attention, the possibility that the mitochondrial ancestor had to overcome potential predated/non-self recognizing systems has received less attention. The existence of mitochondria-related bacteria able to escape innate immunity suggest some lines of thought to address this point.

Keywords: virulence · pathogenicity · innate immunity

EDOUARD CHATTON (1883-1947): LIFE AND WORK

Marie-Odile Soyer-Gobillard

Oceanological Observatory "Laboratoire Arago", Banyuls-sur-mer, France

mog66@wanadoo.fr

Edouard Chatton contributed to our knowledge of single-celled protists, especially ciliates and dinoflagellates, free-living and/or symbiotic, in relation to the marine invertebrate animals in which they reside. More than the description of numerous new families, genera and species, more than the description of their life cycle, he anticipated some of great concepts of cell biology: (1) the fundamental difference between prokaryote and eukaryote protists, long time before use of the electron microscope, (2) the reproductive ability of the system kinetosome-centriole, the homology of the kinetosome with the mitotic centriole of animal cells, (3) the different kinds of mitotic systems... He trained more than thirty students-collaborators among them André Lwoff and Jacques Monod, who won the Nobel Prize of Medicine. Later, the great cell biologist Hans Ris and also myself, we completed Chatton's descriptions which he made with the light microscopes of that time on the dino- and syndinian mitosis: but we had at our disposal sophisticated electron microscopes, biochemical and molecular techniques to try to understand mitotic machinery and complex chromosome structure.

Keywords: prokaryotes · eukaryotic microbes · cell biology

EXTREMOPHILES, THEN AND NOW: DIVERSITY AND PHYSIOLOGY

Milton S. da Costa

Universidade de Coimbra, Coimbra, Portugal

milton@ci.uc.pt

Microbiologists were, as it would be expected, initially interested in microorganisms that caused disease or participated in useful fermentations. Infectious diseases like tuberculosis, pneumonia, influenza were rampant and caused numerous deaths. Organisms involved in food production or that caused their spoilage were economically important and therefore studied. Other organisms had to wait to be discovered and studied. The term “Extremophile” was apparently coined by R. M. Macelroy in 1974 to denote organisms that grow under extreme conditions of temperature, pH, extreme hydrostatic pressure, high salt concentrations or which survive extreme doses of gamma radiation. In many instances the term has been used in connection with biotechnological studies on organisms which might produce enzymes or metabolic products with properties not found in organisms that grow under “milder” environmental conditions. We now generally define extremophiles as organisms that grow in environments of low biodiversity, although it is still difficult to circumscribe microbial environments and we still know little about the diversity of these environments. The first thermophiles and halophiles were studied because they were important in food spoilage, this being the case with thermophilic Gram-positive bacteria which spoil canned products and red-pigmented extremely halophilic archaea which grow on and spoil salted fish. In time, microbiologists began to correlate these unusual organisms with specific natural environments. The ecological perspective led to the accelerated isolation and study of these organisms, because microbiologist knew where to look for so-called extremophiles. The later development of 16S rRNA gene sequence analysis, led us to understand the evolutionary implications of these organisms in terms of the origin of life and adaptation to harsh growth conditions. Moreover, some of these organisms have produced important enzymes for industrial processes and the Taq polymerase (from *Thermus aquaticus*), for example, led to the development of an era of molecular biology-based studies based on PCR-based methodologies. An ecological perception that slightly halophilic thermophilic organisms like, mesophilic counterparts, also accumulate compatible solutes during osmotic adaptation led to the identification of a large number of novel small organic solutes that are generally not found in mesophilic organisms. Some of these compatible solutes, namely mannosylglycerate and di-*myo*-inositol-phosphate may also contribute to growth at supraoptimal temperatures. The examination of genes coding for the enzymes involved in the synthesis of mannosylglycerate also led to identification of genes in mycobacteria whose products might represent targets for drug therapy. We have in a sense come full circle by studying thermophiles, slightly halophilic thermophilic organisms and then mycobacteria, which are not considered extremophiles.

Keywords: extremophiles · thermophiles · halophiles · extreme radiation resistance · compatible solutes

“LIFE’S UNITY AND FLEXIBILITY”: THE ECOLOGICAL LINK

Ricardo Guerrero

University of Barcelona, Spain

rguerrero@iec.cat

In 1956, Albert J. Kluyver (1888–1956) and his former student, Cornelis B. van Niel (1897–1985), published *The Microbe's Contribution to Biology*, a small book based on the John M. Prather Lectures that the authors had delivered at Harvard University in April 1954. Kluyver, the father of comparative biochemistry, promulgated the idea of the unity of life and the use of microorganisms to elucidate biochemical pathways and energy transformations. The purpose of the lectures was to consider how biologists' outlook on life would have differed if they had remained unaware of all forms of life invisible to the naked eye. It is clear that this attitude would inevitably have led to a serious under-evaluation of life's potentialities. Prokaryotic microorganisms were the first inhabitants of Earth, which is 4.55 billion years old, and biopoiesis may have taken place on our planet as early as 3.85 billion years ago. While the known original features of our two nearest neighbors in the Solar System, Venus and Mars, might have been conducive to the appearance of life, it probably could not have been maintained on either of those planets. However, something special happened on Earth that allowed life to persist: the establishment of ecosystems among prokaryotes, or ecopoiesis. Without the early cycling of matter, nascent prokaryotic life on Earth would have exhausted our planet's elements and life would have become extinct less than 300 million years later. Over the first two billion years of prokaryotic evolution, almost all metabolic strategies came into being. Prokaryotes are the basis upon which other forms of life have arisen. Symbiotic associations among prokaryotes were the progenitors of all the complex and varied biological forms that followed and now exist on Earth, giving place to the eukaryotic cell. Microbial symbioses with animals, plants, and other microorganisms are wide-ranging in their variety and common in natural communities. These symbioses are essential to the livelihood of both the microorganism and its partners. Without microbial symbionts, most animals and plants could not survive in natural environments. Microbes inhabit all possible locations in which life exists, from those offering “ideal” conditions for growth (from the point of view of “macroorganisms”, of course) to those characterized by extreme conditions. The ubiquity of microorganisms is based on three major characteristics: their small size, which facilitates their dispersal; their metabolic versatility and flexibility; and their genetic plasticity (horizontal transfer), which allows them to tolerate and adapt quickly to unfavorable and/or changing environments. “Life is a special property of matter at a certain stage of complexity” (Kluyver). All life is connected by the cycling of matter and all organisms are connected through the web of ecosystems. Microbial ecology provides a most useful approach to understand the inherent unity in the apparent diversity of life. It is the study of natural processes, specifically, the interactions between microorganisms, and between microorganisms and other species and the environment. The study of microbial communities has raised questions about their composition, structure, and stability and about the activities and functions of their individual inhabitants. In the past, knowledge of microorganisms in the environment depended mainly on studies of axenic cultures in the laboratory. However, most microorganisms have so far resisted cultivation efforts. From the majority of habitats studied, less than 1% of the microorganisms observed by microscopy have been cultivated. Consequently, molecular biological techniques to detect and identify microorganisms by molecular markers, such as 16S rRNA or functional genes, are increasingly being used to explore microbial diversity and to analyze the structure of microbial communities. This has initiated an exciting era in microbial ecology. We are becoming aware that microorganisms constitute the basis for the functioning of the biosphere, especially through their cycling of elements, which affects the quality of all life on this planet as well as the shaping Earth's oceans and atmospheres. It is also a unique time in the history of science, as in the coming years the interaction of technological advances with the exponential increase in knowledge of the true extent of microbial diversity will allow significant advances in microbiology—and in biology and other sciences in general.

Keywords: ecopoiesis · symbiosis · microbial communities

HEAVY METALS, BACTERIA AND ENVIRONMENT

José A. Gil

University of León, Spain

degjgs@unileon.es

Many metals and metalloids play specific and essential roles in all living organisms, but when present in high concentrations produce severe threat to biota and human health. The contamination of soil, water and air by toxic metals is a growing environmental problem all over the world due to activities of metal processing, mining industry, burning of fossils fuels, uncontrolled landfilling of wastes, and agriculture or medical uses. Unlike organic contaminants, which can be degraded into harmless chemical species, metals and metalloids can not be destroyed but they can be immobilized or transformed into less toxic forms. Arsenic is an extremely toxic metalloid that adversely affects human health. It enters the water supply from geochemical sources (mining of arsenopyrite gold ores or leaching from geological formations), from anthropomorphic sources, such as medical chemotherapeutics agents, agricultural (arsenical-containing fungicides, pesticides and herbicides), and industrial uses. The toxicity of arsenate (AsV) and arsenite (AsIII) have been associated with increased risk of skin, kidney, lung, and bladder cancer. The ubiquity of arsenic in the environment had lead to the evolution of arsenic defense mechanisms, and the most common microbial mechanism is based on the presence of the arsenic resistance operon (*ars*). This operon encodes for (i) an enzyme involved in arsenate reduction *ArsC*, (ii) an arsenite permease *ArsB*, and (iii) a regulatory protein *ArsR*. *Corynebacterium glutamicum*, a microorganism used for the industrial production of amino acids and nucleotides, is one of the most arsenic-resistant microorganisms described up to date (12 mM arsenite and >500 mM arsenate). Analysis of the *C. glutamicum* genome revealed the presence of two complete *ars* operons (*ars1* and *ars2*) which show the typical three gene structure *arsRBC*. Operon *ars1* contains an additional *arsC* gene (*arsC1'*), located downstream from *arsC*. In addition, two orphan genes (*arsB3* and *arsC4*) were located scattered in the chromosome of *C. glutamicum*. The involvement of both *ars* operons in arsenic resistance in *C. glutamicum* was confirmed by gene disruption experiments of the three arsenite permease genes present in its genome. Wild-type and *arsB3* insertional mutant *C. glutamicum* strains were able to grow in 12 mM arsenite, whereas *arsB1* and *arsB2* *C. glutamicum* insertional mutants were resistant to 4 mM and 9 mM arsenite, respectively. The double *arsB1-arsB2* insertional mutant was resistant to only 0.4 mM arsenite and 10 mM arsenate. Gene amplification assays of operons *ars1* and *ars2* in *C. glutamicum* revealed that the recombinant strains containing the *ars1* operon were resistant to up to 60 mM arsenite, this being one of the highest levels of bacterial resistance to arsenite so far described. Blast searches and protein alignments analysis reveal three different types of arsenate reductases in *C. glutamicum*. The product of the orphan gene *arsC4* seems to belong to the *E. coli* *ArsC* family. *ArsC1'* shares characteristic with *Streptomyces* *ArsC*, whereas *ArsC1* and *ArsC2* are different to the arsenate reductases described up to date. *arsC* gene disruption analysis and complementation studies will reveal the role of each protein in the reduction *C. glutamicum* arsenate. Tools for genetic manipulation of *C. glutamicum* were developed in our laboratory since 1980, and using this technology we are constructing *C. glutamicum* strains able to remove arsenic from contaminated water.

Keywords: *Corynebacterium* · arsenic resistance · bioremediation

**FROM PATHOGENESIS TO GENETICS TO EVOLUTION AND BACK AGAIN:
SALMONELLA'S CONTRIBUTIONS TO BIOLOGY**

Stanley Maloy

San Diego State University, San Diego, CA, USA

smaloy@sciences.sdsu.edu

Scientists initially became attracted to *Salmonella* for medical reasons. *Salmonella* are a common cause of gastroenteritis, a disagreeable affliction that has been a desultory part of the universal human experience. Certain *Salmonella* are even more reprehensible, causing the potential lethal disease Typhoid fever. The desire to determine which particular strain of *Salmonella* was responsible for a disease outbreak led to the use of phage typing. In 1952 these medical tools led to the discovery of transduction, the transfer of genomic DNA between different strains. Although later discovered in other bacteria, the efficiency of gene exchange between *Salmonella* by the phage P22 quickly turned *Salmonella enterica* sv. Typhimurium from a medical problem to a model genetic organism. The ease of isolating and characterizing *Salmonella* mutants led to the genetic dissection of many biosynthetic pathways and provided insights into how bacteria regulate gene expression in response to environmental conditions. Detailed analysis of the histidine biosynthetic genes led to the development of the Ames test, a quick and inexpensive approach to evaluate potential carcinogens using bacteria. The ease of genetic analysis by P22 also led to the discovery of transposons in bacteria and their use as genetic tools – applications with tremendous impact on the field of microbiology. Genetic mapping the numerous mutants provided novel insights into bacterial chromosome structure and evolution. In addition to the ease of genetics, because individual cells in a culture of *Salmonella* are much more uniform than most other bacteria (including *Escherichia coli*), *Salmonella* became a favorite organism of scientists studying bacterial growth. These tools also provided new approaches to study *Salmonella* pathogenesis. Clever application of genetic and molecular tools elucidated many fundamental aspects of how *Salmonella* interacts with an infected host to cause disease, insights with broad applicability in other bacterial pathogens as well. Recently the genome sequences of multiple strains of *Salmonella* have been determined, providing a detailed snapshot of evolutionary changes that distinguish closely related bacteria. Thus, from the initial interest in *Salmonella* as a medical nuisance, studies on *Salmonella* over the last 50 years have provided key insights into bacterial physiology, genetics, cell biology, and evolution. Nevertheless, there are many important questions about *Salmonella* that remain unanswered. Recent discoveries suggest that *Salmonella* may cause chronic human diseases such as atherosclerosis, but the mechanisms remain obscure. We have identified mechanisms that may be responsible for the adaptation of *Salmonella* to new niches, but we have not yet demonstrated cause and effect. Although we have learned a lot about how *Salmonella* grows in laboratory media and in an animal host, we know little about how *Salmonella* survives in the outside environment. We understand simple regulatory networks, but do not yet understand how multiple environmental signals are integrated to produce the proper response. In short, although *Salmonella* remains an important human pathogen, *Salmonella* has also contributed greatly to our understanding of biology and will continue to contribute novel insights well into the future.

Keywords: phage · transposons · Ames test · genome rearrangements

PNEUMOCOCCUS BIOLOGY

Rubén López

Centro de Investigaciones Biológicas, CSIC, Madrid, Spain

rubenconcha@telefonica.net

The study of the biology of *Streptococcus pneumoniae* (the pneumococcus) had been a central issue in medicine during many decades since it caused more health problems than cardiovascular diseases and cancer put together until the use of antibiotics became generalized in the mid 1940s. Many fundamental contributions to the history of the microbiology should credit this bacterium: the capsular precipitin reaction; its major play in the development of immunology through the identification of polysaccharide as antigens; and, mainly, the demonstration by genetic transformation that genes are composed of DNA, which has meant the greatest impact on biology from the study of bacteria. However, the present importance of this historic bacterium comes from the concern over pneumococcal disease caused by multidrug-resistant strains. Infectious diseases are currently the third cause of death in the United States and the leading cause of morbidity worldwide with the pneumococcus being the main cause of pneumonia, meningitis, and bloodstream infections in the elderly, the young, and immunocompromised individuals. In this presentation, I bring about also a short analysis of the most reliable contributions to the basic knowledge on this bacterium from 1970s until the mid 1980s when major topics on *S. pneumoniae* concentrated on the study of the peculiarities of genetic transformation, including competence development (a physiological characteristic that permeates the cells to incorporate exogenous DNA), and recombination between resident and exogenous DNA that lead to the explosion of current knowledge about pneumococcus. Furthermore, I will also focus on a brief report about the contributions of our group to dissect the molecular basis underlying three main virulence factors like lytic enzymes, pneumococcal phages, and the molecular organization of the genes coding for the capsular polysaccharides. The importance of analysing these issues in depth might contribute to establishing a wide range of clinical applications since the existing antipneumococcal vaccines have limited efficacy and attempts to fight pneumococcal infections through more generalized use of antibiotics seems unrealistic in the long-term. This assumption is supported because of the genetic plasticity of this microorganism and the gene flow in natural populations that result in a shift in capsular type or in the rapid spread of antibiotic-resistant isolates and appearance of novel antibiotic resistance 'determinants'. In addition, because *S. pneumoniae* is a human commensal it may not be sound to perturb the normal microbiota with unpredictable long-term consequences. Finally, the role of vectors including conjugative transposons and bacteriophage needs to be addressed in a clinical setting with basic scientific experimentation. Recently, phages and phage products have been proposed as an alternative (or complement) to the available antibiotics.

Keywords: *Streptococcus pneumoniae* · capsular polysaccharide · cell wall hydrolases · phage · virulence factors

VIRUS CONTRIBUTION TO BIOLOGY

Esteban Domingo

Centro de Biología Molecular “Severo Ochoa” (CSIC-UAM),
Universidad Autónoma de Madrid, Cantoblanco, Spain

edomingo@cbm.uam.es

Viruses contributed to biology as soon as they were recognised as biological entities associated with human, animal and plant disease. The influence of viruses has often been linked to contributions made by cellular microbes, a recognition of the importance of interdisciplinary and transdisciplinary science. A remarkable precedent of vaccination was variolation, practiced by ancient civilizations as a means to attenuate the severity of smallpox epidemics. Vaccination unveiled basic principles of immunology, and eventually resulted in the eradication of the dreaded smallpox towards the end of the 20th century, with the last clinical case reported in Somalia in 1977. Smallpox eradication is one of the major achievements in health sciences. Early in the 20th century a connection was made between virus and cancer, a finding which anticipated the concept that cell behaviour can be profoundly modified by external, replicating entities. One of the major impacts of virology on biology resulted from the use of bacteriophages as experimental systems for the study of replication of genetic material, and its expression in the processes of transcription and translation. In this respect, the work of Adams, Hershey, Delbrück and Luria represented the origins of molecular biology, an essential step for later developments in biology. Progress in bacteriophage genetics occurred while the nature of the genetic material and its structure were being unveiled with key participation of bacteriology. The different perceptions of the nature of viruses, as their composition and replication mechanisms were being disclosed, are illustrated by a number of definitions published from 1957 until 1967 by Luria, Lwoff, and others. In a few years, definitions evolved from referring to “entities” to “elements of genetic material”. In the second part of the 20th century, an additional, salient contribution of Virology was the discovery of reverse transcriptase, or RNA- dependent DNA polymerase. This new enzymatic activity ended the so called “dogma of molecular biology” that asserted that the flow of genetic information had to go from DNA to RNA to protein. The characterization of plasmid and viral vectors, the discovery of restriction enzymes and DNA ligases, the new methods for rapid nucleotide sequencing, and retrotranscription, set the basis for the development of genetic engineering, with its multiple implications for health science and modern biotechnology. At the onset of the 21st century, viruses continue to influence biology in a number of fronts. They are used in research on gene delivery, and the slowly moving field of gene therapy. A potential new development on the horizon is the use of viruses as model systems for studies on biological complexity. This potential application stems from the recognition of the extreme genetic and phenotypic diversity of viral populations, in particular the high mutation rates and quasispecies dynamics of viruses that have RNA as genetic material. Viruses, because of their limited complexity, may be adequate experimental model systems to understand the molecular basis of the internal interactions that determine emergent features of biological systems. However, this possible chapter of the contribution of virus to biology is yet to be written.

Keywords: virus · molecular biology · biological complexity

YEAST CONTRIBUTION TO BIOLOGY

Enrique Herrero

University of Lleida, Spain

Enric.Herrero@cmb.UdL.es

Yeasts have played an essential role in the development of Chemistry and Biology since late 18th century when Lavoisier described the chemical changes occurring during alcoholic fermentation. The studies of Cagniard-Latour, Kützing and Schwann in the first half of 19th century and those of Pasteur and Berthelot in the second half of that century represented a shift from a chemical to a biological focusing in the study of fermentation. Even more, they settled the foundations of biochemistry as a biological science. However, during the next hundred years the yeast (in particular *Saccharomyces cerevisiae*) were not employed basically as a model to establish central biological principles and to study general cellular processes, but were contemplated as organisms useful for the transformation of organic matter and production of beverages. That is, considering the dichotomy of the studies of Pasteur/Berthelot (basic versus applied outputs), emphasis was given during the next decades for the industrial applications of yeasts. Nevertheless, these same developments were establishing the basis for the contribution of yeasts to the development of cell biology as has occurred during the last thirty years. During the first decades of the 20th century, industrial strains of *S. cerevisiae* were genetically manipulated to improve their performance in industrial processes. Some of these strains derived into the 'laboratory strains' that more recently have been employed for the study of biological processes at the molecular and cellular level. DNA manipulation techniques were easily adapted from the seventies of the 20th century thanks to the development of different types of plasmids that can be stably propagated in *S. cerevisiae*. Thus, these plasmids together with the large number of mutant strains resulting from 'direct genetics' approaches allowed employing *S. cerevisiae* as a model microorganism that in some aspects has substituted (or complemented) *Escherichia coli* in analysis of biological processes. The knowledge on the functioning of the eukaryotic cell cycle based on yeast studies is a good example for this. With that background, it is not strange that *Saccharomyces cerevisiae* became the first eukaryotic organism whose genome was totally sequenced in 1997. This represented a revolution on the approaches to study the biology of the cell, as it allowed the shift to 'reverse genetics' for functional analysis of gene products. The huge accumulation of biological data on structure, function and interaction between the gene products of *S. cerevisiae* has marked the more recent step towards Systems Biology, that is, approaching the cell (or organism) as an integrated and complex network of components interacting among them. But yeasts are not only 'models', they are organisms existing in nature, which interact with other organisms and transform the environment. The genetic and molecular biology tools can now be extended for the study of other yeast species such as *Candida albicans*, *Yarrowia lipolytica* or *Pichia polymorpha*, that are also important as pathogens or transformers of organic matter.

Keywords: yeast · fermentation · genomics · cell cycle · biomedicine

THE RISE OF MICROBIAL ECOLOGY

Thomas M. Schmidt

Michigan State University, East Lansing, MI, USA

tschmidt@msu.edu

The 1956 publication of “The Microbe’s Contribution to Biology” provided biologists with an overview of microbial life, emphasizing the core metabolic unity of microbes coupled to their exceptional capacity to adapt to a dramatic range of environments. The principles set forth in this book served as the basis for the emerging scientific discipline of microbial ecology. While the book highlights the value of pure cultures for providing a framework for understanding the vast metabolic potential of microbes, extrapolation from pure cultures to natural environments has been overshadowed by microbiologists’ inability to culture many of the microbes seen in natural environments. A combination of genomic approaches is now providing a culture-independent view of the microbial world, revealing a more diverse and dynamic than anticipated. As methods for determining the diversity of microbial communities become increasingly accessible, a major challenge to microbial ecologist is to link the structure of microbial communities with their functions. Establishing the links between structure and function frequently requires integration of classical and contemporary approaches in microbiology. This presentation will highlight several examples from aquatic and terrestrial ecosystems, where culture and culture-independent based methods are providing an enhanced appreciation for the microbe’s contribution to the evolution and maintenance of life on Earth.

Keywords: metabolic diversity · structure and function · microbial communities

MARINE GENOMICS

Carlos Pedrós-Alió

Marine Sciences Institute, CMIMA, CSIC, Barcelona, Spain

cpedros@icm.csic.es

Neither genomics nor marine microbial ecology existed at the time of publication of “The Microbe’s contribution to biology”. However, there is a parallel between the chapters in the book and the role of current marine genomics: in both cases a deeper knowledge of microbes was an eye opener that revolutionized our understanding of life’s possibilities. Marine microbial ecology can be considered to have started in the 1970s, when it was shown that most respiration in the oceans was in the bacterial size fractions and when bacteria were shown to be very abundant. Nowadays, marine microorganisms are considered to be responsible for half of the total primary production on the planet and the 10^{29} bacteria present in the oceans are considered to be responsible for more than 95% of the total respiration. The change of perspective, therefore, has been spectacular. The application of genomic approaches to marine microbial ecology in the past ten years has caused another Copernican revolution. Thanks to such techniques, novel functions have been discovered, a large diversity of microorganisms has been uncovered, and the meaning of concepts such as species, genome or niche has been challenged. There are three main approaches currently being used. First, marine microorganisms can be isolated in pure culture and their genomes can be completely sequenced. Until one year ago, most sequenced genomes belonged to bacteria of medical interest. However, thanks to the initiative of the Gordon and Betty Moore Foundation, over 150 genomes of marine bacteria have been sequenced in the last year. Of course, the main caveat is that many of the bacteria isolated in pure cultures are not the most important in nature. However, these genomes offer a wealth of information that can be used to interpret the results from the other two approaches. For example, the complete genomes of four cyanobacteria have offered profound insight about what is a species and what is an ecological niche. Second, large fragment of environmental DNA can be carefully extracted and cloned in appropriate vectors such as fosmids or BAC libraries. These large fragments of DNA contain several genes. If a gene for 16S rDNA is found in one clone the bacterium can be identified, and the neighboring genes can be cloned. In this way, for example, the existence of a novel function was discovered in an uncultivated bacterium. One clone from one of such libraries had the 16S rDNA gene of SAR86 (a cluster of sequences retrieved from many oceans but with no representative in pure culture). A gene coding for a protein similar to halorhodopsin was found in the same clone. Upon study, this protein (named proteorhodopsin) was shown to use light to create a proton gradient and thus, an unknown group of bacteria, SAR86, was shown to have a novel function (phototrophy). The third approach involves fragmenting the environmental DNA into small fragments and cloning of such fragments in conventional vectors. This is called shotgun cloning. In this way, DNA fragment can be sequenced without previous screening. This allows for discovery of novel genes regardless of their origin. The drawback is that it requires massive sequencing to analyze the thousands of clones generated from a single sample and that it is difficult to reassemble genomes from the many small fragments. Application of this approach to a sample from the Sargasso Sea by the J. Craig Venter Foundation, has revealed over 100,000 genes, many of them of unknown functions. In one of the most typical examples, this approach has increased by at least one order of magnitude the number of proteorhodopsin genes known. All together, the application of these techniques to marine microbes is revolutionizing our view of life

Keywords: shotgun cloning · fosmids · BAC libraries

PLANT-MICROBE RELATIONSHIPS. APPLICATIONS OF BENEFICIAL MICROORGANISMS IN PLANT DISEASE CONTROL

Emilio Montesinos

Institute for Food Technology-CeRTA-CIDSAV, University of Girona, Spain

emonte@intea.udg.es

Plants constitute an excellent ecosystem for microorganisms from the highly variable aerial part to the more stable root system. Plants and microbes have co-evolved, and developed strategies to live in association through commensalistic, beneficial or detrimental interactions. Plants, like humans and other animals, also become sick due to infections that cause severe losses limiting food production in the world. The discovery of microbes as causal agents of infectious diseases in plants was in most cases contemporary to the establishment of the basic principles of Microbiology by Pasteur and Koch around 1876. However, very often this is ignored in many textbooks. Also, several plant diseases affecting crops of economic and as food importance, have been responsible of agricultural losses that in some cases lead to severe famine. The Irish famine due to potato late blight in 1846 and Bengal famine due to brown spot of rice in 1943 are examples having deep influence in human development. The 11,000 diseases that have been described in plants are caused by 120 genera of fungi, 30 types of viruses, and eight genera of bacteria. Since the Green Revolution most of plant diseases have been under control by synthetic chemical pesticides. In spite of its high efficacy on disease control these compounds have health and environmental non-target effects. A new approach of disease control have emerged based on beneficial microorganisms associated to plants. Many plant associated microbes are able to colonize or compete for nutrients and sites of pathogen interaction, or to exert antagonism through antimicrobial compounds, develop hyperparasitism or direct interference against pathogens, interfere with pathogen signals, or induce systemic acquired resistance (SAR) in the plant host. However, most strains developed as biocontrol agents exhibit a poor ecological fitness or suppose a potential toxicological risk or environmental impact, and only few have arrived on the market of biopesticides. Approaches based on high-throughput screening in environmental samples like detection of marker gene expression or intracellular screen of metagenomic libraries of cloned DNA, are expected to improve the isolation and development of new biocontrol agents. Also, a new generation of chemical compounds have emerged that elicit plant defence responses but do not exhibit antimicrobial activity, or consist of antimicrobial peptides from synthetic or natural origin. Transgenic plants and domesticated beneficial microorganisms have been produced with engineered genes encoding defective pathogen components, gene silencing systems, HR elicitors or overexpressing R genes, PR proteins, antimicrobial peptides or quorum-sensing regulator genes. However, some of these technologies have biosafety, environmental and consumer concerns that may limit its use.

Keywords: plant pathogens · hyperparasitism · biological control

PROKARYOTIC TAXONOMY: IN SEARCH OF A NATURAL SYSTEM, OR DOES ONE EVEN EXIST?

Gary J. Olsen

University of Illinois, Urbana, IL, USA

gary@phylo.life.uiuc.edu

For over one hundred years, microbiologists wanted, but knew that they did not have, a natural system of classification for microorganisms. While the Zoologists and Botanists had some confidence that their classifications had at least some evolutionary basis, microbiologists had to make do with a determinative system. With the advent of molecular phylogeny in the 1960's, and its application to microorganisms in the 1970's, we got our first objective picture of a complete tree of life. One of the most profound consequences was the recognition by Carl Woese that prokaryotes are not a phylogenetic group: Bacteria are as far removed from Archaea as they are from Eucarya. Subsequent work has repeatedly suggested that, if anything, Archaea and Eucarya share a more recent common ancestor than do Archaea and Bacteria. For many years, some workers questioned the data and methods, arguing that the result was simply wrong. This position has largely faded, though it continues to be revived in new forms. Others have argued that while it is true that Archaea and Bacteria are distinct groups, this fact should have reduced nomenclatural status; that, in essence, we should stick to an "unnatural" classification. Since this always devolves to a question of personal taste, one can merely disagree. The last 10 years have seen the rise of a new, scientifically more interesting, challenge. Even as analyses of full genome sequences have confirmed time and again nearly every phylogenetic group described by Woese 20 or more years ago, other analyses have revealed that most genes have at some point in their history been horizontally transferred. Thus, most genes in a genome do share a common history. This has led to the questioning of the very existence of a tree of life, and along with it, the existence of a natural system. I will argue that horizontal gene transfer does not eliminate a tree-of-life, although it certainly makes it harder to infer. At the same time, the ability to share innovations throughout the biosphere has had a profound impact on the evolution of life.

Keywords: bacterial taxonomy · Archaea · Bacteria · Eukarya phylogeny