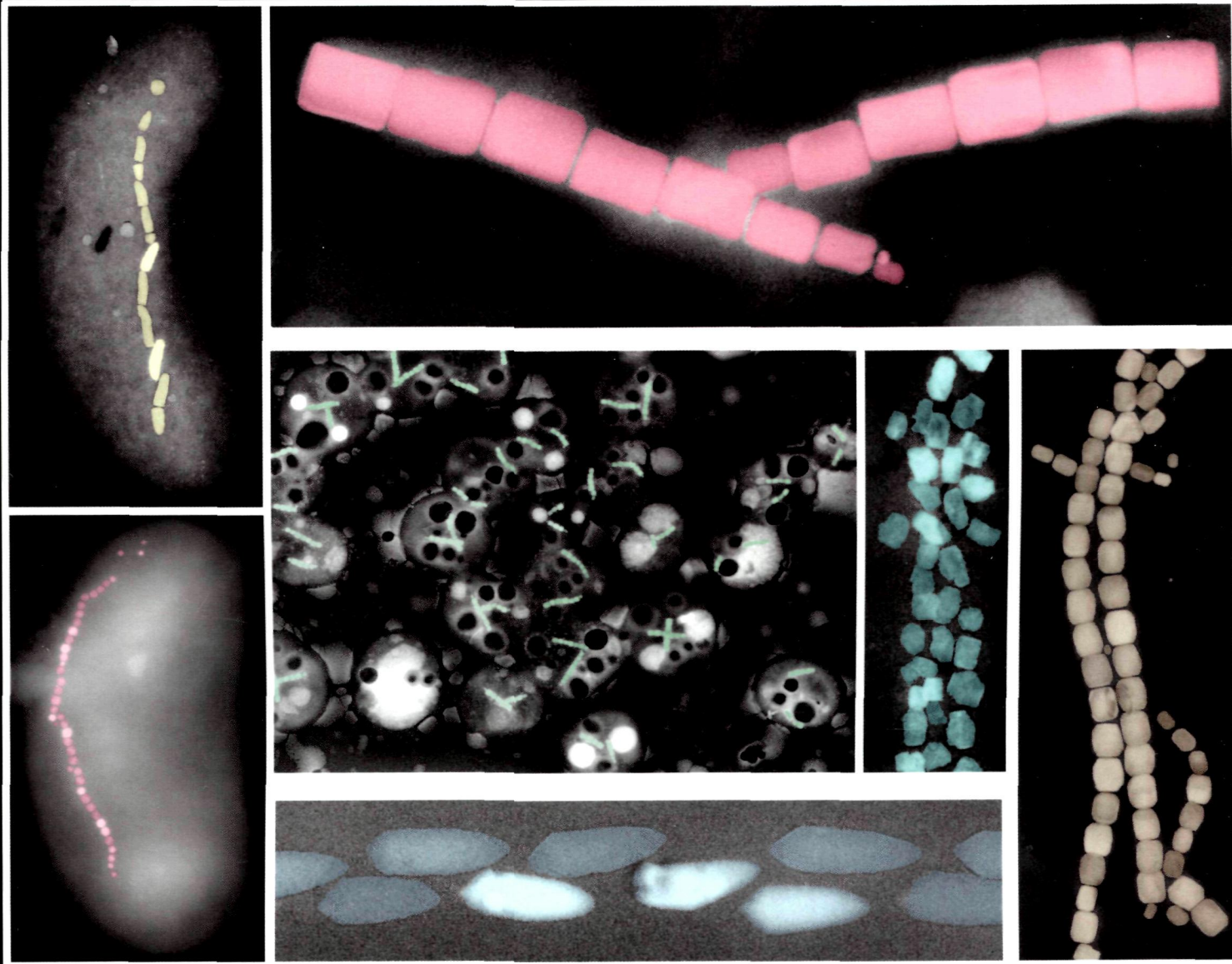


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MICROBIOLOGY AND MOLECULAR BIOLOGY REVIEWS



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## CONTENTS/SUMMARIES

### REVIEWS

#### **Type IV Pili in Gram-Positive Bacteria**

323–341

Stephen Melville, Lisa Craig

**Summary:** Type IV pili (T4P) are surface-exposed fibers that mediate many functions in bacteria, including locomotion, adherence to host cells, DNA uptake (competence), and protein secretion and that can act as nanowires carrying electric current. T4P are composed of a polymerized protein, pilin, and their assembly apparatuses share protein homologs with type II secretion systems in eubacteria and the flagella of archaea. T4P are found throughout Gram-negative bacterial families and have been studied most extensively in certain model Gram-negative species. Recently, it was discovered that T4P systems are also widespread among Gram-positive species, in particular the clostridia. Since Gram-positive and Gram-negative bacteria have many differences in cell wall architecture and other features, it is remarkable how similar the T4P core proteins are between these organisms, yet there are many key and interesting differences to be found as well. In this review, we compare the two T4P systems and identify and discuss the features they have in common and where they differ to provide a very broad-based view of T4P systems across all eubacterial species.

#### **Patterns and Processes of Microbial Community Assembly**

342–356

Diana R. Nemergut, Steven K. Schmidt, Tadashi Fukami, Sean P. O'Neill, Teresa M. Bilinski, Lee F. Stanish, Joseph E. Knelman, John L. Darcy, Ryan C. Lynch, Phillip Wickey, Scott Ferrenberg

**Summary:** Recent research has expanded our understanding of microbial community assembly. However, the field of community ecology is inaccessible to many microbial ecologists because of inconsistent and often confusing terminology as well as unnecessarily polarizing debates. Thus, we review recent literature on microbial community assembly, using the framework of Vellend (*Q. Rev. Biol.* 85:183–206, 2010) in an effort to synthesize and unify these contributions. We begin by discussing patterns in microbial biogeography and then describe four basic processes (diversification, dispersal, selection, and drift) that contribute to community assembly. We also discuss different combinations of these processes and where and when they may be most important for shaping microbial communities. The spatial and temporal scales of microbial community assembly are also discussed in relation to assembly processes. Throughout this review paper, we highlight differences between microbes and macroorganisms and generate hypotheses describing how these differences may be important for community assembly. We end by discussing the implications of microbial assembly processes for ecosystem function and biodiversity.

#### **Functions, Compositions, and Evolution of the Two Types of Carboxysomes: Polyhedral Microcompartments That Facilitate CO<sub>2</sub> Fixation in Cyanobacteria and Some Proteobacteria**

357–379

Benjamin D. Rae, Benedict M. Long, Murray R. Badger, G. Dean Price

**Summary:** Cyanobacteria are the globally dominant photoautotrophic lineage. Their success is dependent on a set of adaptations collectively termed the CO<sub>2</sub>-concentrating mechanism (CCM). The purpose of the CCM is to support effective CO<sub>2</sub> fixation by enhancing the chemical conditions in the vicinity of the primary CO<sub>2</sub>-fixing enzyme, *D*-ribulose 1,5-bisphosphate carboxylase/oxygenase (RubisCO), to promote the carboxylase reaction and suppress the oxygenase reaction. In cyanobacteria and some proteobacteria, this is achieved by encapsulation of RubisCO within carboxysomes, which are examples of a group of proteinaceous bodies called bacterial microcompartments. Carboxysomes encapsulate the CO<sub>2</sub>-fixing enzyme within the selectively permeable protein shell and simultaneously encapsulate a carbonic anhydrase enzyme for CO<sub>2</sub> supply from a cytoplasmic bicarbonate pool. These bodies appear to have arisen twice and undergone a process of convergent evolution. While the gross structures of all known carboxysomes are ostensibly very similar, with shared gross features such as a selectively permeable shell layer, each type of carboxysome encapsulates a phylogenetically distinct form of RubisCO enzyme. Furthermore, the specific proteins forming structures such as the protein shell or the inner RubisCO matrix are not identical between carboxysome types. Each type has evolutionarily distinct forms of the same proteins, as well as proteins that are entirely unrelated to one another. In light of recent developments in the study of carboxysome structure and function, we present this review to summarize the knowledge of the structure and function of both types of carboxysome. We also endeavor to cast light on differing evolutionary trajectories which may have led to the differences observed in extant carboxysomes.

**Pathogenesis of Human Enterovirulent Bacteria: Lessons from Cultured, Fully Differentiated Human Colon Cancer Cell Lines**

380–439

Vanessa Liévin-Le Moal, Alain L. Servin

Summary: Hosts are protected from attack by potentially harmful enteric microorganisms, viruses, and parasites by the polarized fully differentiated epithelial cells that make up the epithelium, providing a physical and functional barrier. Enterovirulent bacteria interact with the epithelial polarized cells lining the intestinal barrier, and some invade the cells. A better understanding of the cross talk between enterovirulent bacteria and the polarized intestinal cells has resulted in the identification of essential enterovirulent bacterial structures and virulence gene products playing pivotal roles in pathogenesis. Cultured animal cell lines and cultured human nonintestinal, undifferentiated epithelial cells have been extensively used for understanding the mechanisms by which some human enterovirulent bacteria induce intestinal disorders. Human colon carcinoma cell lines which are able to express in culture the functional and structural characteristics of mature enterocytes and goblet cells have been established, mimicking structurally and functionally an intestinal epithelial barrier. Moreover, Caco-2-derived M-like cells have been established, mimicking the bacterial capture property of M cells of Peyer's patches. This review intends to analyze the cellular and molecular mechanisms of pathogenesis of human enterovirulent bacteria observed in infected cultured human colon carcinoma enterocyte-like HT-29 subpopulations, enterocyte-like Caco-2 and clone cells, the colonic T84 cell line, HT-29 mucus-secreting cell subpopulations, and Caco-2-derived M-like cells, including cell association, cell entry, intracellular lifestyle, structural lesions at the brush border, functional lesions in enterocytes and goblet cells, functional and structural lesions at the junctional domain, and host cellular defense responses.

**The TetR Family of Regulators**

440–475

Leslie Cuthbertson, Justin R. Nodwell

Summary: The most common prokaryotic signal transduction mechanisms are the one-component systems in which a single polypeptide contains both a sensory domain and a DNA-binding domain. Among the >20 classes of one-component systems, the TetR family of regulators (TFRs) are widely associated with antibiotic resistance and the regulation of genes encoding small-molecule exporters. However, TFRs play a much broader role, controlling genes involved in metabolism, antibiotic production, quorum sensing, and many other aspects of prokaryotic physiology. There are several well-established model systems for understanding these important proteins, and structural studies have begun to unveil the mechanisms by which they bind DNA and recognize small-molecule ligands. The sequences for more than 200,000 TFRs are available in the public databases, and genomics studies are identifying their target genes. Three-dimensional structures have been solved for close to 200 TFRs. Comparison of these structures reveals a common overall architecture of nine conserved  $\alpha$  helices. The most important open question concerning TFR biology is the nature and diversity of their ligands and how these relate to the biochemical processes under their control.

**Mechanism of Homologous Recombination and Implications for Aging-Related Deletions in Mitochondrial DNA**

476–496

Xin Jie Chen

Summary: Homologous recombination is a universal process, conserved from bacteriophage to human, which is important for the repair of double-strand DNA breaks. Recombination in mitochondrial DNA (mtDNA) was documented more than 4 decades ago, but the underlying molecular mechanism has remained elusive. Recent studies have revealed the presence of a Rad52-type recombination system of bacteriophage origin in mitochondria, which operates by a single-strand annealing mechanism independent of the canonical RecA/Rad51-type recombinases. Increasing evidence supports the notion that, like in bacteriophages, mtDNA inheritance is a coordinated interplay between recombination, repair, and replication. These findings could have profound implications for understanding the mechanism of mtDNA inheritance and the generation of mtDNA deletions in aging cells.

**Ecology, Diversity, and Evolution of Magnetotactic Bacteria**

497–526

Christopher T. Lefèvre, Dennis A. Bazylinski

Summary: Magnetotactic bacteria (MTB) are widespread, motile, diverse prokaryotes that biomineralize a unique organelle called the magnetosome. Magnetosomes consist of a nano-sized crystal of a magnetic iron mineral that is enveloped by a lipid bilayer membrane. In cells of almost all MTB, magnetosomes are organized as a well-ordered chain. The magnetosome chain causes the cell to behave like a motile, miniature compass needle where the cell aligns and swims parallel to magnetic field lines. MTB are found in almost all types of aquatic environments, where they can account for an important part of the bacterial biomass. The genes responsible for magnetosome biomineralization are organized as clusters in the genomes of MTB, in some as a magnetosome genomic island. The functions of a number of magnetosome genes and their associated proteins in magnetosome synthesis and construction of the magnetosome chain have now been elucidated. The origin of magnetotaxis appears to be monophyletic; that is, it developed in a common ancestor to all MTB, although horizontal gene transfer of magnetosome genes also appears to play a role in their distribution. The

purpose of this review, based on recent progress in this field, is focused on the diversity and the ecology of the MTB and also the evolution and transfer of the molecular determinants involved in magnetosome formation.

## What a Difference a Dalton Makes: Bacterial Virulence Factors Modulate Eukaryotic Host Cell Signaling Systems via Deamidation

527–539

Erica J. Washington, Mark J. Banfield, Jeffery L. Dangl

**Summary:** Pathogenic bacteria commonly deploy enzymes to promote virulence. These enzymes can modulate the functions of host cell targets. While the actions of some enzymes can be very obvious (e.g., digesting plant cell walls), others have more subtle activities. Depending on the lifestyle of the bacteria, these subtle modifications can be crucially important for pathogenesis. In particular, if bacteria rely on a living host, subtle mechanisms to alter host cellular function are likely to dominate. Several bacterial virulence factors have evolved to use enzymatic deamidation as a subtle posttranslational mechanism to modify the functions of host protein targets. Deamidation is the irreversible conversion of the amino acids glutamine and asparagine to glutamic acid and aspartic acid, respectively. Interestingly, all currently characterized bacterial deamidases affect the function of the target protein by modifying a single glutamine residue in the sequence. Deamidation of target host proteins can disrupt host signaling and downstream processes by either activating or inactivating the target. Despite the subtlety of this modification, it has been shown to cause dramatic, context-dependent effects on host cells. Several crystal structures of bacterial deamidases have been solved. All are members of the papain-like superfamily and display a cysteine-based catalytic triad. However, these proteins form distinct structural subfamilies and feature combinations of modular domains of various functions. Based on the diverse pathogens that use deamidation as a mechanism to promote virulence and the recent identification of multiple deamidases, it is clear that this enzymatic activity is emerging as an important and widespread feature in bacterial pathogenesis.

## ERRATUM

### Pyrophosphate-Fueled Na<sup>+</sup> and H<sup>+</sup> Transport in Prokaryotes

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Alexander A. Baykov, Anssi M. Malinen, Heidi H. Luoto, Reijo Lahti

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*Cover photograph* (Copyright 2013, American Society for Microbiology. All Rights Reserved.): Shown are false-colored transmission electron microscope images of magnetotactic bacteria and magnetosome chains. Magnetotactic bacteria in the middle-left panel and the leftmost panels are approximately 1 to 2  $\mu\text{m}$  long. The top left panel (bullet-shaped magnetosomes colored in yellow) shows a thermophilic, vibrioid magnetotactic bacterium found in brackish hot springs within the Great Boiling Springs geothermal field in Gerlach, Nevada. The bottom left panel (cuboctahedral magnetosomes colored in pink) shows a cell of the cultured strain BW-2 isolated from a brackish, sulfidic spring at Badwater Basin at Death Valley, California. The middle-left panel (magnetosomes colored in green) are magnetotactic cocci collected from the Calanque de Morgiou in Marseille, France. Magnetosomes are generally about 35 to 120 nm in size. Bullet-shaped and octahedral magnetosomes are composed of magnetite, while the chain made of pleomorphic magnetosomes (middle-right panel) is composed of greigite. The top right panel (magnetosomes colored in pink) shows 2 magnetosome chains found in a magnetotactic coccus collected from the Pointe Rouge marina, Marseille. The middle-right panel (magnetosomes colored in blue) shows a chain of pleomorphic magnetosomes found in a large, greigite-producing rod-shaped bacterium collected from a spring at ambient temperature in the Great Boiling Springs geothermal field in Gerlach, Nevada. The bottom middle panel (magnetosomes colored in blue) shows a chain of bullet-shaped magnetosomes in the cultured, alkaliphilic magnetotactic bacterium strain AV-1 isolated from a brackish, hyperalkaline spring in Armagosa Valley, California. The bottom right panel (magnetosomes colored in brown) shows a bundle composed of 2 or 3 magnetosome chains found in a large rod-shaped bacterium isolated from the Calanque de Morgiou, Marseille, France. (See related article on p. 497.)