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REVIEWS

Replication Fork Stalling at Natural Impediments. Ekaterina V. Mirkin and Sergei M. Mirkin.....	13–35
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Summary: Accurate and complete replication of the genome in every cell division is a prerequisite of genomic stability. Thus, both prokaryotic and eukaryotic replication forks are extremely precise and robust molecular machines that have evolved to be up to the task. However, it has recently become clear that the replication fork is more of a hurdler than a runner: it must overcome various obstacles present on its way. Such obstacles can be called natural impediments to DNA replication, as opposed to external and genetic factors. Natural impediments to DNA replication are particular DNA binding proteins, unusual secondary structures in DNA, and transcription complexes that occasionally (in eukaryotes) or constantly (in prokaryotes) operate on replicating templates. This review describes the mechanisms and consequences of replication stalling at various natural impediments, with an emphasis on the role of replication stalling in genomic instability.

Surprising Arginine Biosynthesis: a Reappraisal of the Enzymology and Evolution of the Pathway in Microorganisms. Ying Xu, Bernard Labedan, and Nicolas Glansdorff.....	36–47
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*Summary: Major aspects of the pathway of de novo arginine biosynthesis via acetylated intermediates in microorganisms must be revised in light of recent enzymatic and genomic investigations. The enzyme N-acetylglutamate synthase (NAGS), which used to be considered responsible for the first committed step of the pathway, is present in a limited number of bacterial phyla only and is absent from Archaea. In many Bacteria, shorter proteins related to the Gcn5-related N-acetyltransferase family appear to acetylate L-glutamate; some are clearly similar to the C-terminal, acetyl-coenzyme A (CoA) binding domain of classical NAGS, while others are more distantly related. Short NAGSs can be single gene products, as in *Mycobacterium* spp. and *Thermus* spp., or fused to the enzyme catalyzing the last step of the pathway (argininosuccinase), as in members of the *Alteromonas-Vibrio* group. How these proteins bind glutamate remains to be determined. In some Bacteria, a bifunctional ornithine acetyltransferase (i.e., using both acetylornithine and acetyl-CoA as donors of the acetyl group) accounts*

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for glutamate acetylation. In many Archaea, the enzyme responsible for glutamate acetylation remains elusive, but possible connections with a novel lysine biosynthetic pathway arose recently from genomic investigations. In some Proteobacteria (notably Xanthomonadaceae) and Bacteroidetes, the carbamoylation step of the pathway appears to involve *N*-acetylornithine or *N*-succinylornithine rather than ornithine. The product *N*-acetylcitrulline is deacetylated by an enzyme that is also involved in the provision of ornithine from acetylornithine; this is an important metabolic function, as ornithine itself can become essential as a source of other metabolites. This review insists on the biochemical and evolutionary implications of these findings.

Central Roles of Small GTPases in the Development of Cell Polarity in Yeast and Beyond. Hay-Oak Park and Erfei Bi. 48–96

Summary: The establishment of cell polarity is critical for the development of many organisms and for the function of many cell types. A large number of studies of diverse organisms from yeast to humans indicate that the conserved, small-molecular-weight GTPases function as key signaling proteins involved in cell polarization. The budding yeast *Saccharomyces cerevisiae* is a particularly attractive model because it displays pronounced cell polarity in response to intracellular and extracellular cues. Cells of *S. cerevisiae* undergo polarized growth during various phases of their life cycle, such as during vegetative growth, mating between haploid cells of opposite mating types, and filamentous growth upon deprivation of nutrition such as nitrogen. Substantial progress has been made in deciphering the molecular basis of cell polarity in budding yeast. In particular, it becomes increasingly clear how small GTPases regulate polarized cytoskeletal organization, cell wall assembly, and exocytosis at the molecular level and how these GTPases are regulated. In this review, we discuss the key signaling pathways that regulate cell polarization during the mitotic cell cycle and during mating.

Biosynthesis of Ether-Type Polar Lipids in Archaea and Evolutionary Considerations. Yosuke Koga and Hiroyuki Morii. 97–120

Summary: This review deals with the *in vitro* biosynthesis of the characteristics of polar lipids in archaea along with preceding *in vivo* studies. Isoprenoid chains are synthesized through the classical mevalonate pathway, as in eucarya, with minor modifications in some archaeal species. Most enzymes involved in the pathway have been identified enzymatically and/or genomically. Three of the relevant enzymes are found in enzyme families different from the known enzymes. The order of reactions in the phospholipid synthesis pathway (glycerophosphate backbone formation, linking of glycerophosphate with two radyl chains, activation by CDP, and attachment of common polar head groups) is analogous to that of bacteria. *sn*-Glycerol-1-phosphate dehydrogenase is responsible for the formation of the *sn*-glycerol-1-phosphate backbone of phospholipids in all archaea. After the formation of two ether bonds, CDP-archaeol acts as a common precursor of various archaeal phospholipid syntheses. Various phospholipid-synthesizing enzymes from archaea and bacteria belong to the same large CDP-alcohol phosphatidyltransferase family. In short, the first halves of the phospholipid synthesis pathways play a role in synthesis of the characteristic structures of archaeal and bacterial phospholipids, respectively. In the second halves of the pathways, the polar head group-attaching reactions and enzymes are homologous in both domains. These are regarded as revealing the hybrid nature of phospholipid biosynthesis. Precells proposed by Wächtershäuser are differentiated into archaea and bacteria by spontaneous segregation of enantiomeric phospholipid membranes (with *sn*-glycerol-1-phosphate and *sn*-glycerol-3-phosphate backbones) and the fusion and fission of precells. Considering the nature of the phospholipid synthesis pathways, we here propose that common phospholipid polar head groups were present in precells before the differentiation into archaea and bacteria.

Insertion Sequence Diversity in Archaea. J. Filée, P. Siguier, and M. Chandler. 121–157

Summary: Insertion sequences (ISs) can constitute an important component of prokaryotic (bacterial and archaeal) genomes. Over 1,500 individual ISs are included at present in the ISfinder database (www-is.biotoul.fr), and these represent only a small portion of those in the available prokaryotic genome sequences and those that are being discovered in ongoing se-

quencing projects. In spite of this diversity, the transposition mechanisms of only a few of these ubiquitous mobile genetic elements are known, and these are all restricted to those present in bacteria. This review presents an overview of ISs within the archaeal kingdom. We first provide a general historical summary of the known properties and behaviors of archaeal ISs. We then consider how transposition might be regulated in some cases by small antisense RNAs and by termination codon readthrough. This is followed by an extensive analysis of the IS content in the sequenced archaeal genomes present in the public databases as of June 2006, which provides an overview of their distribution among the major archaeal classes and species. We show that the diversity of archaeal ISs is very great and comparable to that of bacteria. We compare archaeal ISs to known bacterial ISs and find that most are clearly members of families first described for bacteria. Several cases of lateral gene transfer between bacteria and archaea are clearly documented, notably for methanogenic archaea. However, several archaeal ISs do not have bacterial equivalents but can be grouped into Archaea-specific groups or families. In addition to ISs, we identify and list nonautonomous IS-derived elements, such as miniature inverted-repeat transposable elements. Finally, we present a possible scenario for the evolutionary history of ISs in the Archaea.

Colicin Biology. Eric Cascales, Susan K. Buchanan, Denis Duché, Colin Kleanthous, Roland Lloubès, Kathleen Postle, Margaret Riley, Stephen Slatin, and Danièle Cavard	158–229
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Summary: Colicins are proteins produced by and toxic for some strains of *Escherichia coli*. They are produced by strains of *E. coli* carrying a colicinogenic plasmid that bears the genetic determinants for colicin synthesis, immunity, and release. Insights gained into each fundamental aspect of their biology are presented: their synthesis, which is under SOS regulation; their release into the extracellular medium, which involves the colicin lysis protein; and their uptake mechanisms and modes of action. Colicins are organized into three domains, each one involved in a different step of the process of killing sensitive bacteria. The structures of some colicins are known at the atomic level and are discussed. Colicins exert their lethal action by first binding to specific receptors, which are outer membrane proteins used for the entry of specific nutrients. They are then translocated through the outer membrane and transit through the periplasm by either the Tol or the TonB system. The components of each system are known, and their implication in the functioning of the system is described. Colicins then reach their lethal target and act either by forming a voltage-dependent channel into the inner membrane or by using their endonuclease activity on DNA, rRNA, or tRNA. The mechanisms of inhibition by specific and cognate immunity proteins are presented. Finally, the use of colicins as laboratory or biotechnological tools and their mode of evolution are discussed.

Functional Taxonomy of Bacterial Hyperstructures. Vic Norris, Tanneke den Blaauwen, Armelle Cabin-Flaman, Roy H. Doi, Rasika Harshey, Laurent Janniere, Alfonso Jimenez-Sanchez, Ding Jun Jin, Petra Anne Levin, Eugenia Mileykovskaya, Abraham Minsky, Milton Saier, Jr., and Kirsten Skarstad	230–253
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Summary: The levels of organization that exist in bacteria extend from macromolecules to populations. Evidence that there is also a level of organization intermediate between the macromolecule and the bacterial cell is accumulating. This is the level of hyperstructures. Here, we review a variety of spatially extended structures, complexes, and assemblies that might be termed hyperstructures. These include ribosomal or “nucleolar” hyperstructures; transertion hyperstructures; putative phosphotransferase system and glycolytic hyperstructures; chemosignaling and flagellar hyperstructures; DNA repair hyperstructures; cytoskeletal hyperstructures based on EF-Tu, FtsZ, and MreB; and cell cycle hyperstructures responsible for DNA replication, sequestration of newly replicated origins, segregation, compaction, and division. We propose principles for classifying these hyperstructures and finally illustrate how thinking in terms of hyperstructures may lead to a different vision of the bacterial cell.

AUTHOR'S CORRECTION

The Bacterial Actin-Like Cytoskeleton. Rut Carballido-López	254
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