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Review

Phosphatidylcholine biosynthesis and function in bacteria ☆

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ABSTRACT

Phosphatidylcholine (PC) is the major membrane-forming phospholipid in eukaryotes and is estimated to be present in about 15% of the domain *Bacteria*. Usually, PC can be synthesized in bacteria by either of two pathways, the phospholipid *N*-methylation (Pmt) pathway or the phosphatidylcholine synthase (Pcs) pathway. The three subsequent enzymatic methylations of phosphatidylethanolamine are performed by a single phospholipid *N*-methyltransferase in some bacteria whereas other bacteria possess multiple phospholipid *N*-methyltransferases each one performing one or several distinct methylation steps. Phosphatidylcholine synthase condenses choline directly with CDP-diacylglycerol to form CMP and PC. Like in eukaryotes, bacterial PC also functions as a biosynthetic intermediate during the formation of other biomolecules such as choline, diacylglycerol, or diacylglycerol-based phosphorus-free membrane lipids. Bacterial PC may serve as a specific recognition molecule but it affects the physicochemical properties of bacterial membranes as well. This article is part of a Special Issue entitled Phospholipids and Phospholipid Metabolism.

1. Introduction

Phosphatidylcholine (PC) is the major membrane-forming phospholipid in eukaryotes and can be synthesized by either of two pathways, the methylation pathway or the CDP-choline pathway [1]. Bacteria such as the well-studied *Escherichia coli* or *Bacillus subtilis* have long served as model organisms for Gram-negative and Gram-positive bacteria, respectively, and both have phosphatidylethanolamine (PE), phosphatidylglycerol (PG) and cardiolipin (CL) as major membrane-forming phospholipids [2]. Both "model bacteria", *E. coli* and *B. subtilis*, are devoid of PC and other membrane phospholipids traditionally regarded as typically eukaryotic such as sphingolipids [3], phosphatidylinositol (PI), or methylated derivatives of PE such as monomethyl-PE (MMPE), and dimethyl-PE (DMPE), that occur in some bacteria [4]. For a long time it was believed that PC occurs only in a few specialized bacteria, such as photosynthetic bacteria containing extensive internal membrane structures or bacteria living in association with eukaryotes [5,6]. We previously estimated than more than 10% of the all bacteria possess PC as a membrane lipid [4] and we support this by our present estimate by which at least 15% of the bacteria have the ability to synthetize PC. The relative amount of PC detected in different bacterial species varies widely and ranges from a few percent of the total membrane lipid (0-4% in *Pseudomonas aeruginosa*) to up to 73% in *Acetobacter aceti* [4,7].

Although individual biosynthetic steps of the CDP-choline pathway for PC synthesis exist in some bacteria, catalyzed by the *licAC*-encoded products that permit the formation of phosphocholine or CDP-choline [4], the only bacterial example for which a complete CDP-choline pathway for PC synthesis has been proposed is the case of the spirochaete *Treponema denticola* [8]. In more general terms, the two different pathways for PC biosynthesis occurring more frequently in bacteria are the phospholipid *N*-methylation (Pmt) pathway and the phosphatidylcholine synthase (Pcs) pathway. In the *N*-methylation pathway, phosphatidylethanolamine is methylated three times to yield PC involving one or more phospholipid *N*-methyltransferases [4,9], whereas in the PC synthase pathway, choline condenses directly with CDP-diacylglycerol to form PC and CMP [10,11]. Several mutants of different PC-containing bacteria have been generated that are devoid of detectable PC. However, the extent to which the absence of PC affects other observable phenotypes depends on the respective bacterial system and may be severe, as in the case of *Sinorhizobium meliloti* [12], to hardly detectable, as in the case of *P. aeruginosa* [13]. Examples are presented where bacterial PC functions as a biosynthetic intermediate during the formation of other biomolecules and where bacterial PC may serve as a specific recognition molecule. We discuss how bacterial PC may affect the physicochemical properties of bacterial membranes.

Abbreviations: CL, cardiolipin; CPT, choline phosphotransferase; DAG, diacylglycerol; DMPE, dimethylphosphatidylethanolamine; MMPE, monomethylphosphatidylethanolamine; PAF, platelet-activating factor; PC, phosphatidylcholine; Pcs, phosphatidylcholine synthase; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; PI, phosphatidylinositol; Pmt, phospholipid *N*-methyltransferase; PS, phosphatidylserine; SAM, *S*-adenosylmethionine; SAH, *S*-adenosylhomocysteine

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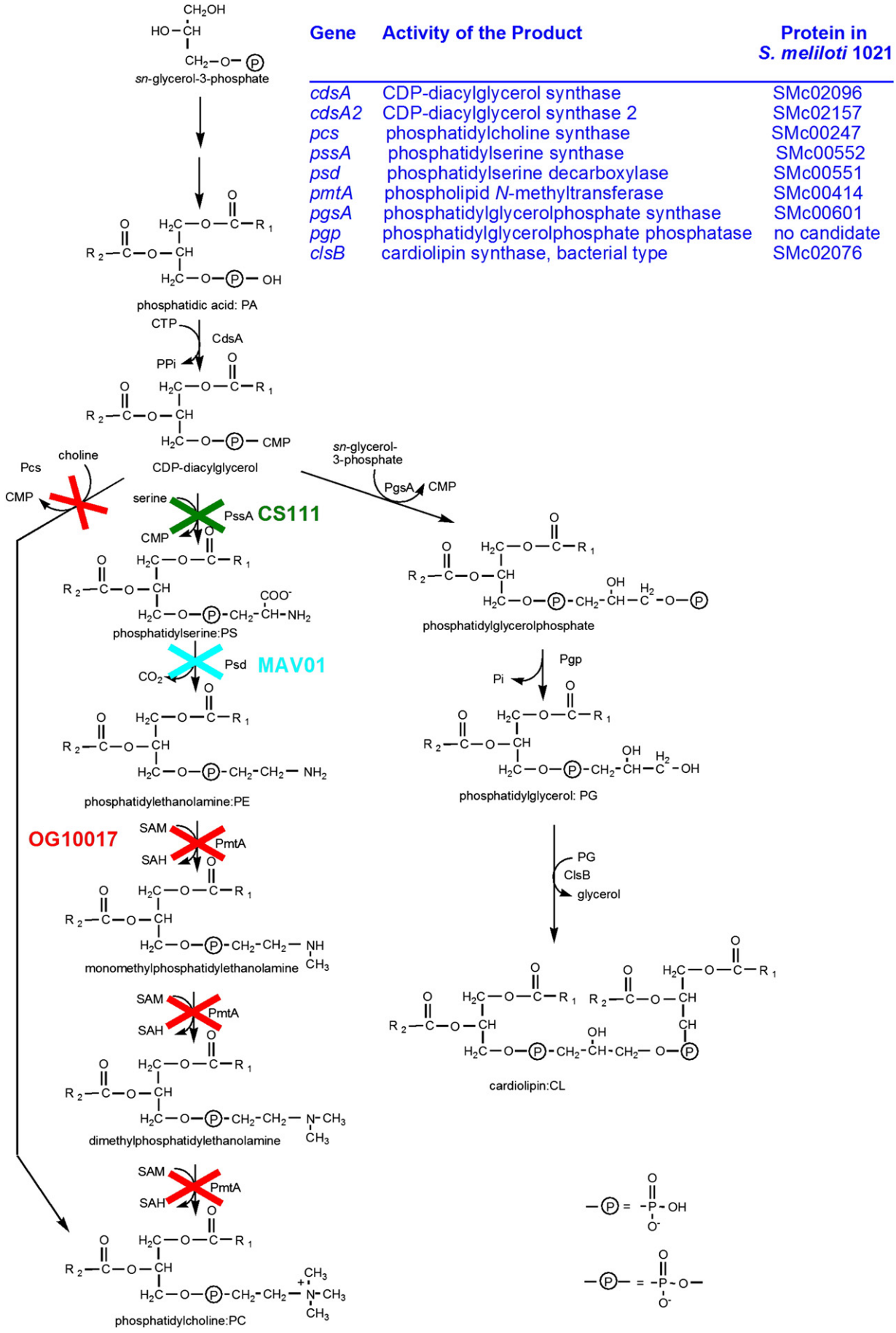

Fig. 1. Model of glycerophospholipid biosynthesis in *Sinorhizobium meliloti* (for details see text).