

An elusive marine photosynthetic bacterium is finally unveiled

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In the early 2000s, the realization that a significant fraction of the so-called heterotrophic marine bacterioplankton is capable of phototrophy has challenged our views of the carbon and energy budgets in the oceans (1) and, consequently, the biosphere. Because of their widespread occurrence and high abundance, bacterioplankton represent large pools of major elements and are catalysts in many biogeochemical cycles of global significance. In 2000–2002, a new picture of marine aerobic anoxygenic phototrophs (AAnPs) in the oceans was revealed. Using biophysical techniques, Kolber *et al.* (2, 3) detected a significant signal originating from these organisms in different regions of the World Ocean. These findings came as a big surprise because this type of photosynthesis was believed to be limited to a few organisms living in specialized ecological niches (4, 5). Based on cultivation studies (3–8), these newly discovered AAnPs were thought to be limited to members of *Alphaproteobacteria*. This notion was challenged in 2002 when a study based on environmental genomics (9) suggested that some marine AAnPs genes likely originated from members of *Gammaproteobacteria* (10). The work of Fuchs *et al.* (11) in this issue of PNAS is the first to unequivocally assign these elusive AAnP genes to a cultured member of *Gammaproteobacteria*.

The results offer a glimpse of the physiological adaptations and ecology of organisms that we now consider as typical marine bacterioplankton. Before the application of cultivation-independent technique analyses in the early 1990s, marine bacterioplankton was studied mainly after cultivation in rich media, and most isolated organisms were members of a limited set of copiotrophic (i.e., organisms adapted to growth in high substrate concentrations) *Gammaproteobacteria* and *Bacteroidetes*. Cloning and sequencing of 16S rRNA genes (12–15) and direct probing for these genes in the environment (16, 17) challenged the importance of these organisms and also led to the discovery of novel environmentally significant groups (18, 19). The findings also propelled the development and application of alternative cultivation techniques for bacterioplankton (20–23)

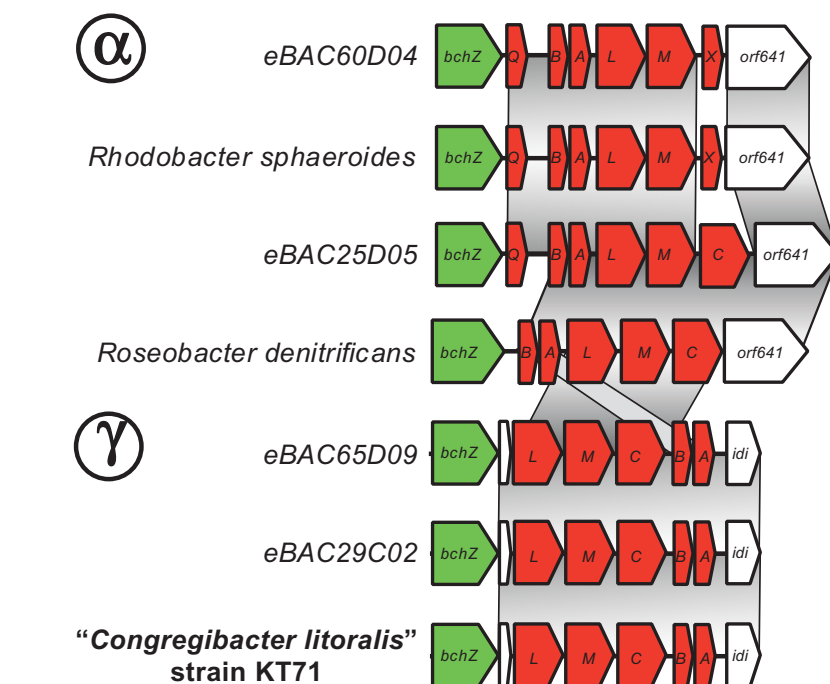


Fig. 1. Diversity of puf operons. Homologous regions are connected by dark gray areas. Puf genes and other reaction center genes are marked in red; green identifies bchZ genes, and white indicates nonphotosynthetic or hypothetical proteins with unknown function. *Alphaproteobacteria* (Upper) and *Gammaproteobacteria* (Lower) groups are indicated. Examples are from puf operons of cultured bacteria and environmental BAC sequences currently available in GenBank.

that resulted in the cultivation of many organisms that were previously known only from cultivation-independent studies. The KT71 strain described by Fuchs *et al.* (11) represents an environmentally significant clade (NOR5/OM60) that has been brought to cultivation by using low-nutrient media (24) and that, like *Pelagibacter ubique* (25) and *Silicibacter pomeroyi* (26), now has its full genomic sequence uncovered.

The sequencing of KT71 was part of the Gordon and Betty Moore Foundation's marine microbiology initiative launched in 2004 (www.moore.org/microgenome), in which >200 marine bacteria have or are in the process of full genome sequencing aiming to "produce a better understanding of the ocean's basic biological and chemical processes." Full genome sequencing analysis revealed that KT71 is, in fact, closely related to the mysterious gammaproteobacterial AAnP group detected in 2002 because its photosynthetic operon is identical to that of environ-

mental BAC clones from Monterey Bay in California (Fig. 1). Based on physiological tests and genomic information, these organisms are likely photoheterotrophs, organisms that use light as an energy source while exploiting organic compounds as their carbon and energy source. Genomic evidence for photoheterotrophy includes the presence of genes involved in bacteriochlorophyll-based phototrophy but the lack of key genes for autotrophic carbon fixation of the Calvin cycle, the reductive citrate cycle, or the reductive acetyl-CoA pathway. Despite the fact that these organisms do not fix significant amounts of carbon dioxide, photoheterotrophs still have the potential to affect carbon budgets in the

Author contributions: M.T.S. and O.B. wrote the paper.

The authors declare no conflict of interest.

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