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The Importance of Prophage in the Persistence of Commensal Bacteria within Human Oral Cavity

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Short Commentary

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SHORT COMMENTARY

The next-generation sequencing technology has revealed the staggering abundance and diversity of bacteriophage (phage) within human-associated microbiome [1,2]. Phages, both lytic and temperate, have been considered an integral part of human microbiome and their role in affecting bacterial physiology, modulating oral microbial communities have been suspected based on our understanding of phage-bacterial interaction in environmental microbial community. However, the empirical data on the bacteria-phage interaction and physiological and ecological role of phages in human microbiome, particularly oral microbiome, are lacking due to the limited number of phages that have been successfully isolated and characterized.

In a recent study, we reported the characterization of xhp1, a novel linear plasmid-like prophage identified based on genomic analysis from a human oral commensal isolate, *Actinomyces odontolyticus* subsp. *actinosynbacter* strain XH001. Prophage xhp1 can be induced and re-infects xhp1-cured XH001. The spontaneous induction of xhp1, particularly during biofilm formation, leads to the lysis of a subpopulation of bacterial hosts and the release of eDNA that promotes biofilm assembly [3]. This was the first report of a linear plasmid-like prophage identified from human oral microbiome, as well as the first line of evidence showing the impact of prophage on biofilm formation of a human oral commensal bacterium, which could potentially contribute to bacterium's persistence within the oral cavity.

The linear plasmid-like prophage is quite unique, and currently, only a few examples of such phages from bacteria are known, including the best-studied linear plasmid-like prophage N15 [4] of *Escherichia coli*. Intriguingly, unlike other known linear plasmid-like prophages which encode telomerase to replicate their genomes, xhp1 might use a different mechanism to replicate its linear genome through terminal-protein-primed DNA synthesis and subsequent endonucleolytic processing, which leads to a free terminal 3'-overhang in the xhp1 linear genome. The phylogenetic analysis also revealed limited similarity between xhp1 and the other linear plasmid-like phages, suggesting that xhp1 might belong to a unique group of phages. The discovery of this unique type of linear plasmid-like prophage within human oral microbiome is reflective of the astounding diversity of phage types revealed by metagenomic studies.

The impact of temperate phages on the physiology of environmental bacteria, as well as the pathogenicity of certain pathogenic bacterial species during their infection has been well-documented [5]. Temperate phages have been shown to contribute to bacterial adaptation during infection through a variety of mechanisms, including lysogenic conversion, alteration of toxins production and secretion as well as contribution to biofilm formation [6]. Particularly, the enhanced bacterial biofilm formation due to spontaneous induction of prophage has been well-documented and regarded as one of the key mechanisms to increase bacterial competitiveness [6].

Since the initial observation of released prophage in the cultivation medium of *Bacillus megaterium* lysogens due to spon-

taneous induction in 1950s [7], accumulating evidence from a variety of environmental bacterial species and human pathogens has demonstrated the positive impact of spontaneous prophage induction, often accompanied by lysis of a small percentage of bacterial cells, on the fitness of bacterial population [6]. Specifically, phage-induced lysis generally leads to an accumulation of extracellular DNA (eDNA), which is an important constituent of robust biofilms in diverse bacterial species, thus allowing them to persist within certain environments, or promoting virulence in pathogenic bacterial strains during their infection.

The capability to form biofilm is crucial in bacterial survival in environmental niches as well as host-associated microbial community. Particularly, considering the constant washing action of salivary flow, it is essential for human oral commensal bacteria to be able to form robust biofilm to their persistence within human oral cavity. Our study revealed one of the potential mechanisms that could be used by oral commensal bacterial to facilitate their biofilm formation. There are over 700 common oral bacterial species, with 200-300 bacterial species in each person's oral cavity [8]. Recent genome-based analysis revealed that DNA of viral origin represents a highly frequent element of bacterial genomes and accounts for up to 20% of the whole bacterial genome, many of which encode fully functional prophages [9]. Thus, spontaneous prophage induction could be a common, well-conserved mechanism for enhancing biofilm formation in many oral commensal species, an intriguing hypothesis warrants further investigation.

In addition to isolating and characterizing more oral phages and investigating their impact on their bacterial hosts physiology *in vitro*, future oral phage studies should also focus on better understanding of phage-bacterial host dynamics *in vivo* within multispecies community to obtain comprehensive knowledge regarding the phage's impact on the ecology of host-associated microbial community.

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