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Review

Q6Q1 A conserved chemical dialog of mutualism: lessons from squid and vibrio

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Abstract

Microorganisms shape, and are shaped by, their environment. In host–microbe associations, this environment is defined by tissue chemistry, which reflects local and organism-wide physiology, as well as inflammatory status. We review how, in the squid–vibrio mutualism, both partners shape tissue chemistry, revealing common themes governing tissue homeostasis in animal–microbe associations.

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1. Introduction

Animals and plants have evolved in a sea of microbes [43]. Some of these microbes form beneficial and co-evolved alliances with specific host tissues, from which both partners may derive benefits such as nutrient acquisition or defense [43]. In recent years, it has become clear that the composition of an organism's microbiota is structured by the host's tissue environment [23]. Host-tissue chemistry reflects both underlying physiological function and inflammatory status (for an in-depth review of tissue homeostasis, refer to [9]). The balance of these two factors varies, even within tissues of the same organ system. For example, the intestinal epithelium of animals is much more tolerant of inflammation-inducing microbial products in the colon (a major site of immune maturation), than in the ileum (the primary site of nutrient absorption) [49]. Thus, tissue chemistry and physiology can present significant selective pressures on the evolution of mutualism. In turn, the interaction of the normal microbiota with the innate immune system is a key mechanism that shapes the tissue environment, and mediates the activation of

adaptive immunity [32]. From this perspective, the relationship between the innate immune response and the microbiota is at the core of the acquisition, development, and maintenance of microbial symbionts.

Invertebrate animal models have long been critical to the study of innate immunity/microbe interactions, beginning in the 1800's, when Metchnikoff first observed phagocytosis in starfish larvae. Since this time, these invertebrate models have provided a window into the mechanisms by which the innate immune system maintains homeostasis, and have already revealed cornerstones of the chemical dialogue that underlies stability: for example, toll-like receptors, a major class of sensors of bacterial products, were first discovered during studies of the fruit fly [26]. It is likely that the strategies of innate immune recognition used by other branches of invertebrate phylogeny, such as annelids, nematodes, and mollusks, have much to reveal about the conserved strategies of mutualism [53,21]. In this review, we focus on the molluscan branch of metazoan phylogeny and, specifically, on what the squid *Euprymna scolopes* has revealed about how its innate immune system and its co-evolved microbial symbiont, *Vibrio fischeri*, orchestrate the initiation, development, and maintenance of mutualism. A discussion of the mechanisms underlying these processes is not within the scope of the present review; for that, we recommend recent articles on the immune systems of squids

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and other invertebrates [53,21,62]. We focus instead on how the squid–vibrio mutualism has contributed to our understanding of the chemical ‘language’ that forms the negotiation between a microbial symbiont and its host’s innate immune response.

1.1. The squid–vibrio model

E. scolopes forms a specific association with the Gram-negative, bioluminescent, marine gamma-proteobacterium *V. fischeri*. The mutualism takes place in the epithelium-lined crypts of a specialized anatomical structure of the squid called the light organ [73] (Fig. 1A). The functional basis of this mutualism is the bioluminescence provided by *V. fischeri*, which is used for host behaviors. The light organ shares much of the anatomical and physiological features of an eye: a lens and reflector manipulate the intensity and direction of bioluminescence (Fig. 1B), and the supporting epithelial tissue is photoreceptive [44] and expresses genes involved in eye

development [58]. Unlike the eye, which collects and perceives light from the environment, the light organ manipulates the bioluminescence of a dense (10^8 CFU/mature light organ) population of *V. fischeri* [63]. Only *V. fischeri* can colonize this tissue habitat, and a persistent, monospecific population of the symbiont is maintained in the light organ throughout the squid’s ~9-month life. The squid’s immune response is orchestrated primarily by both a population of circulating macrophage-like immune cells, called hemocytes, and tissue-specific responses to microbe-associated molecular patterns (MAMPs) [45,62]. In the following sections, we review our current understanding of the chemical selection for *V. fischeri* that occurs during the initiation, development and maintenance of mutualism.

2. Initiation: the winnowing process

Symbiosis is initiated in a multi-step process, beginning when the newly hatched squid harvests *V. fischeri* cells from the bacterioplankton. Ecological studies have demonstrated that *V. fischeri* is enriched in the squid’s habitat, but still represents only a minor constituent of the total population [40]. Therefore, the challenge for a juvenile squid is two-fold: it must first sample sufficient seawater to encounter *V. fischeri*, and then select cells of this specific symbiont from among the many kinds of other microbes that have been collected, in a process named ‘winnowing’ [56]. Winnowing begins outside of the light organ, in bilateral ciliated fields that are unique to the uncolonized, or aposymbiotic, state. This complex, step-wise progression occurs over a distance of only a hundred microns, highlighting the importance of understanding the nanoscale structure of host-tissue microenvironments. In this section, we review what is known of the chemical exchange that takes place between the partners during winnowing.

2.1. Making first contact

Upon hatching, ventilation of the mantle cavity brings bacterioplankton-rich seawater in contact with the surface of the light organ. Peptidoglycan (PGN) fragments of cell wall released by these bacteria induce a non-specific shedding of sialylated host mucus [52] (Fig. 2A). The acidic glycosylation of the mucins produces a matrix with a pH of ~6.3 [37], in which the bacterioplankton are entrapped. Host antimicrobial peptides/proteins such as galaxin and peptidoglycan recognition-protein 2 (PGRP2), establish an early negative selection against Gram-positive microbes in the mucus [30,74]. Combined with other antimicrobial constituents secreted into the mucus, such as the oxygen carrier and phenoloxidase, hemocyanin [38] and, as yet, uncharacterized factors, the chemistry that defines this first site of host contact results in the exclusion of many seawater bacteria.

2.2. Establishing dominance in the mucus

Aided by the PGN-triggered mucus, *V. fischeri* cells that are drawn into the mantle cavity during ventilation adhere directly

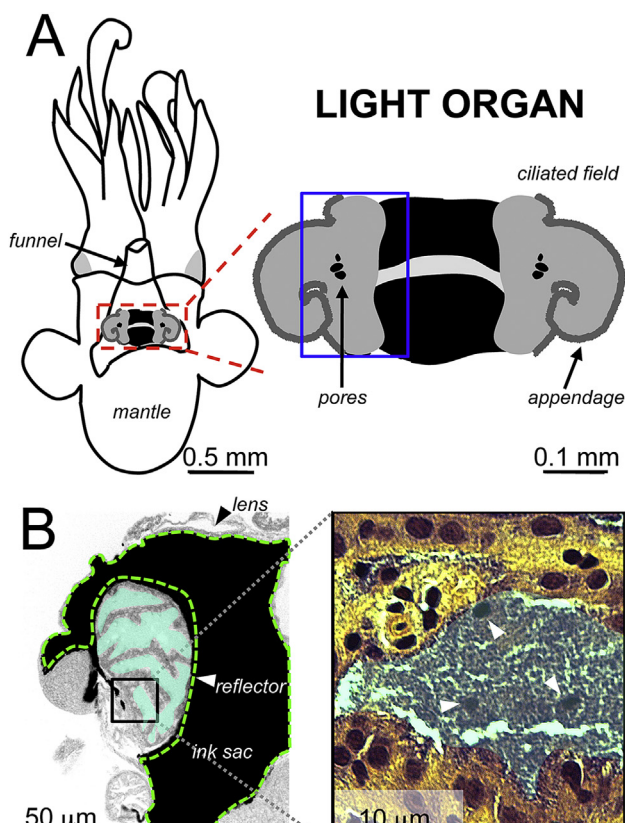


Fig. 1. The anatomy of the juvenile squid–vibrio mutualism. A) The squid’s light organ is the anatomical structure that maintains the bioluminescent symbiont *V. fischeri* and modulates light output. The organ is located underneath the mantle of the squid, just atop the funnel: a structure used to move water into and out of the mantle cavity. The immature light organ (boxed in red, and enlarged at right) has bilateral ciliated fields and appendages. At the base of the appendages are pores, leading into the crypts of the light organ. B) A cross-section of the light organ, boxed in blue in (A), shows that the symbiont (teal) is maintained in extracellular crypts lined with a polarized epithelium that is photoreceptive. Structures surrounding the crypts, such as the reflector (indicated in green dashed lines), ink sac, and lens manipulate the light produced by the symbiont for host behaviors.

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