
Prokaryotic Symbionts of Termite Gut Flagellates: Phylogenetic and Metabolic Implications of a Tripartite Symbiosis

Andreas Brune, Ulrich Stingl

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Introduction

The symbiotic associations of termites with their gut microorganisms have been studied for almost a century. While the earlier work had focused on the intestinal protozoa of lower termites and their role in digestion, the more recent investigations have been directed mainly at the prokaryotic gut microorganisms, their metabolic activities, and the structure and function of the bacterial and archaeal populations. In addition, the application of microsensor techniques has revealed the unexpected dynamics of the physiochemical gut conditions and given the first indications of the spatial organization of the major microbial activities, which has led to the recognition that the gut provides a variety of different microhabitats for its microbiota.

The most important habitats for the prokaryotes in the hindgut of lower termites are provided by the intestinal protozoa. Although it is long known that the gut flagellates are intimately associated with prokaryotes, the significance of this phenomenon has not been fully appreciated. The difficulties surrounding cultivation of the protozoa and the complete absence of pure cultures of the prokaryotic symbionts so far allowed merely a morphological description of the different associations. Their exact nature and the possible benefits for the partners are mostly in the dark. However, with the advent of molecular biology tools and the resulting new possibilities, the interest in the symbiotic associations between prokaryotes and termite gut flagellates has been renewed.

A definitive classification of these associations into the different categories of symbiosis, such as mutualism, parasitism, or commensalism, would require a level of understanding that remains to be reached. This chapter will therefore use the term symbiosis in its broader definition, as it was originally coined by Anton de Bary (1878), which comprises all kinds of associations between different species.

A. Brune

Max Planck Institute for Terrestrial Microbiology, Marburg, Germany

U. Stingl

Department of Microbiology, Oregon State University, Corvallis, Or., USA

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The Termite Gut Microecosystem

The symbiotic digestion of lignocellulose by termites is a complex series of events involving both the host and its intestinal microbiota (Brune 2003, 2005). While the digestive activities in the foregut and midgut seem to be mainly caused by the host, the processes in the hindgut are largely controlled by the symbionts. The recalcitrance of the lignocellulosic diet and the dynamics of physicochemical gut conditions contribute to the heterogeneity of ecological niches and are reflected in a diverse community of prokaryotic and eukaryotic microorganisms.

2.1

Lignocellulose degradation

There is a large body of literature on the decomposition of wood and cellulose by termite gut flagellates, which are essential for the digestion of lignocellulose in lower termite (Radek 1999). By contrast, the majority of prokaryotes in termite guts do not seem to contribute to polymer degradation. They appear to be involved mainly in the fermentation of soluble metabolites released into the gut, which are derived either directly from the food by the digestive enzymes or from the fermentative activity of the intestinal protozoa (Breznak 2000; Ohkuma 2003; Brune 2005).

Lignocellulose is not only difficult to degrade, but it is also an extremely nitrogen-poor substrate that lacks most of the essential nutrients required by the termite, such as amino acids, vitamins, and sterols. The capacity of the intestinal prokaryotes to fix dinitrogen, to assimilate nitrate and ammonia, and to synthesize those amino acids and vitamins essential for the host makes them also an important source of nutrition (Breznak 2000; Machida et al. 2001). The microbial biomass produced in the hindgut is accessed via proctodeal feeding, which serves both the transfer of symbionts among individual termites and nitrogen cycling by subsequent digestion of microbial biomass in the midgut (Fujita et al. 2001).

2.2

The Gut Microenvironment

Based on the oxygen sensitivity and the fermentative metabolism of the intestinal protozoa, the high concentrations of microbial fermentation products, the presence of anaerobic or oxygen-sensitive activities such as methanogenesis and nitrogen fixation, and the isolation of obligately anaerobic bacteria, it was