



## Review

Architecture and assembly of the Type VI secretion system <sup>☆</sup>

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## ABSTRACT

The Type VI secretion system (T6SS) delivers protein effectors to diverse cell types including prokaryotic and eukaryotic cells, therefore it participates in inter-bacterial competition and pathogenesis. The T6SS is constituted of an envelope-spanning complex anchoring a cytoplasmic tubular edifice. This tubular structure is evolutionarily, functionally and structurally related to the tail of contractile phages. It is composed of an inner tube tipped by a spike complex, and engulfed within a sheath-like structure. This structure assembles onto a platform called “baseplate” that is connected to the membrane sub-complex. The T6SS functions as a nano-crossbow: upon contraction of the sheath, the inner tube is propelled towards the target cell, allowing effector delivery. This review focuses on the architecture and biogenesis of this fascinating secretion machine, highlighting recent advances regarding the assembly of the membrane or tail complexes. This article is part of a Special Issue entitled: Protein trafficking and secretion in bacteria. Guest Editors: Anastassios Economou and Ross Dalbey.

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## 1. Introduction

As emphasized in this Special Issue, a number of specialized protein targeting and secretion mechanisms are dedicated to transport proteins or other macromolecules to specific compartments of the bacterial cell or to the external milieu. These mechanisms are not only critical for bacteria to ensure the proper localization and positioning of key processes, but are essential to efficiently induce pathogenesis or colonize an ecological niche. For a bacterium, colonizing a new niche means not only

adapting its fitness but also to entering into competition with other organisms participating in this niche; however, the gain and loss ratio should be strictly controlled as an ecological niche is also efficient when microorganisms coordinate their behaviors. The Type VI secretion system (T6SS) recently emerged as one of the key players in the control of these niches, as the activity of the T6SS might affect prokaryotic cells, simply or highly organized eukaryotic cells. The T6SS delivery mechanism of effector proteins requires a complex apparatus that assembles into the cytoplasm and extends through the bacterial envelope. It is broadly distributed among Gram-negative bacteria but almost exclusively confined to the  $\alpha$ -,  $\beta$ - and  $\gamma$ -proteobacteria subgroups with an over-representation in the  $\gamma$  [1,2]. T6SS components are generally encoded within large clusters of genes and in most instances, the expression of these gene clusters is tightly controlled at the transcriptional, post-transcriptional and/or post-translational levels.

This review summarizes the current knowledge on the structural organization of this secretion apparatus. We refer the readers to excellent recent reviews describing the regulation of T6SS genes, the function, the biological significance and the effector proteins delivered by this apparatus [3–8].

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