

## Active transport across the bacterial outer membrane: The Ton motor complex

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In Gram-negative bacteria, outer membrane (OM) transporters import nutrients by coupling to an inner membrane (IM) protein complex called the Ton complex. The Ton complex consists of TonB, ExbB, and ExbD, and uses the proton motive force (pmf) at the IM to transduce energy to the OM via TonB. Here, we structurally characterize the Ton complex from *E. coli* using X-ray crystallography, electron microscopy, DEER spectroscopy, and crosslinking, revealing a stoichiometry consisting of a pentamer of ExbB, a dimer of ExbD, and at least one TonB. Electrophysiology studies show that the Ton subcomplex forms pH-sensitive cation-selective channels, providing insight to the mechanism by which it may harness the pmf for energy production.