Cryo-ET Analysis of the Yeast Synaptonemal Complex *In-Situ*

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The synaptonemal complex (SC) is the large proteinaceous scaffold that assembles between homologous chromosomes by the end of meiotic prophase. While its functions are numerous -- and mysterious, in yeast the SC is required for the phenomenon known as crossover interference. Knowledge of the native structure of this complex is needed to evaluate how the SC carries out its functions. Traditional electron microscopy and super-resolution light microscopy have revealed that in many organisms, the SC has a ladder-like structure: two rail-like lateral elements are bridged by a set of rung-like transverse filaments. The filaments are connected along their centers by a central element. To determine the 3-D architecture of the SC and nuclear macromolecular complexes in situ, we studied frozen-hydrated meiotic yeast cell cryosections by Volta electron cryotomography and subtomogram analysis. We find the predominant SC motif is a duster-like arrangement of densely packed triple-helical filaments, both of which are also abundant in the polycomplexes of pachytene-arrested cells. There was no evidence for a ladder-like organization. Partial dissolution by 1,6-hexanediol treatment suggests that these triple-helical filaments belong to the central region of the SCs and are most likely the abundant Zip1 transverse element protein. Subtomogram averaging revealed that the SC's triple helix is up to 12-nm thick and has a rise of 5 nm and a pitch of 130 nm. Polymers thinner than the triple helix, such as single or double strands, were not detected; this observation is consistent with the strong self-oligomerization properties of SC proteins. The dense packing of SC subunits supports the notion that the SC's mechanical properties help coordinate the rapid end-to-end communication across synapsed chromosomes. Finally, our study provides a 3-D framework for understanding the other macromolecule machines of meiosis in situ.