

**THE CRYOEM STRUCTURE OF THE SACCHAROMYCES CEREVISIAE  
RIBOSOME MATURATION FACTOR REA1**

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The biogenesis of 60S ribosomal subunits is initiated in the nucleus where rRNAs and proteins form pre-60S particles. These pre-60S particles mature by transiently interacting with various assembly factors. The ~5000 amino-acid AAA+ ATPase Rea1 (or Midasin) generates force to mechanically remove assembly factors from pre-60S particles, which promotes their export to the cytosol. Here we present three Rea1 cryoEM structures. We visualise the Rea1 engine, a hexameric ring of AAA+ domains, and identify an  $\alpha$ -helical bundle of AAA2 as a major ATPase activity regulator. The  $\alpha$ -helical bundle interferes with nucleotide-induced conformational changes that create a docking site for the substrate binding MIDAS domain on the AAA+ ring. Furthermore, we reveal the architecture of the Rea1 linker, which is involved in force generation and extends from the AAA+ ring. The data presented here provide insights into the mechanism of one of the most complex ribosome maturation factors