

## ▲ FIGURE 12-11 Schematic model of the relationship between *E. coli* replication proteins at a growing fork.

(1) A single DnaB helicase moves along the lagging-strand template toward its 3' end, thereby melting the duplex DNA at the fork. (2) One core polymerase (core 1) quickly adds nucleotides to the 3' end of the leading strand as its single-stranded template is uncovered by the helicase action of DnaB. This leading-strand polymerase, together with its  $\beta$ -subunit clamp, remains bound to the DNA, synthesizing the leading strand continuously. (3) A second core polymerase (core 2) synthesizes the lagging strand discontinuously as an

Okazaki fragment (see Figure 12-9b). The two core polymerase molecules are linked via a dimeric  $\tau$  protein. (4) As each segment of the single-stranded template for the lagging strand is uncovered it becomes coated with SSB protein and forms a loop. Once synthesis of an Okazaki fragment is completed, the lagging-strand polymerase dissociates from the DNA but the core remains bound to the  $\tau$ -subunit dimer. The released core polymerase subsequently rebinds with the assistance of another  $\beta$  clamp in the region of the primer for the next Okazaki fragment. See the text for additional details. [Adapted from A. Kornberg, 1988, J. Biol. Chem. **263**:1; S. Kim et al., 1996, Cell **84**:643.]