



◀ **FIGURE 4-10 Three stages in transcription.** During initiation of transcription, RNA polymerase forms a transcription bubble and begins polymerization of ribonucleotides (rNTPs) at the start site, which is located within the promoter region. Once a DNA region has been transcribed, the separated strands reassociate into a double helix, displacing the nascent RNA except at its 3' end. The 5' end of the RNA strand exits the RNA polymerase through a channel in the enzyme. Termination occurs when the polymerase encounters a specific termination sequence (stop site). See the text for details.

polymerases require various protein factors, called **general transcription factors**, to help them locate promoters and initiate transcription. After binding to a promoter, RNA polymerase melts the DNA strands in order to make the bases in the template strand available for base pairing with the bases of the ribonucleoside triphosphates that it will polymerize together. Cellular RNA polymerases melt approximately 14 base pairs of DNA around the transcription start site, which is located on the template strand within the promoter region (step 2). Transcription initiation is considered complete when the first two ribonucleotides of an RNA chain are linked by a phosphodiester bond (step 3).

After several ribonucleotides have been polymerized, RNA polymerase dissociates from the promoter DNA and general transcription factors. During the stage of *strand elongation*, RNA polymerase moves along the template DNA one base at a time, opening the double-stranded DNA in front of its direction of movement and hybridizing the strands behind

it (Figure 4-10, step 4). One ribonucleotide at a time is added to the 3' end of the growing (*nascent*) RNA chain during strand elongation by the polymerase. The enzyme maintains a melted region of approximately 14 base pairs, called the *transcription bubble*. Approximately eight nucleotides at the 3' end of the growing RNA strand remain base-paired to the template DNA strand in the transcription bubble. The elongation complex, comprising RNA polymerase, template DNA, and the growing (nascent) RNA strand, is extraordinarily stable. For example, RNA polymerase transcribes the longest known mammalian genes, containing $\approx 2 \times 10^6$ base pairs, without dissociating from the DNA template or releasing the nascent RNA. **Since RNA synthesis occurs at a rate of about 1000 nucleotides per minute at 37 °C, the elongation complex must remain intact for more than 24 hours to assure continuous RNA synthesis.**

During transcription *termination*, the final stage in RNA synthesis, the completed RNA molecule, or **primary transcript**,