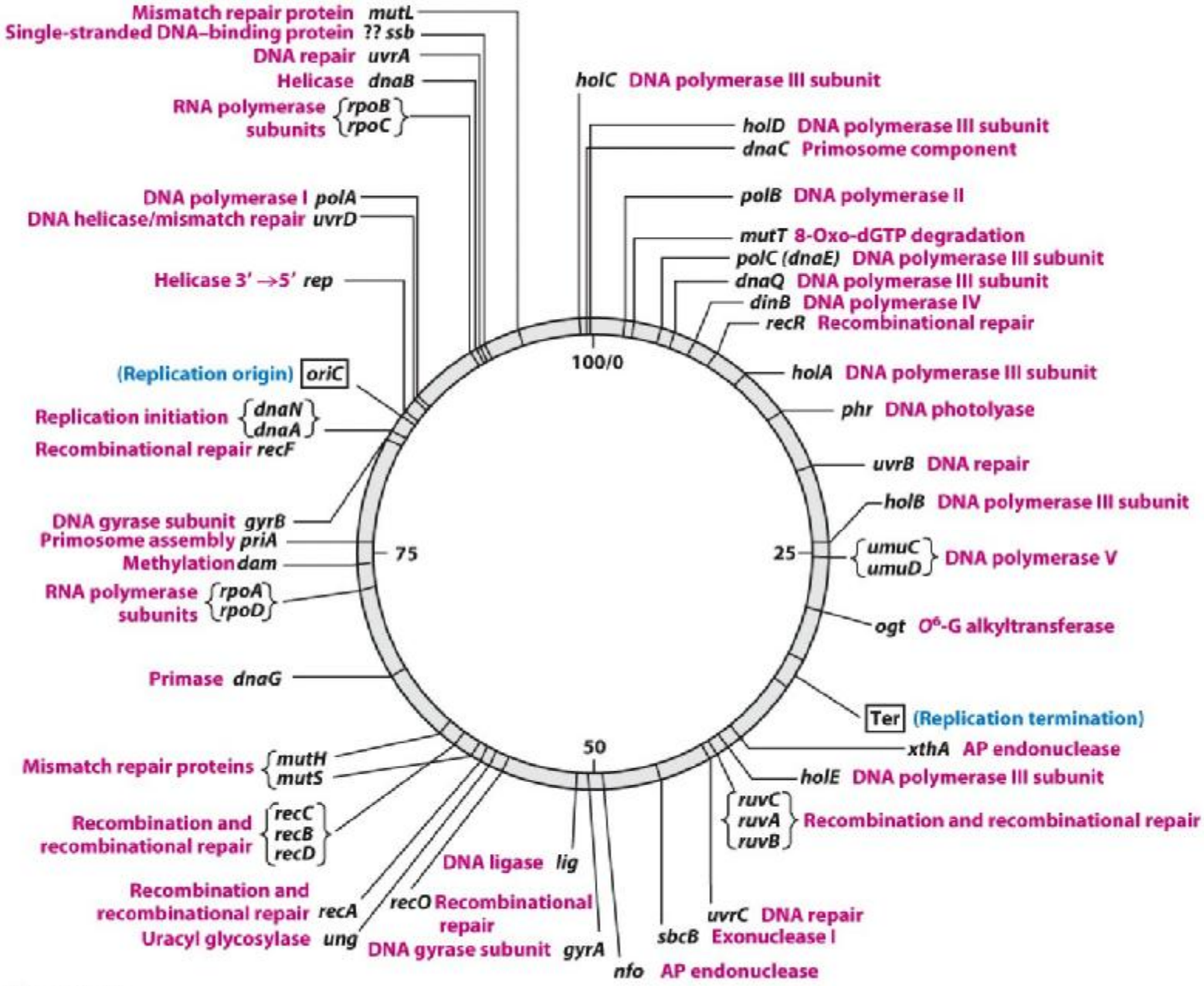

Figure 25-1

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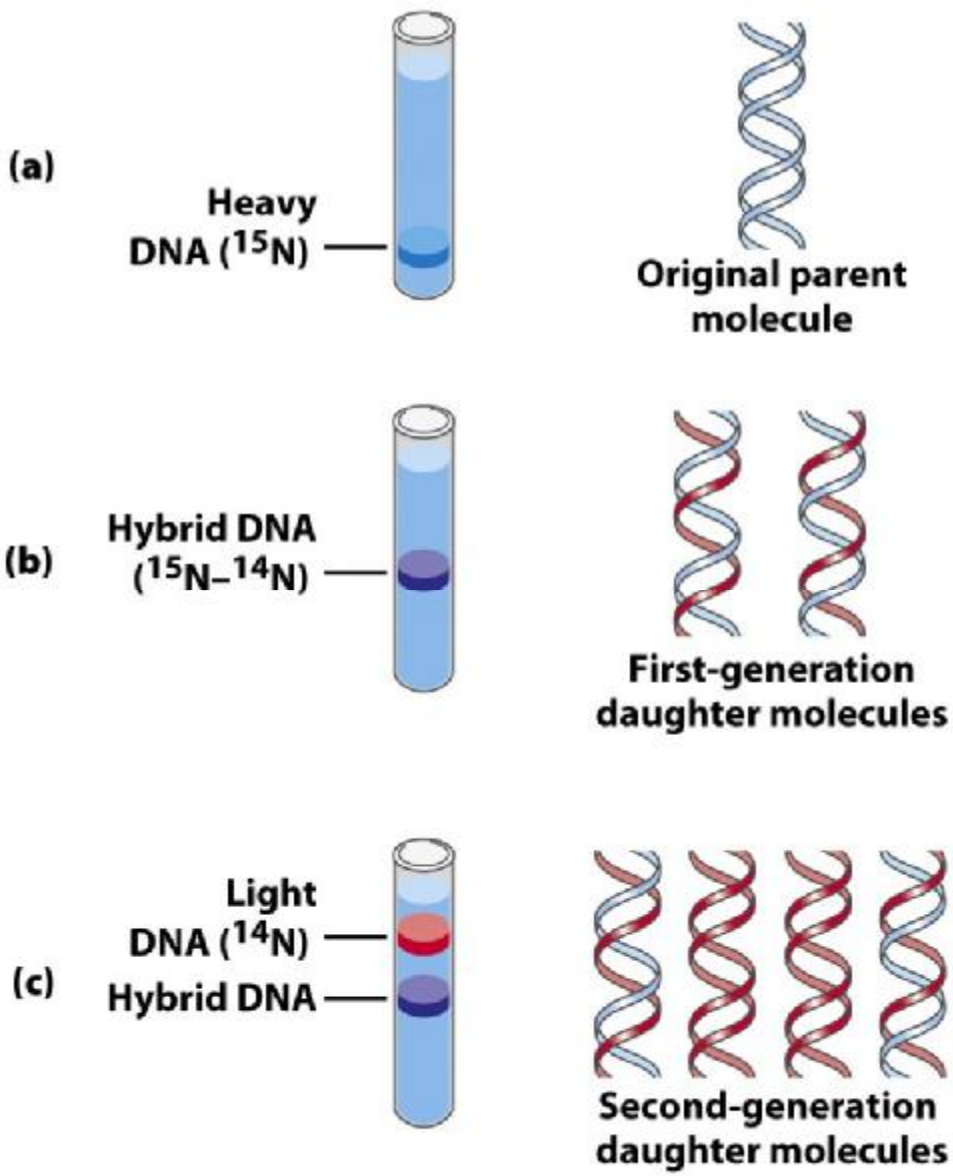

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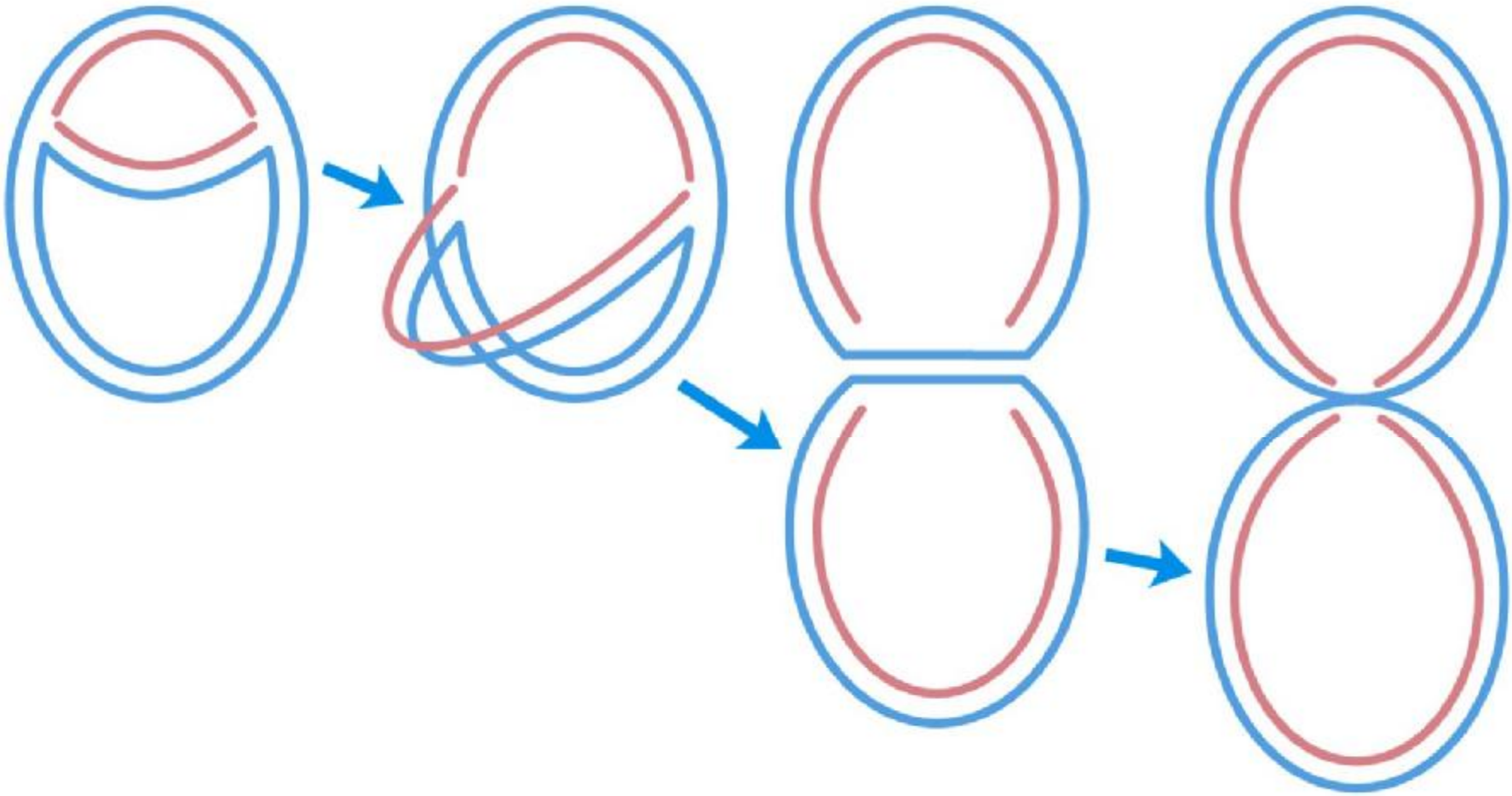

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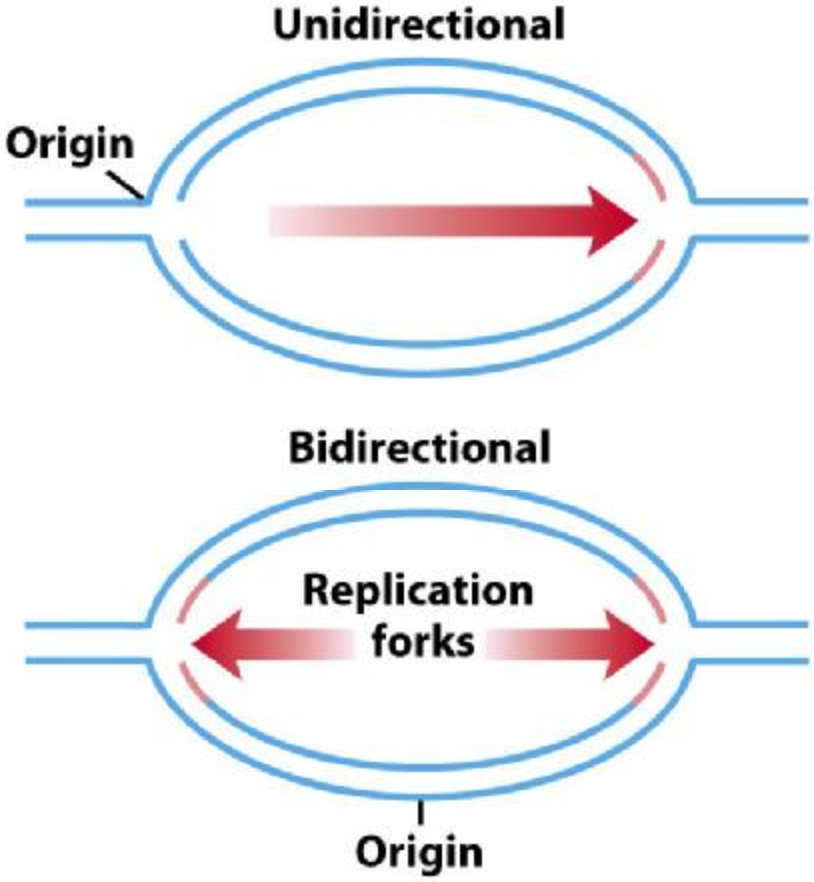

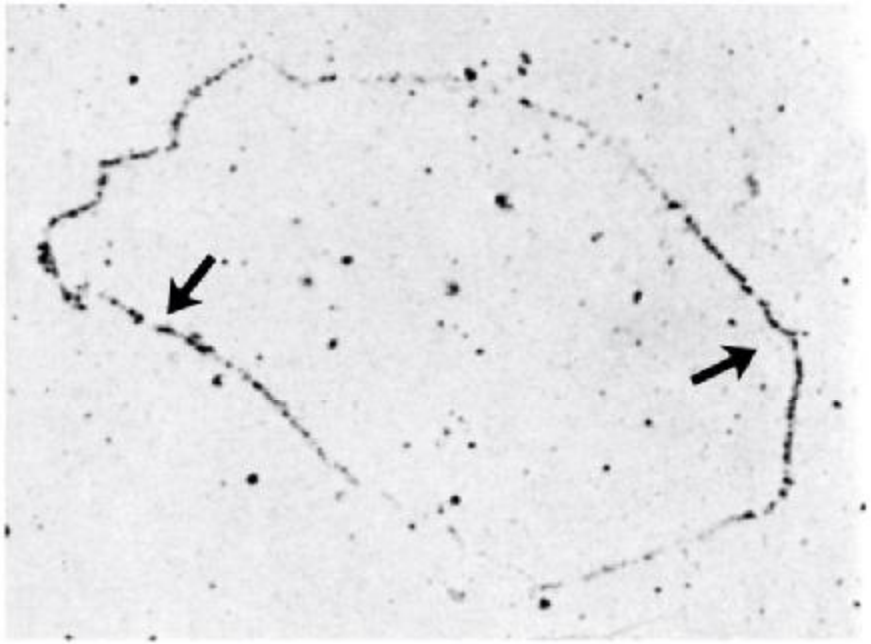

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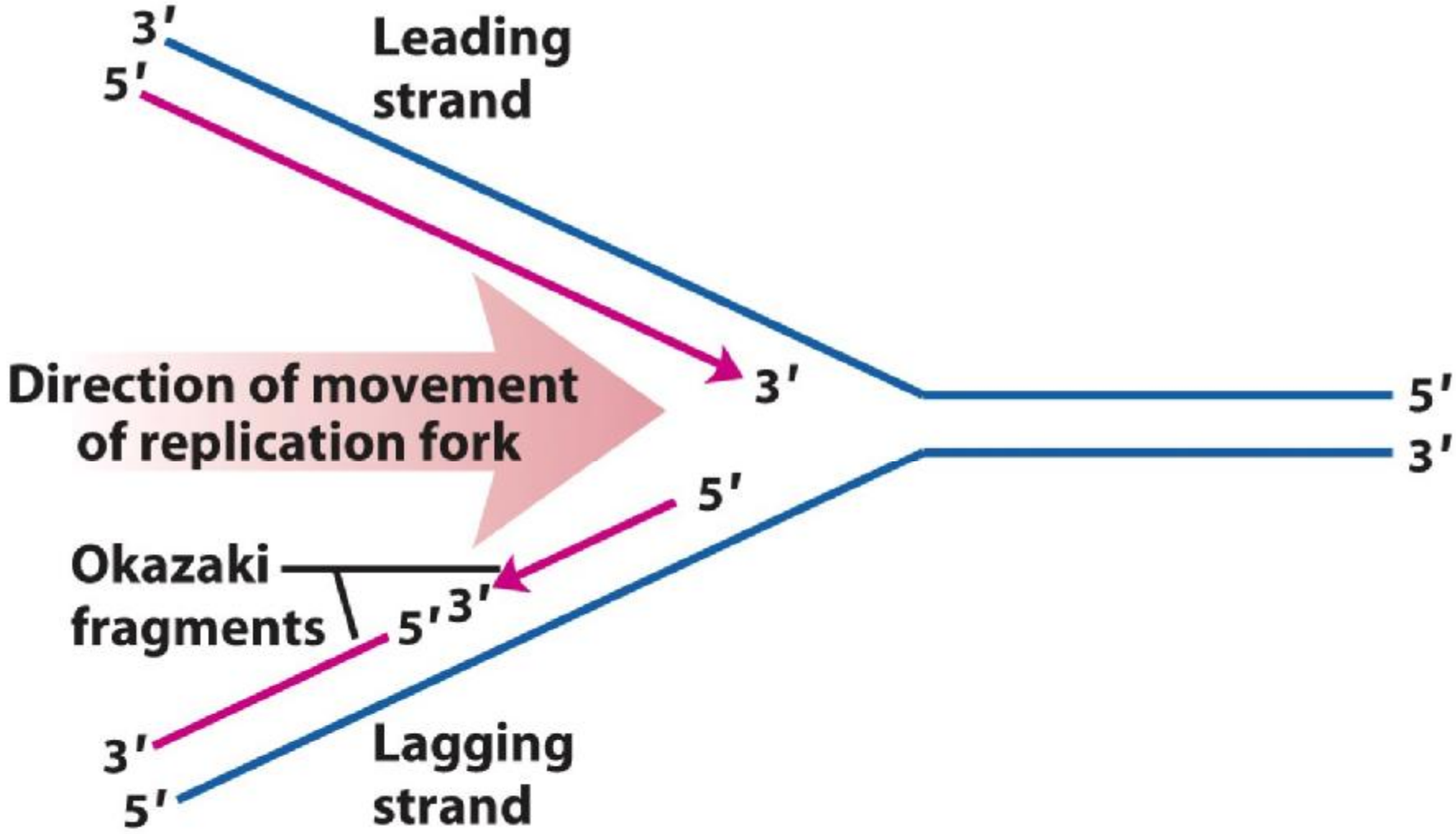

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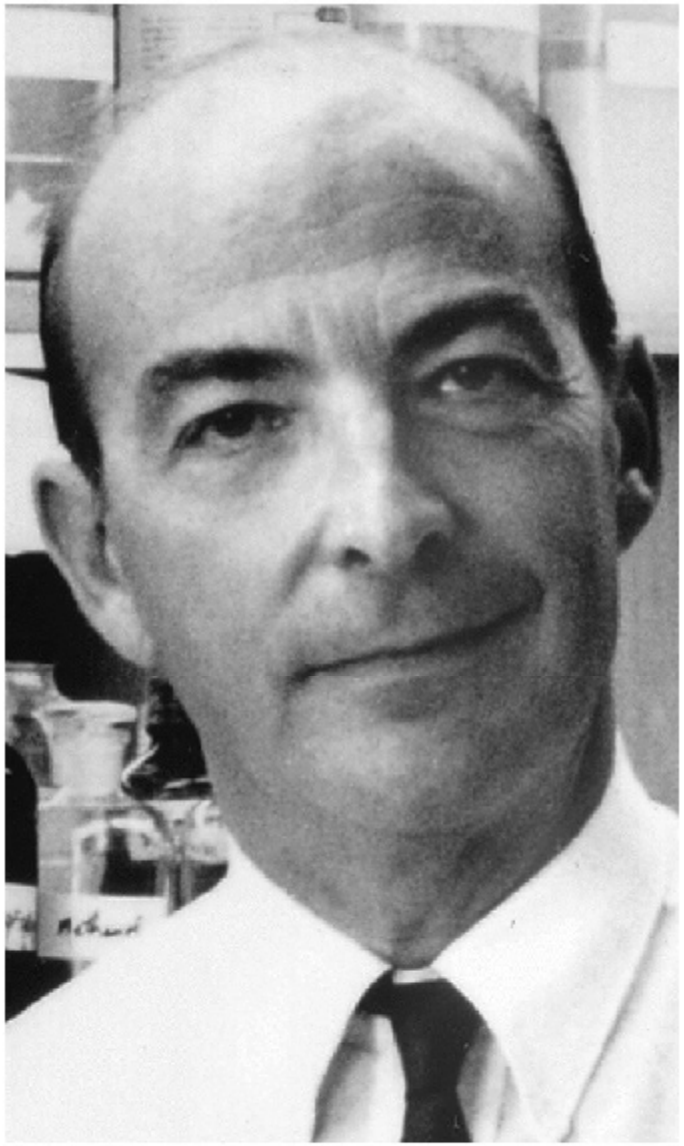

Arthur Kornberg, 1918–2007

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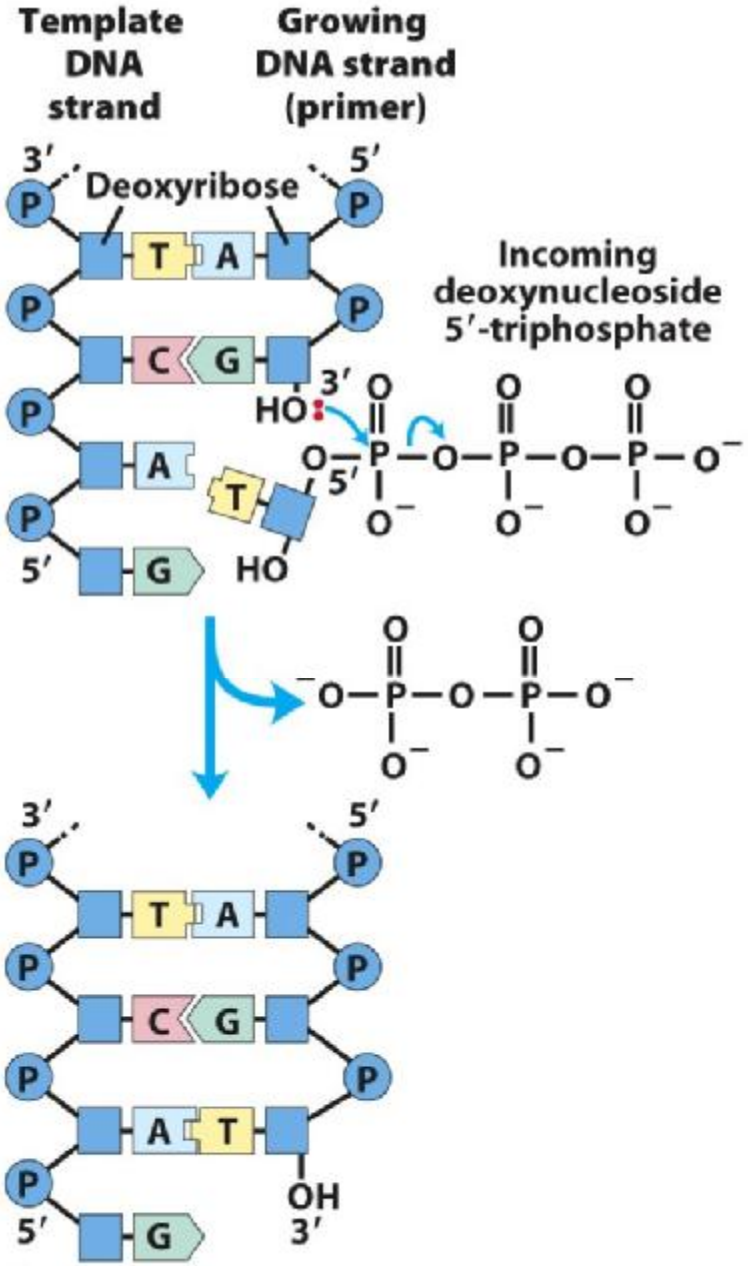

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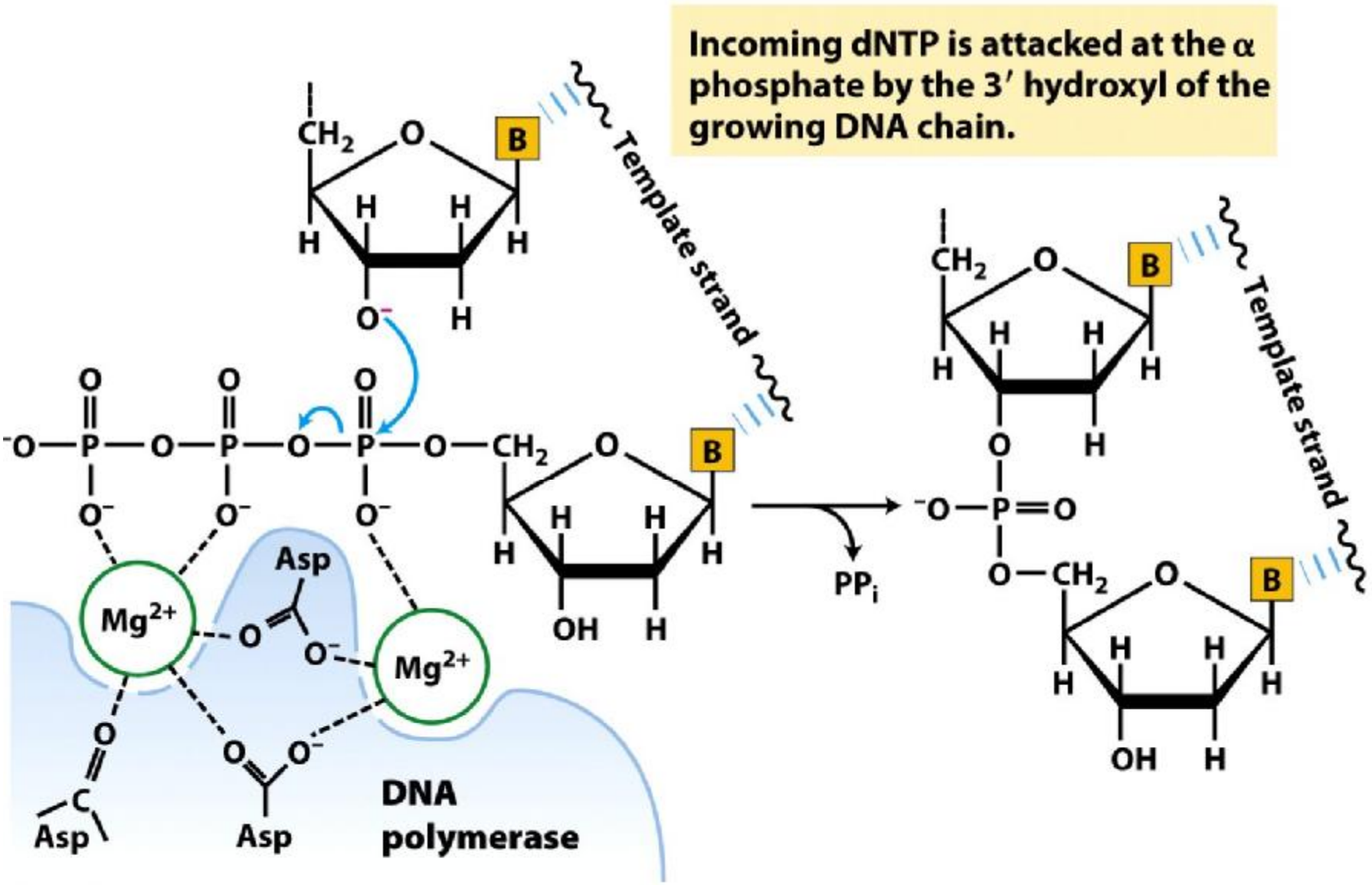

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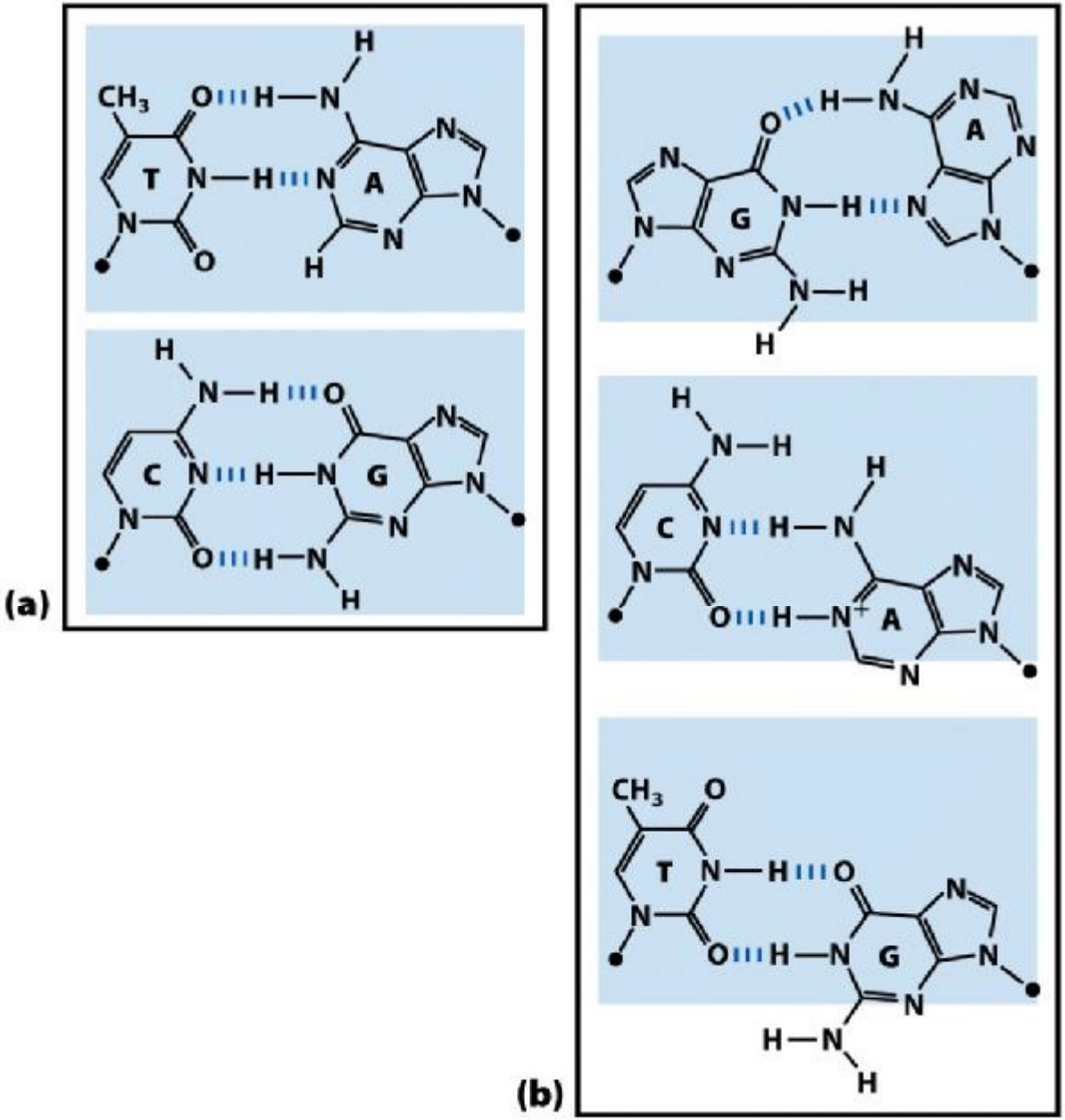

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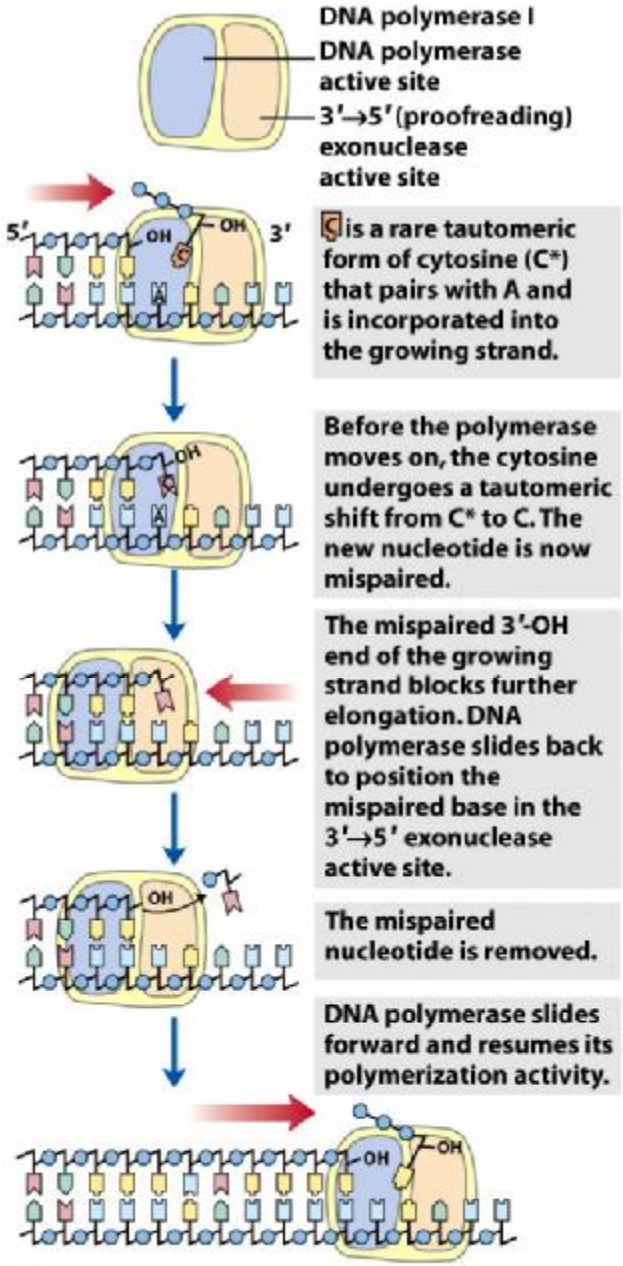

Figure 25-7

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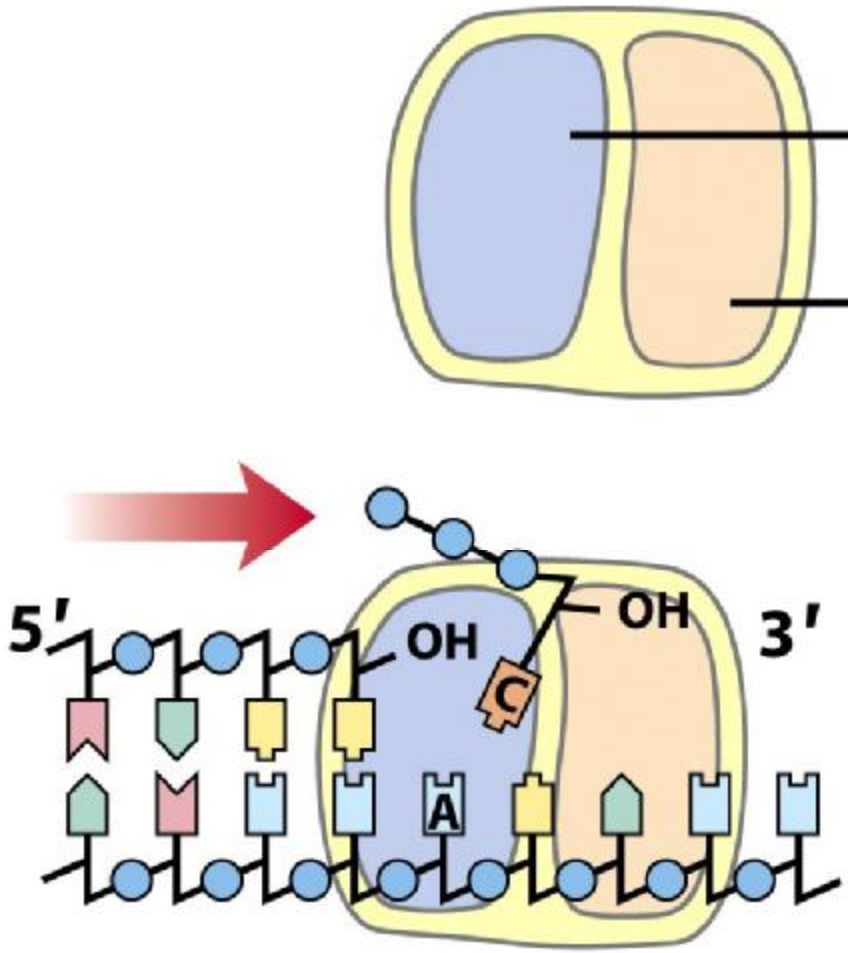

DNA polymerase I

DNA polymerase active site

3′→5′ (proofreading) exonuclease active site

C is a rare tautomeric form of cytosine (C*) that pairs with A and is incorporated into the growing strand.

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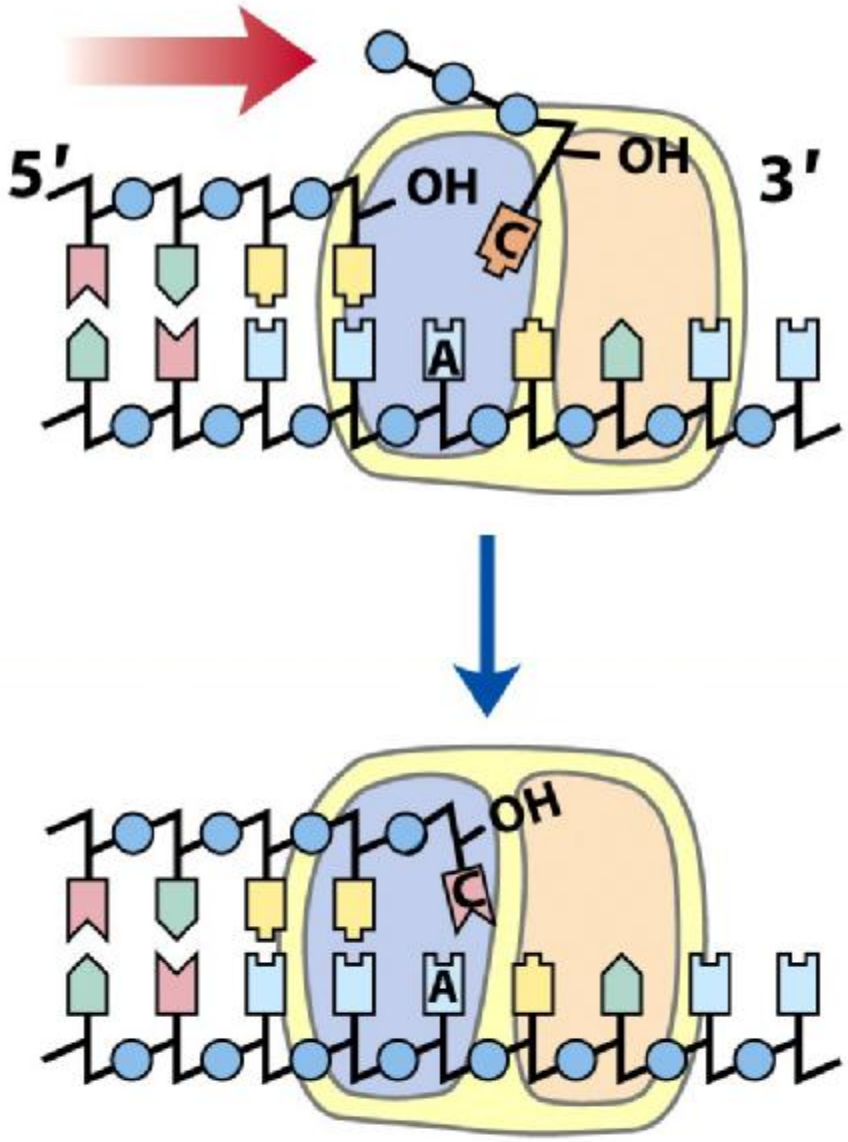

C is a rare tautomeric form of cytosine (C*) that pairs with A and is incorporated into the growing strand.

Before the polymerase moves on, the cytosine undergoes a tautomeric shift from C* to C. The new nucleotide is now mispaired.

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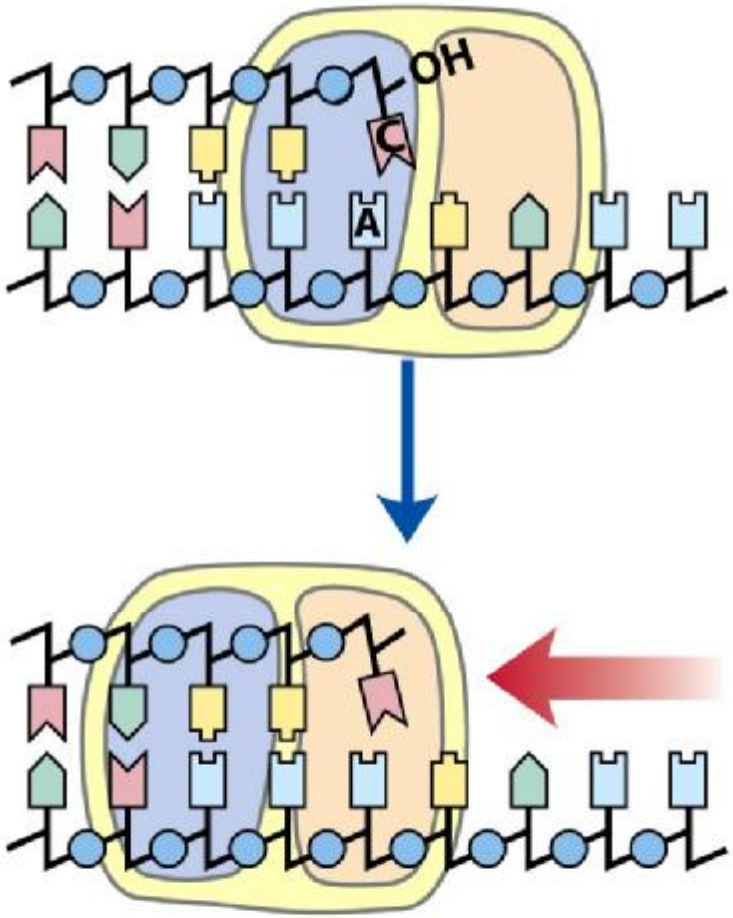

Before the polymerase moves on, the cytosine undergoes a tautomeric shift from C* to C. The new nucleotide is now mispaired.

The mispaired 3′-OH end of the growing strand blocks further elongation. DNA polymerase slides back to position the mispaired base in the 3′→5′ exonuclease active site.

Figure 25-7 part 3
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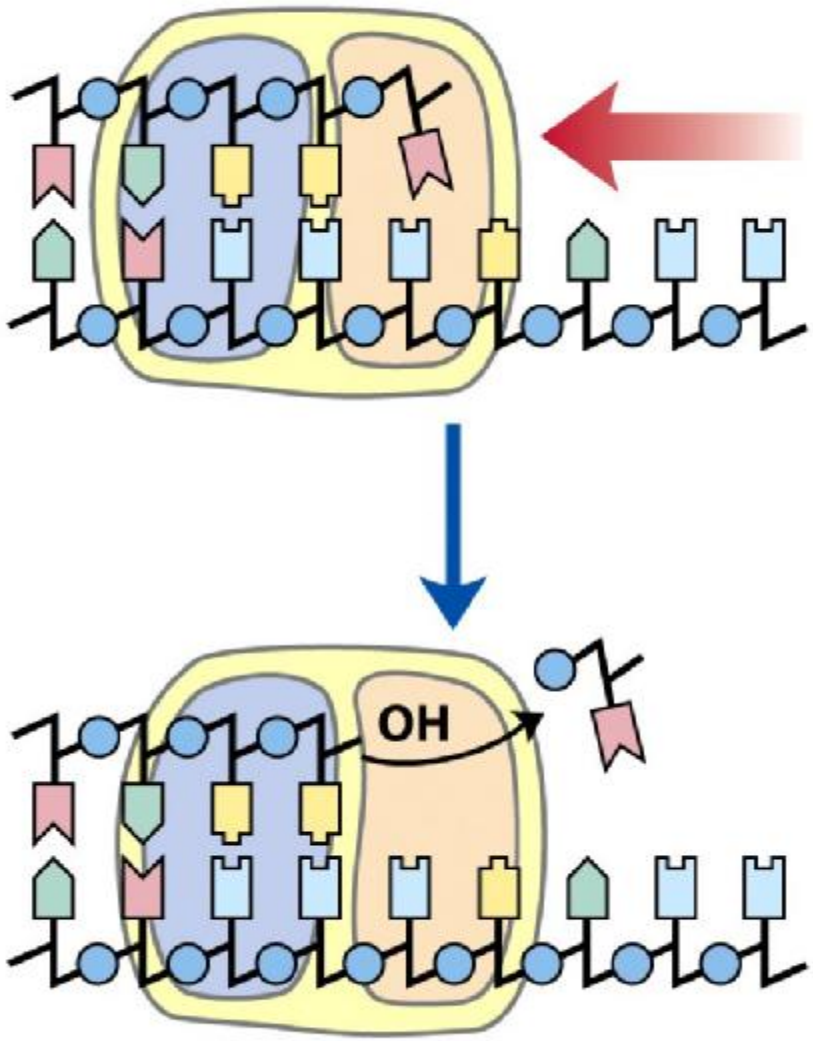

The mispaired 3′-OH end of the growing strand blocks further elongation. DNA polymerase slides back to position the mispaired base in the 3′→5′ exonuclease active site.

The mispaired nucleotide is removed.

Figure 25-7 part 4
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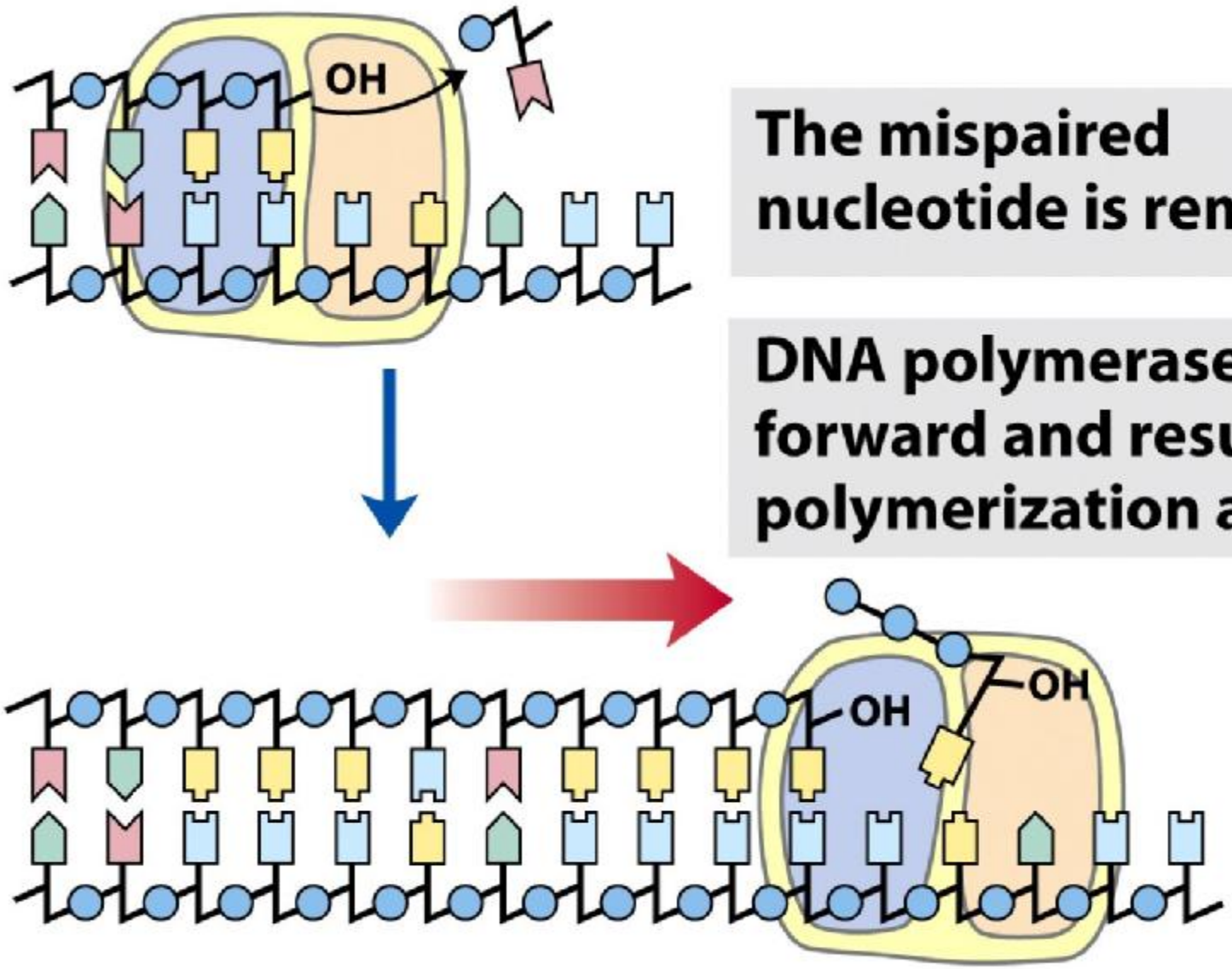

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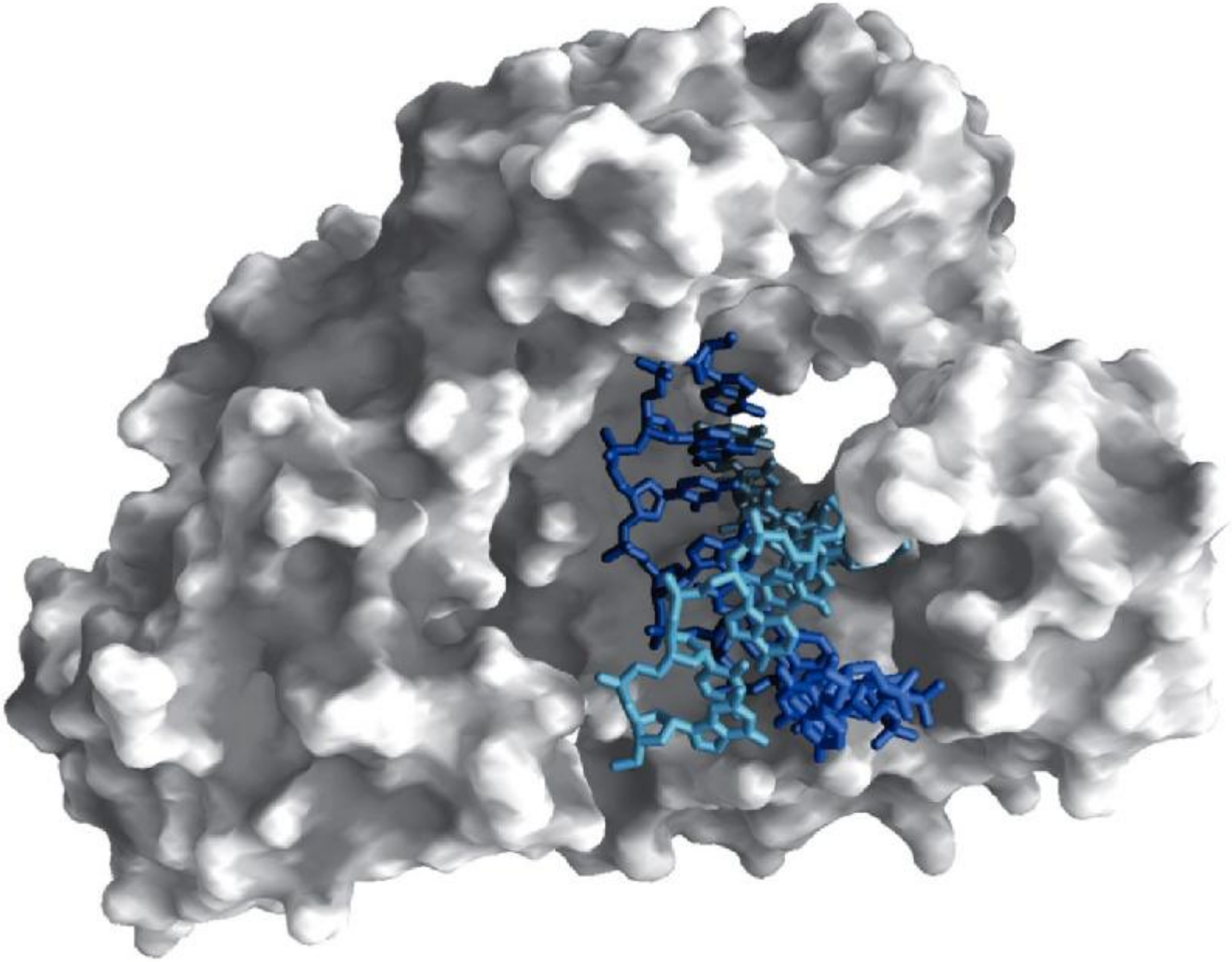

Figure 25-8
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TABLE 25–1 Comparison of Three DNA Polymerases of *E. coli*

	DNA polymerase		
	I	II	III
Structural gene*	*polA*	*polB*	*polC (dnaE)*
Subunits (number of different types)	1	7	≥10
M_r	103,000	88,000†	791,500
3′→5′ Exonuclease (proofreading)	Yes	Yes	Yes
5′→3′ Exonuclease	Yes	No	No
Polymerization rate (nucleotides/s)	16–20	40	250–1,000
Processivity (nucleotides added before polymerase dissociates)	3–200	1,500	≥500,000

*For enzymes with more than one subunit, the gene listed here encodes the subunit with polymerization activity. Note that *dnaE* is an earlier designation for the gene now referred to as *polC*.

†Polymerization subunit only. DNA polymerase II shares several subunits with DNA polymerase III, including the $\beta, \gamma, \delta, \delta', \chi$, and ψ subunits (see Table 25–2).

Table 25-1
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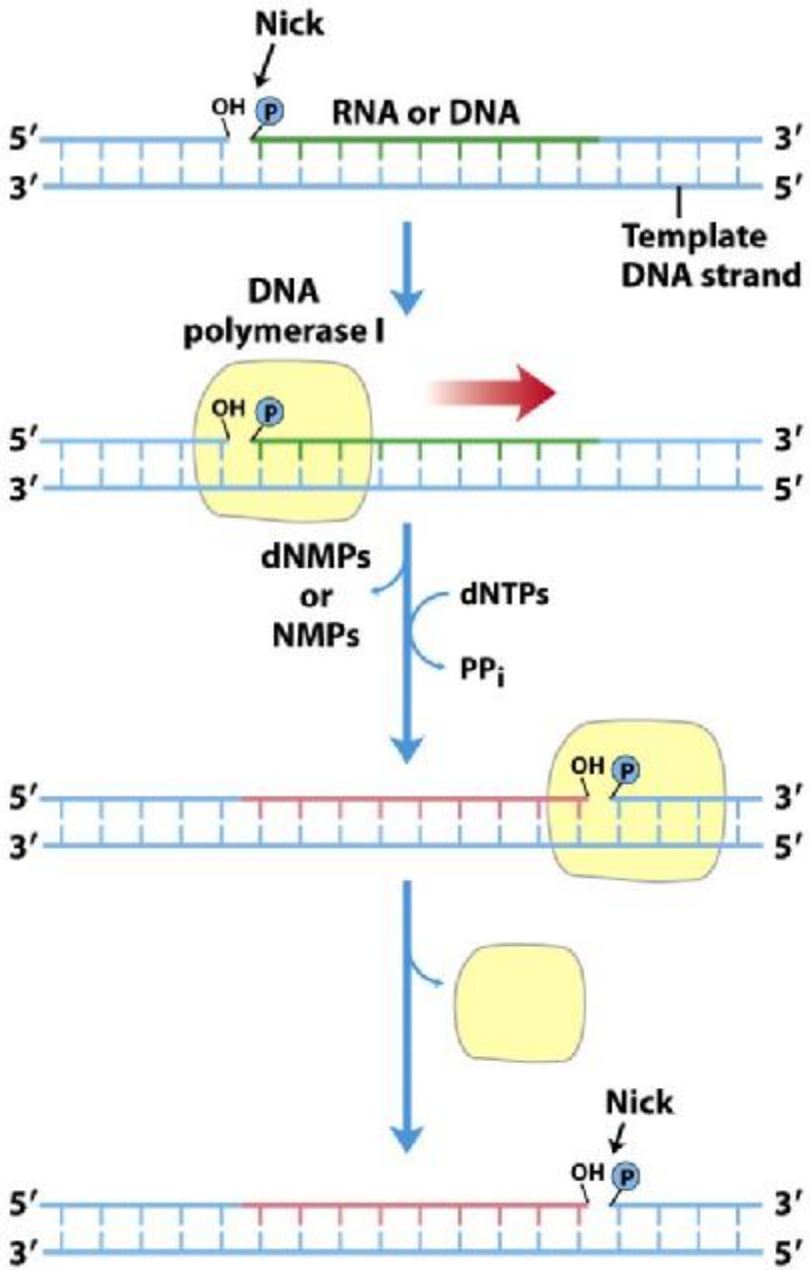

Figure 25-9

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TABLE 25–2 Subunits of DNA Polymerase III of *E. coli*

Subunit	Number of subunits per holoenzyme	M_r of subunit	Gene	Function of subunit	
α	2	129,900	*polC* (*dnaE*)	Polymerization activity	Core polymerase
ε	2	27,500	*dnaQ* (*mutD*)	3′→5′ Proofreading exonuclease	Core polymerase
θ	2	8,600	*holE*	Stabilization of ε subunit	Core polymerase
τ	2	71,100	*dnaX*	Stable template binding; core enzyme dimerization	Clamp-loading (γ) complex that loads β subunits on lagging strand at each Okazaki fragment
γ	1	47,500	*dnaX**	Clamp loader	Clamp-loading (γ) complex that loads β subunits on lagging strand at each Okazaki fragment
δ	1	38,700	*holA*	Clamp opener	Clamp-loading (γ) complex that loads β subunits on lagging strand at each Okazaki fragment
δ'	1	36,900	*holB*	Clamp loader	Clamp-loading (γ) complex that loads β subunits on lagging strand at each Okazaki fragment
χ	1	16,600	*holC*	Interaction with SSB	
ψ	1	15,200	*holD*	Interaction with γ and χ	
β	4	40,600	*dnaN*	DNA clamp required for optimal processivity	

*The γ subunit is encoded by a portion of the gene for the τ subunit, such that the amino-terminal 66% of the τ subunit has the same amino acid sequence as the γ subunit. The γ subunit is generated by a translational frameshifting mechanism (see p. •••) that leads to premature translational termination.

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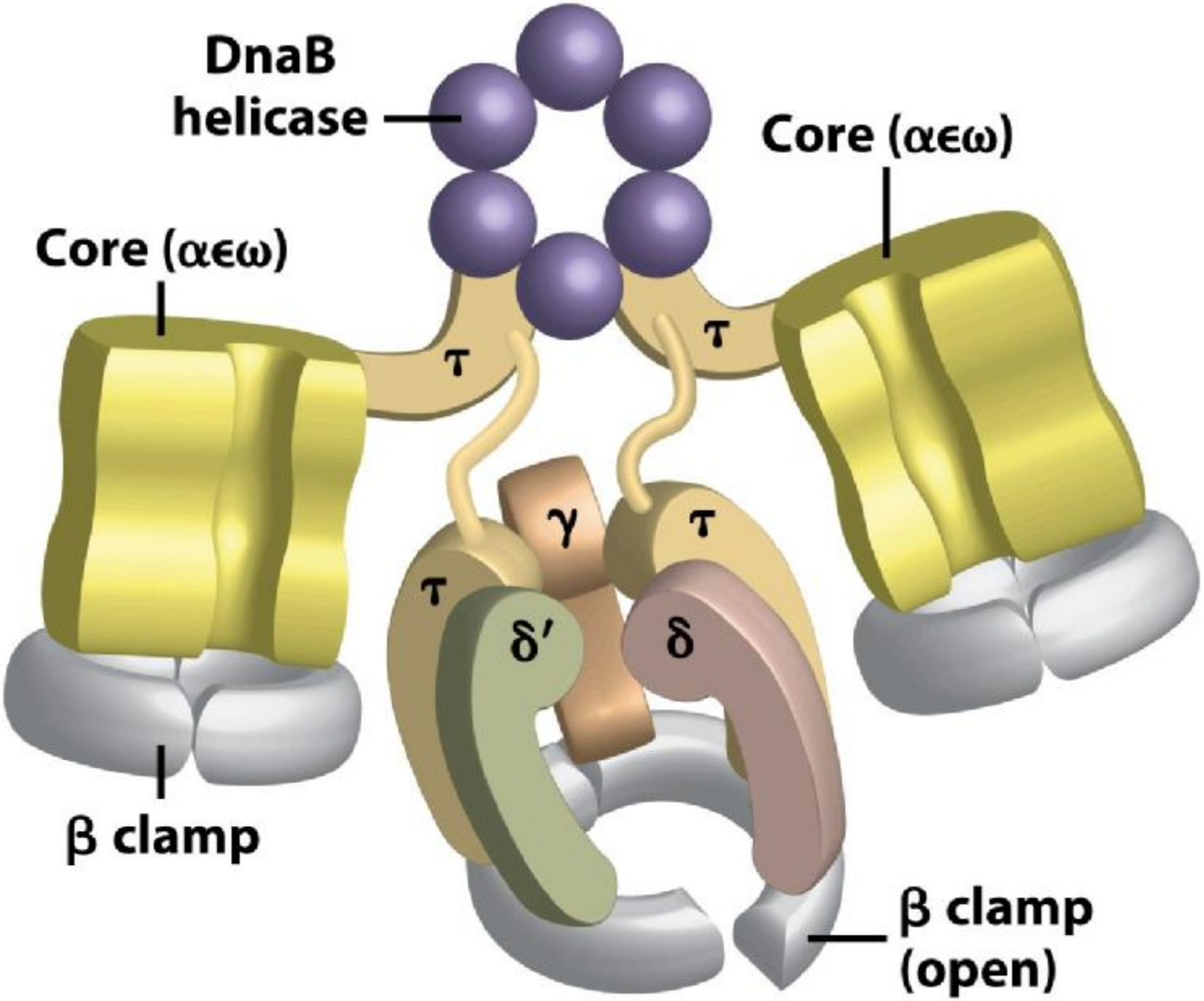

Figure 25-10a
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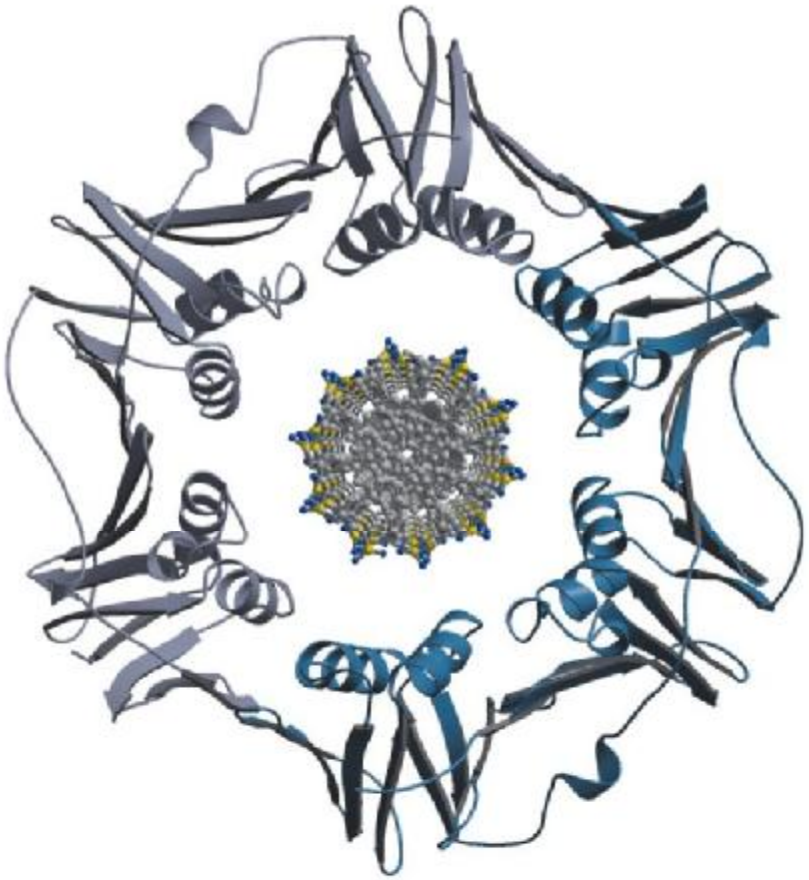
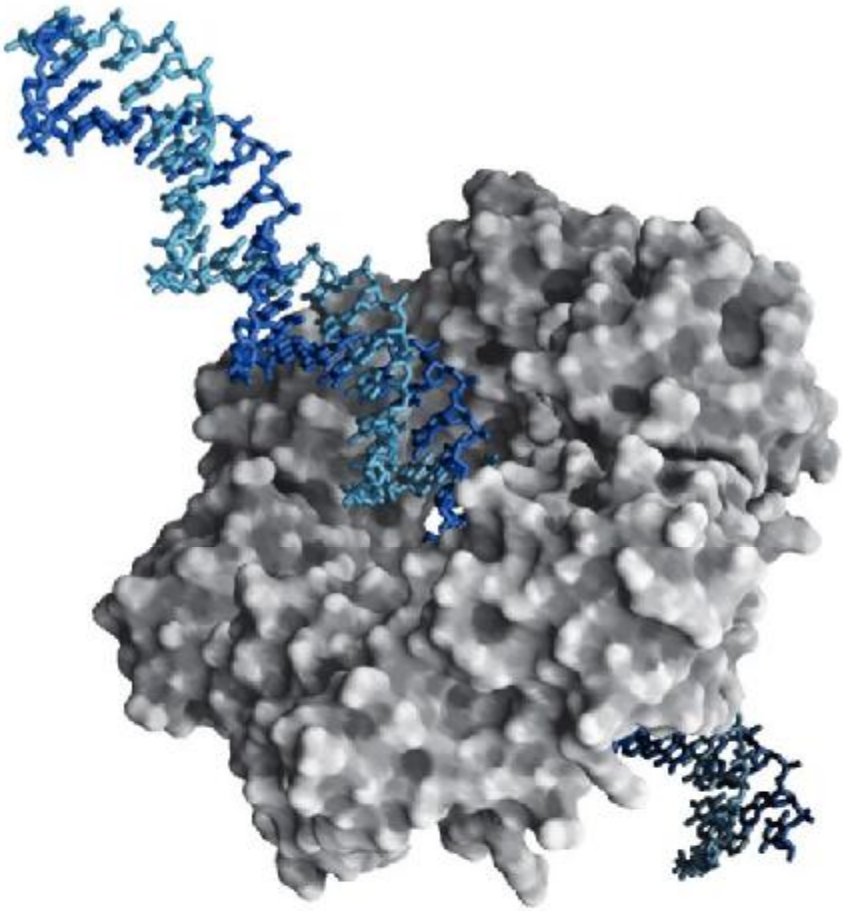


End view



Side view

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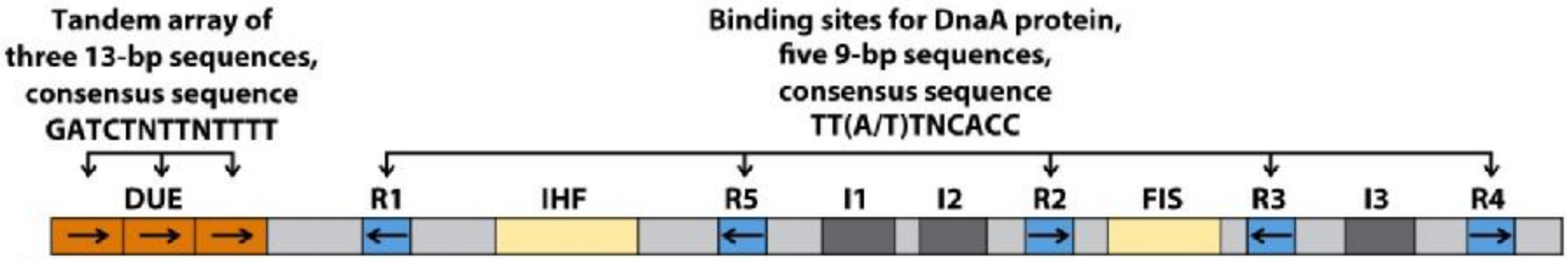

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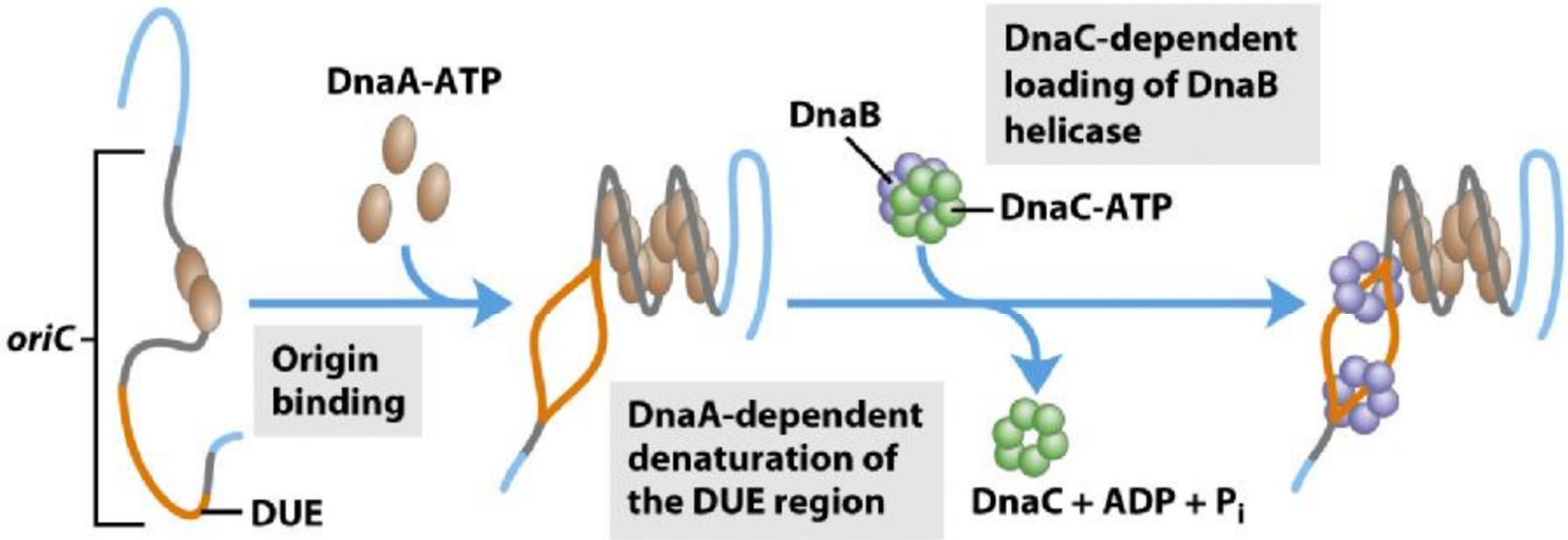
DNA unwinding element (DUE).

IHF (integration host factor)

FIS (factor for inversion stimulation



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DnaA protein, a member of the AAA+ ATPase protein family (-ATPases associated with diverse cellular activities

TABLE 25–3 Proteins Required to Initiate Replication at the *E. coli* Origin

Protein	M_r	Number of subunits	Function
DnaA protein	52,000	1	Recognizes ori sequence; opens duplex at specific sites in origin
DnaB protein (helicase)	300,000	6*	Unwinds DNA
DnaC protein	174,000	6*	Required for DnaB binding at origin
HU	19,000	2	Histonelike protein; DNA-binding protein; stimulates initiation
FIS	22,500	2*	DNA-binding protein; stimulates initiation
IHF	22,000	2	DNA-binding protein; stimulates initiation
Primase (DnaG protein)	60,000	1	Synthesizes RNA primers
Single-stranded DNA-binding protein (SSB)	75,600	4*	Binds single-stranded DNA
DNA gyrase (DNA topoisomerase II)	400,000	4	Relieves torsional strain generated by DNA unwinding
Dam methylase	32,000	1	Methylates (5′)GATC sequences at *oriC*

*Subunits in these cases are identical.

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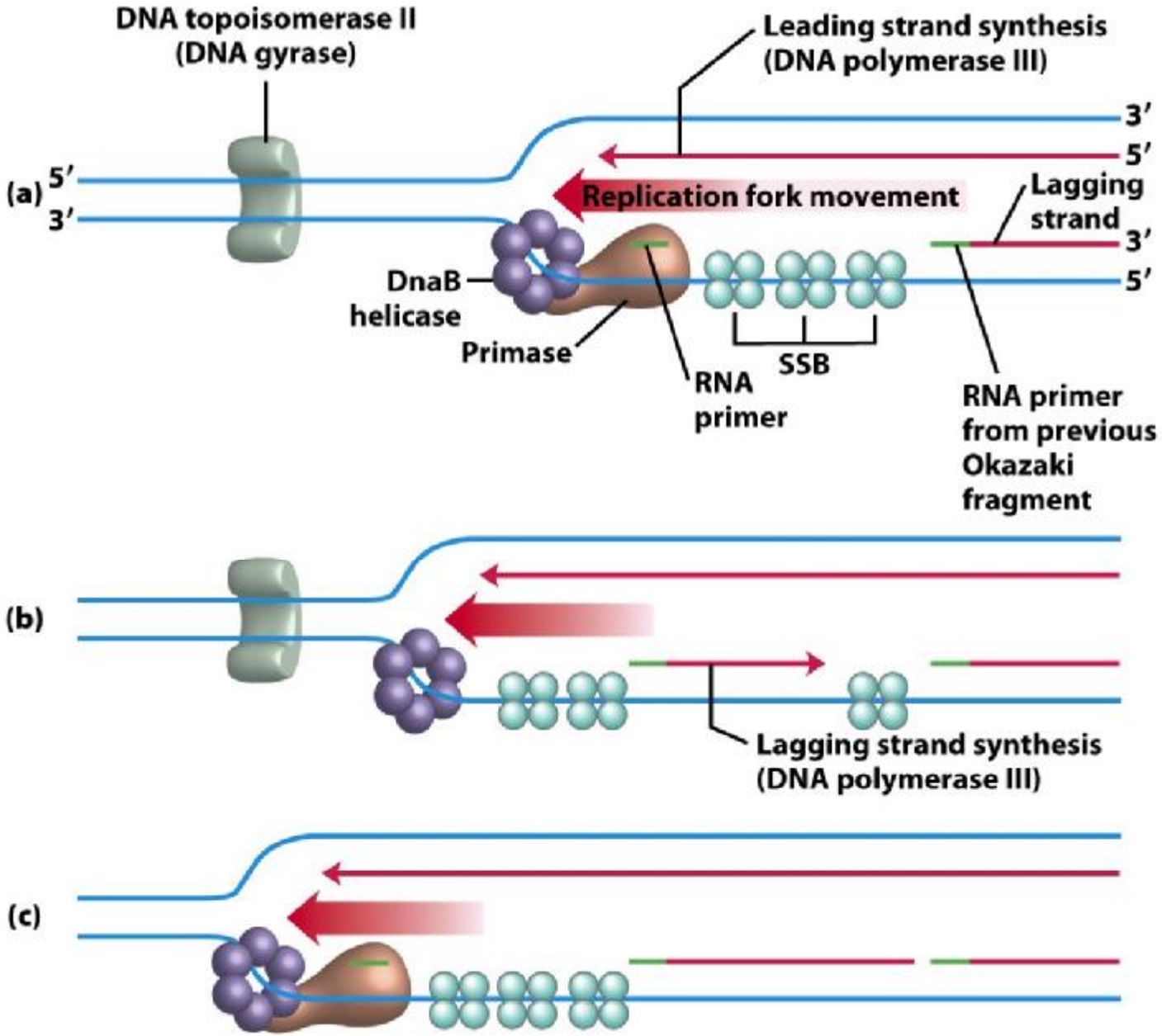

Figure 25-13

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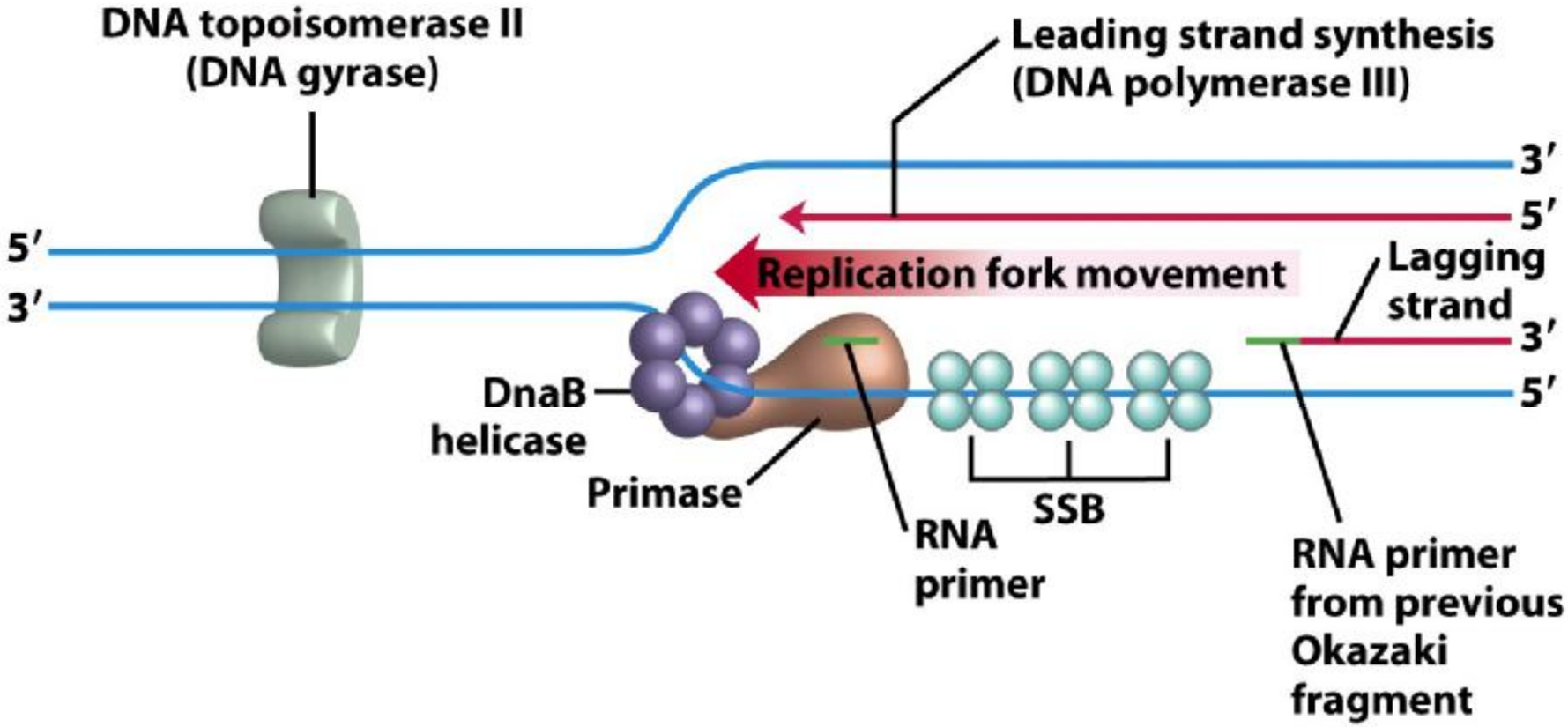

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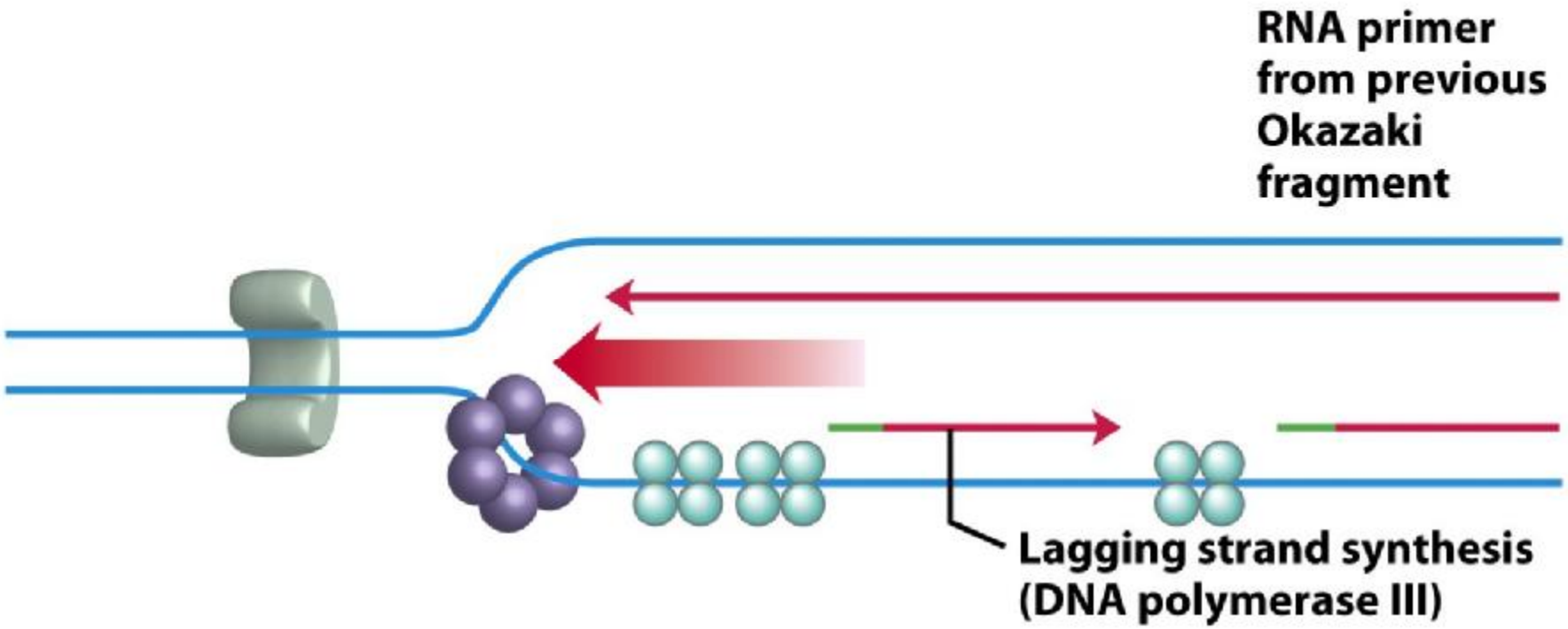

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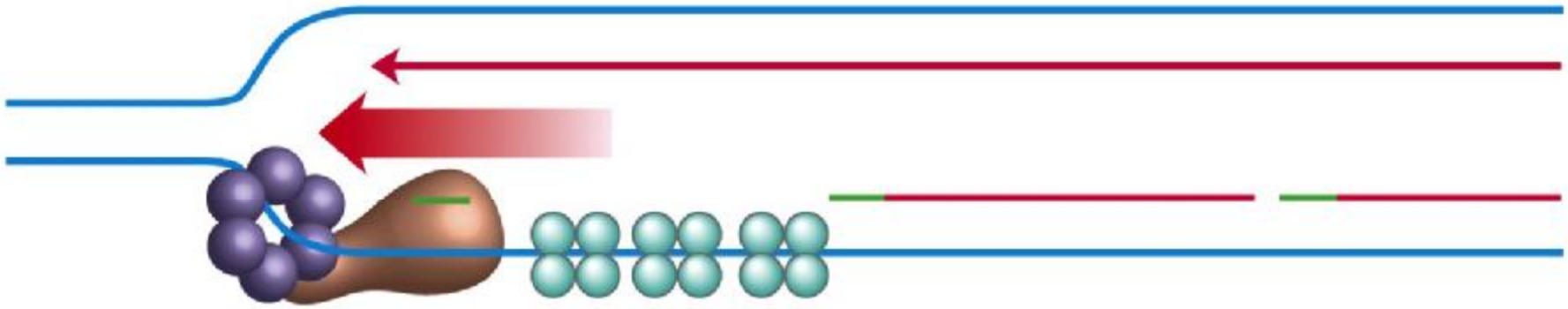

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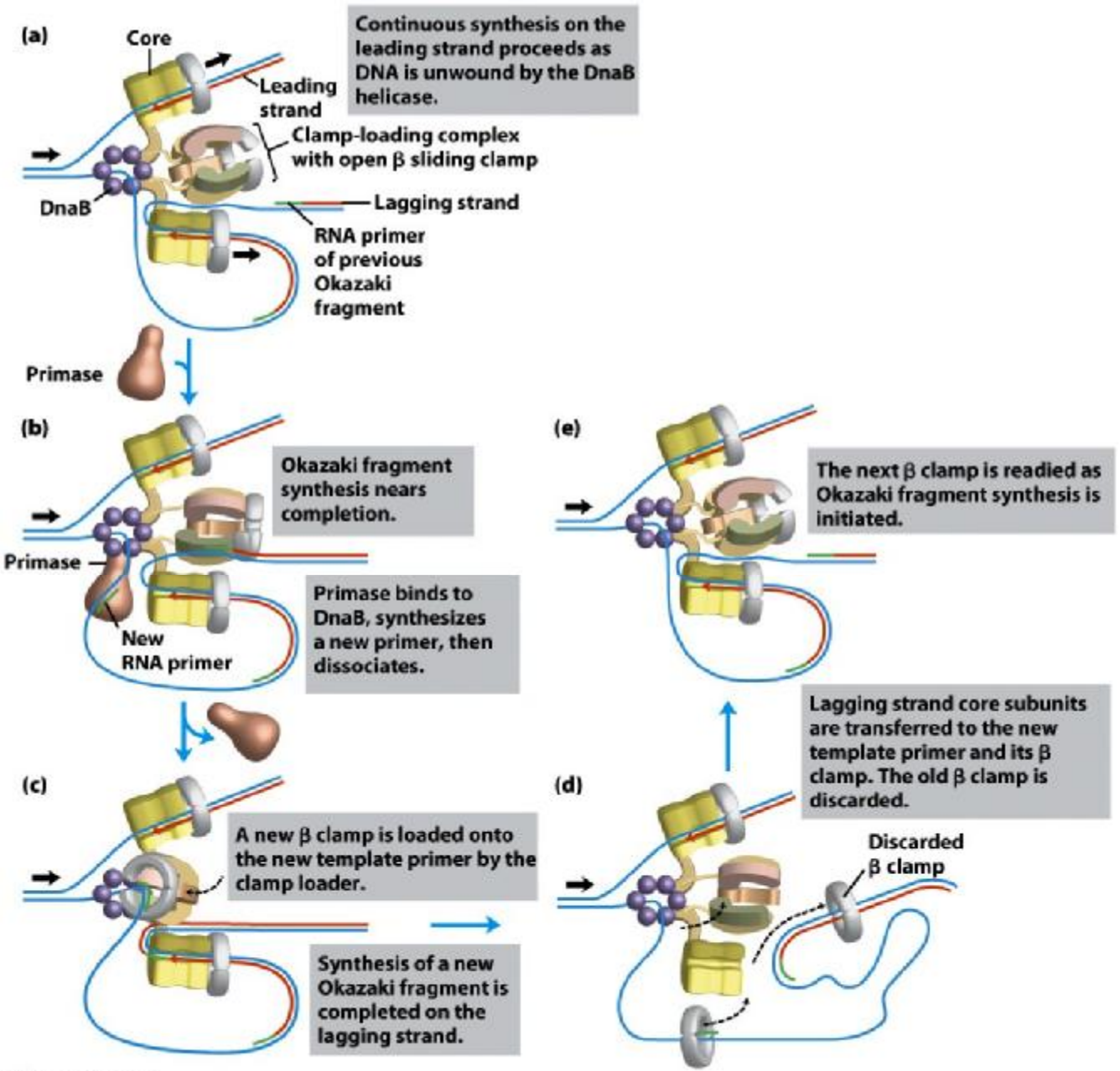

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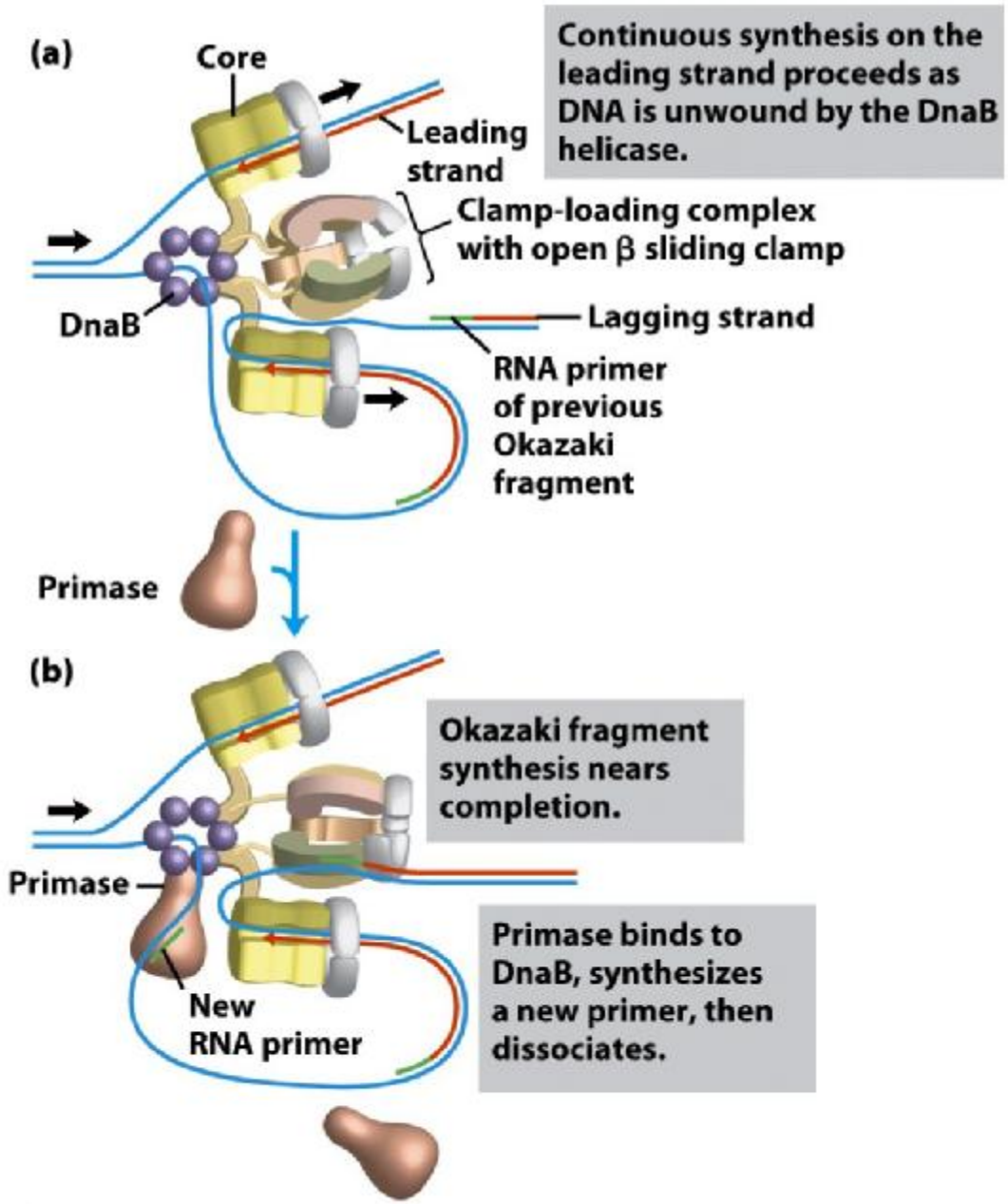

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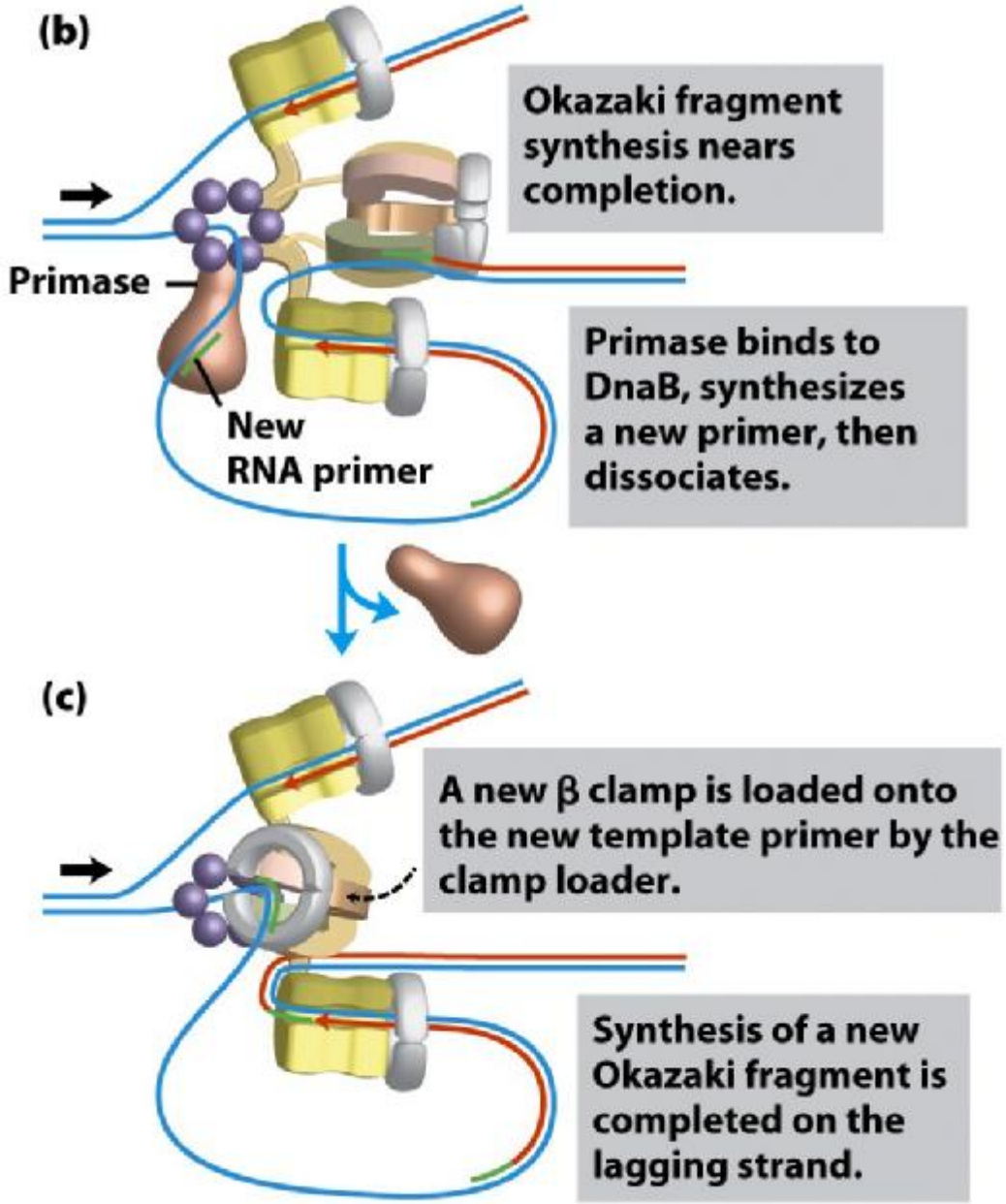

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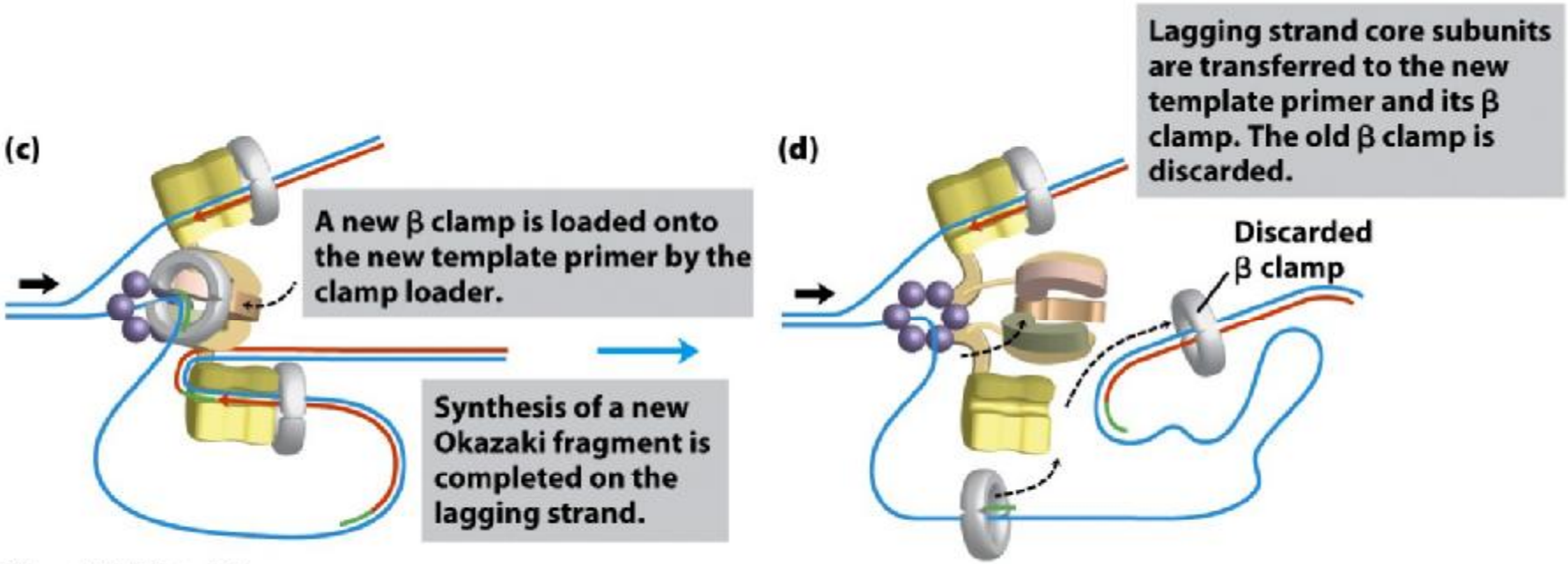

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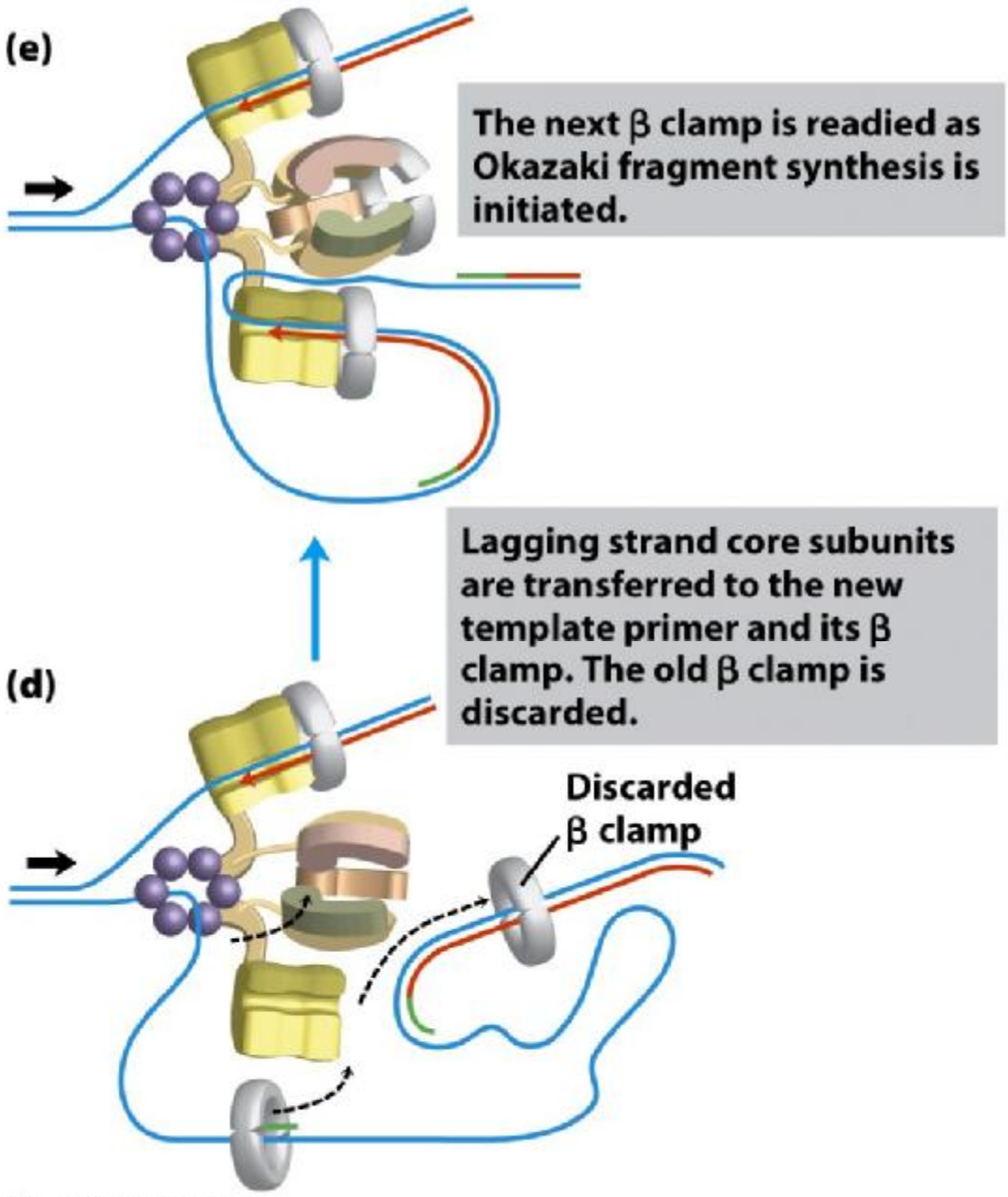

Figure 25-14 part 4

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TABLE 25–4 Proteins of the *E. coli* Replisome

Protein	M_r	Number of subunits	Function
SSB	75,600	4	Binding to single-stranded DNA
DnaB protein (helicase)	300,000	6	DNA unwinding; primosome constituent
Primase (DnaG protein)	60,000	1	RNA primer synthesis; primosome constituent
DNA polymerase III	791,500	17	New strand elongation
DNA polymerase I	103,000	1	Filling of gaps; excision of primers
DNA ligase	74,000	1	Ligation
DNA gyrase (DNA topoisomerase II)	400,000	4	Supercoiling

Source: Modified from Kornberg, A. (1982) *Supplement to DNA Replication*, Table S11–2, W. H. Freeman and Company, New York.

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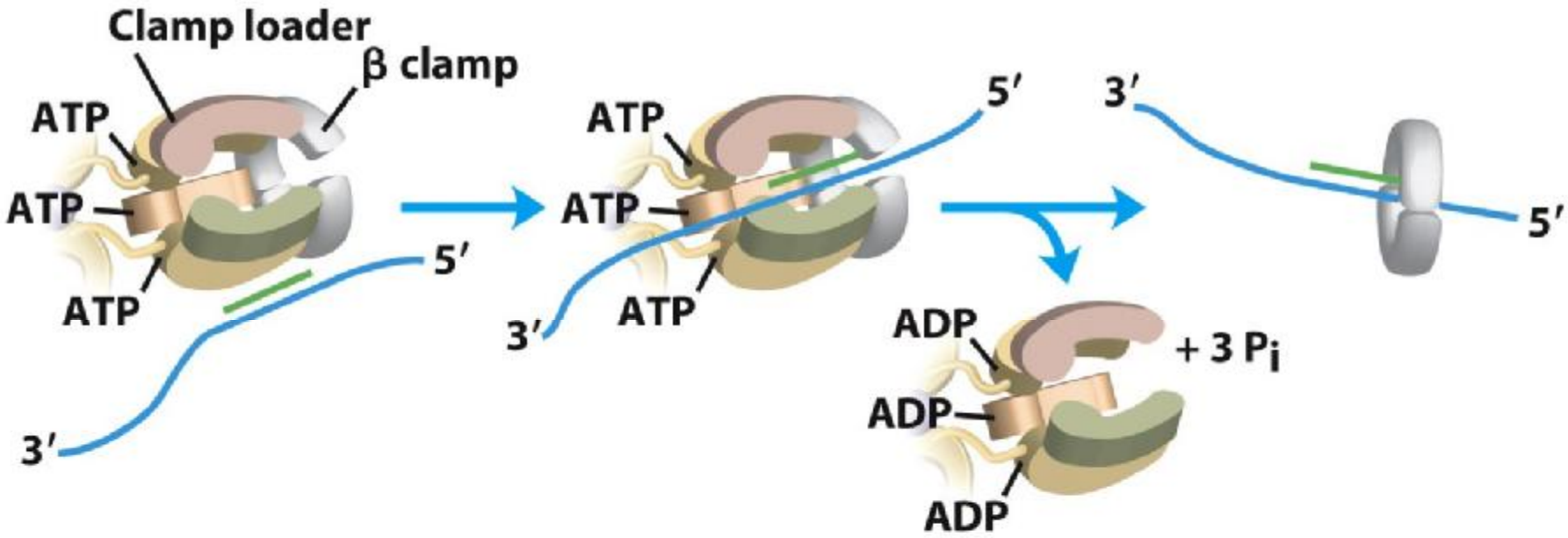

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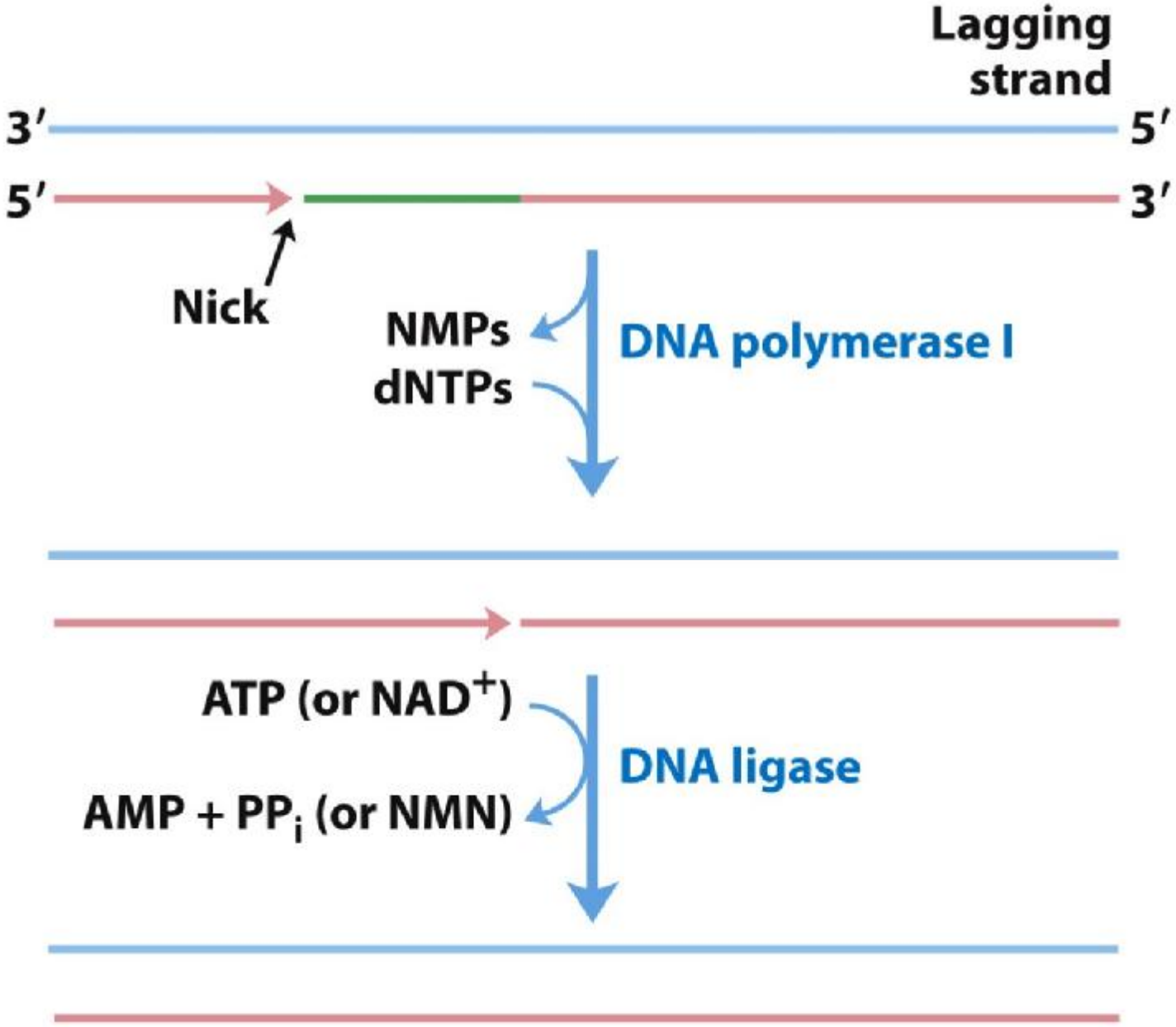

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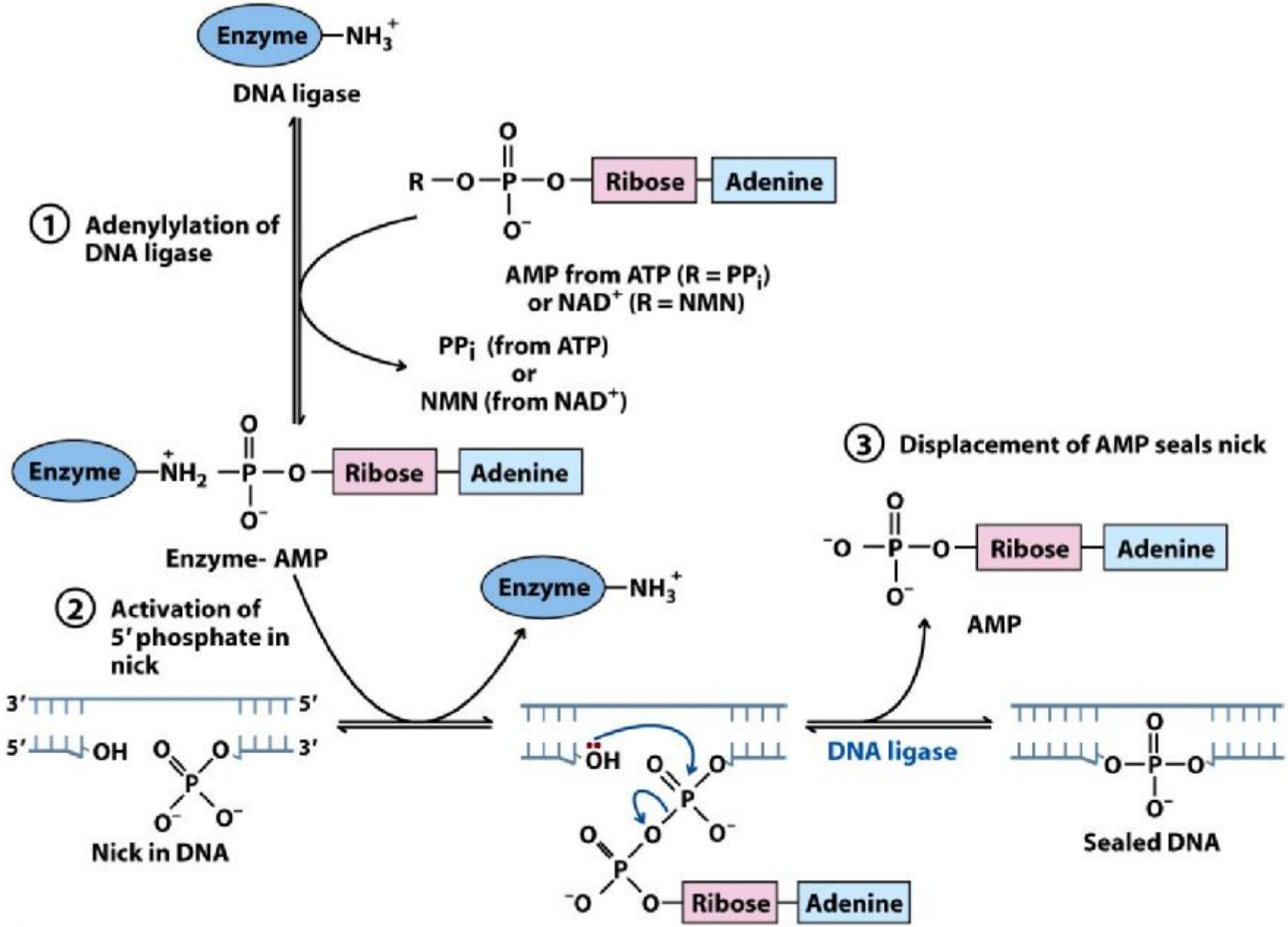

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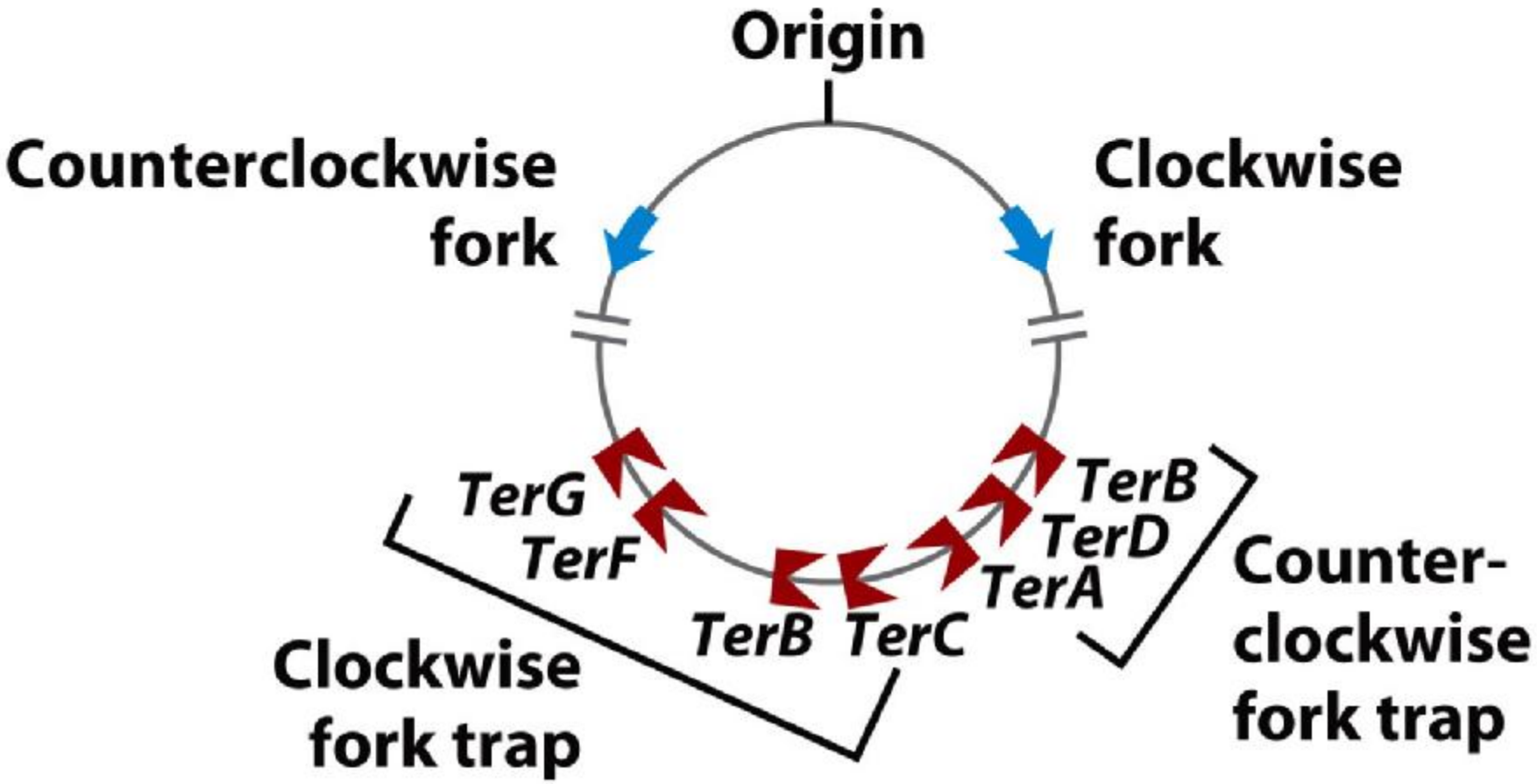
multiple copies of a 20 bp sequence called Ter

The Ter sequences function as binding sites for the protein Tus (terminus utilization substance)



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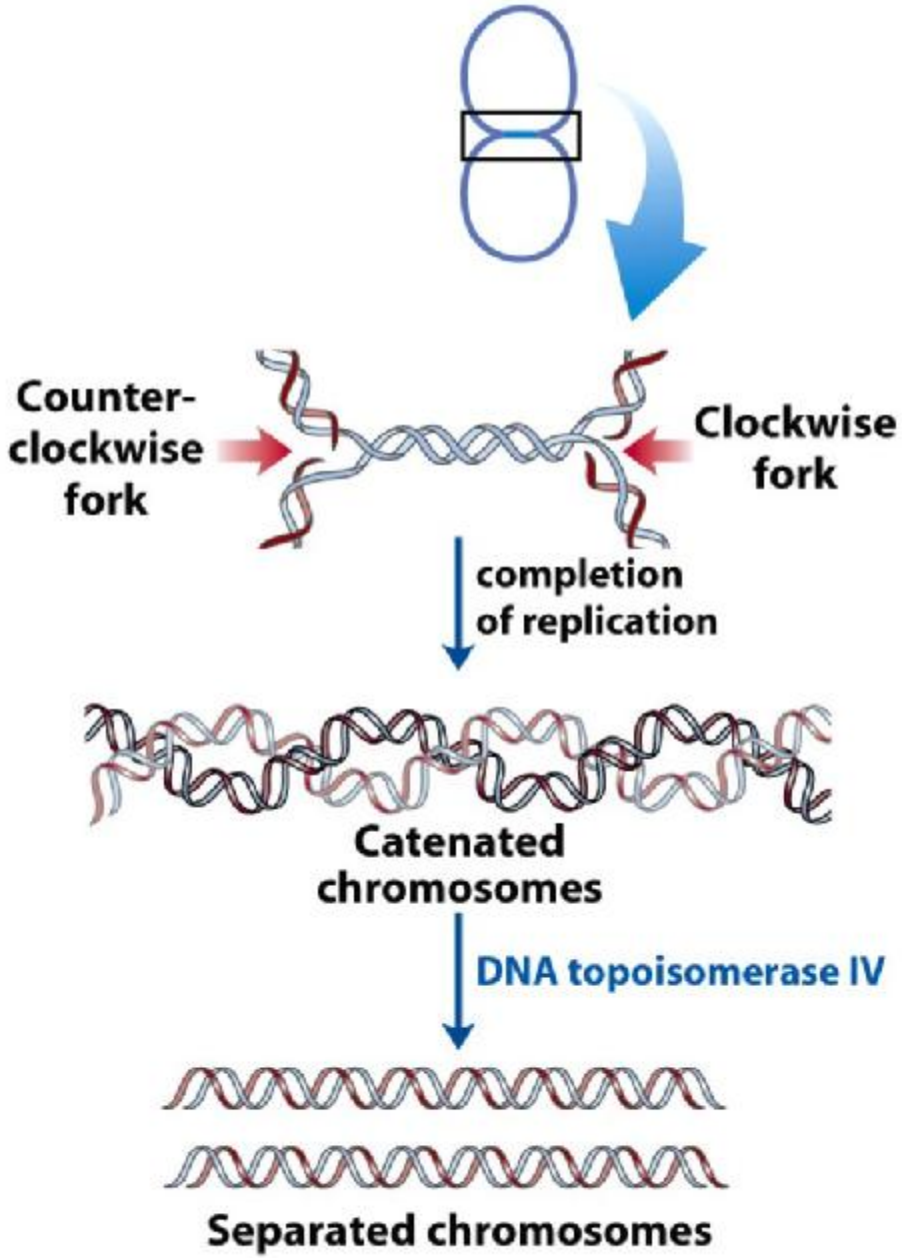

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Replication in Eukaryotic Cells

Origins of replication have a well-characterized structure in some lower eukaryotes but they are much less defined i n higher eukaryotes

Yeast (*Saccharomyces cerevisiae*) has defined replication origins called autonomously replicating sequences (ARS), or replicators.

Yeast replicators span 150 bp and contain several essential conserved sequences. About **400 replicators** are distributed among the 16 chromosomes of the haploid yeast genome

Rate of movement of the replication fork in eukaryotes (~50 nucleotides/s); only one-twentieththh as observed in *E. coli*.

Replication of human chromosomes proceeds bidirectionally from many origins, spaced 30 to 300 kbp apart

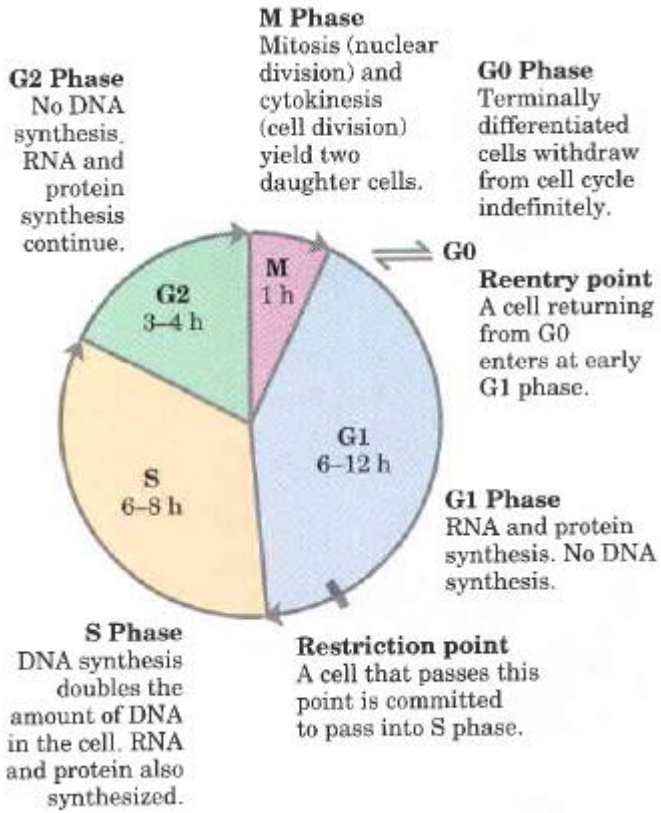
Eukaryotes have several types of DNA polymerases

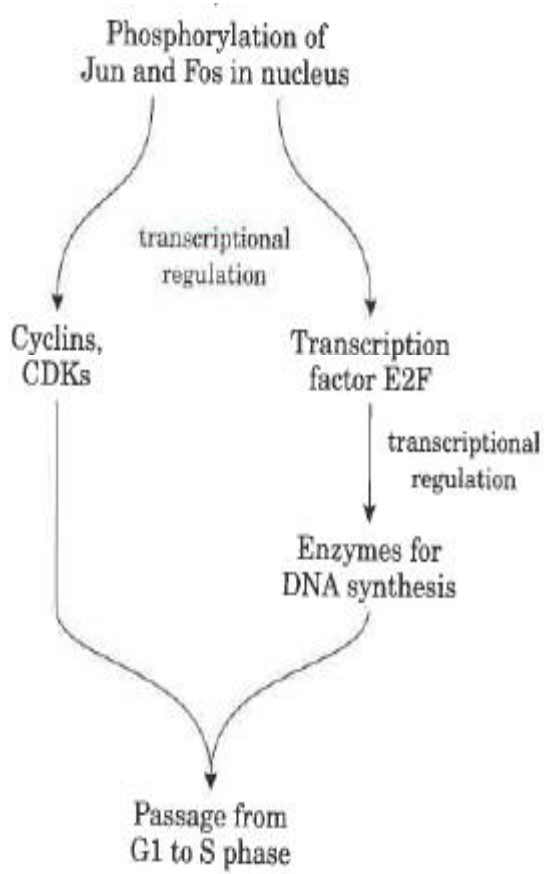
Eukaryotic DNA polymerase	Analogous activity in prokaryotic cells
DNA polymerase α	As primase
DNA polymerase δ	As DNA pol III
DNA polymerase ϵ	As DNA pol I

Regulation of Replication in Eukaryotic Cells

Regulation ensures that all cellular D NA is replicated once per cell cycle. Much of this regulation involves proteins called **cyclins and the cyclin-dependent kinases (CDKs)** with which they form complexes.

The cyclins are rapidly destroyed by ubiquitin-dependent ptroteolysis at the end of the M phase (mitosis), and the absence of cyclins allows the establishment of **pre-replicative complexes (pre-RCs)** on replication initiation sites.


M Phase
Mitosis (nuclear division) and cytokinesis (cell division) yield two daughter cells.
G2 Phase
No DNA synthesis. RNA and protein synthesis continue.
G0 Phase
Terminally differentiated cells withdraw from cell cycle indefinitely.
G0
Reentry point
A cell returning from G0 enters at early G1 phase.
M
1 h
G2
3–4 h
G1
6–12 h
S
6–8 h
G1 Phase
RNA and protein synthesis. No DNA synthesis.
S Phase
DNA synthesis doubles the amount of DNA in the cell. RNA and protein also synthesized.
Restriction point
A cell that passes this point is committed to pass into S phase.


Phosphorylation of Jun and Fos in nucleus
transcriptional regulation
Cyclins, CDKs
Transcription factor E2F
transcriptional regulation
Enzymes for DNA synthesis
Passage from G1 to S phase

In rapidly growing cells, the pre-RC forms at the end of M phase. In slow-growing cells, it does not form until the end of Gl. Formation of the pre-RC renders the cell competent for replication, an event sometimes called **licensing**.

Initiation of replication in all eukaryotes is the loading of the replicative helicase a, heterohexameric complex of minichromosome maintenance (**MCM**) proteins (MCM2 to MCM7)

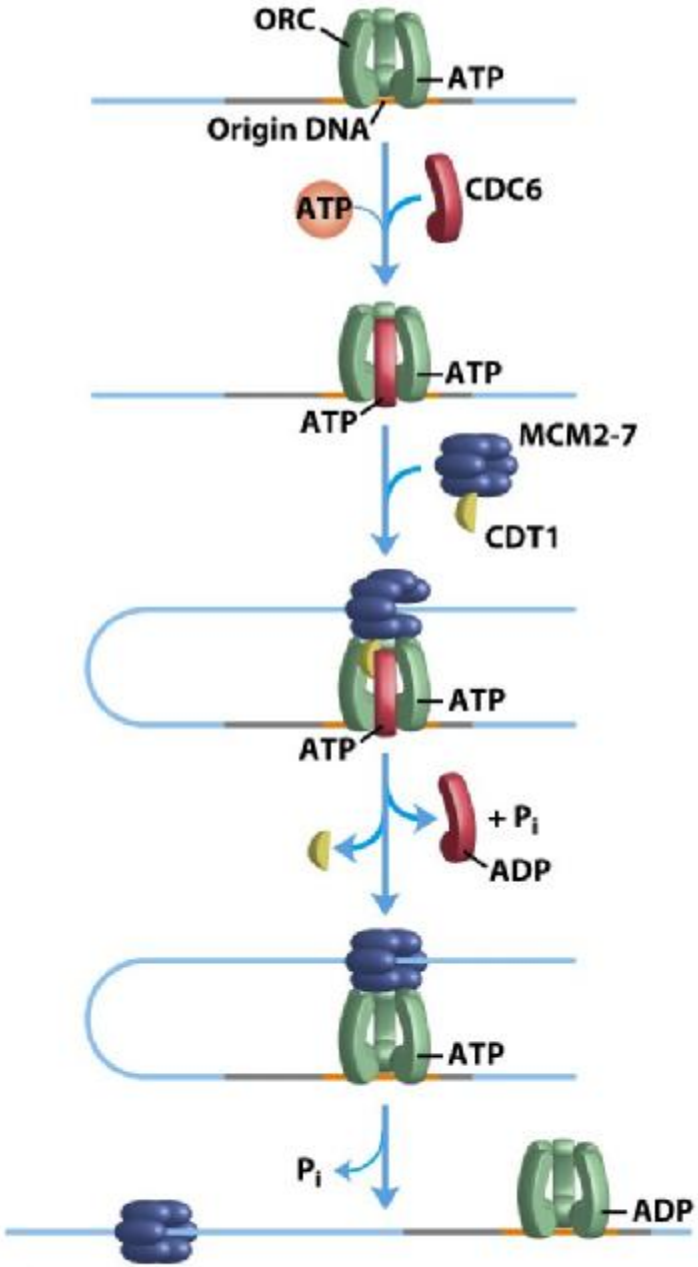


Figure 25-20

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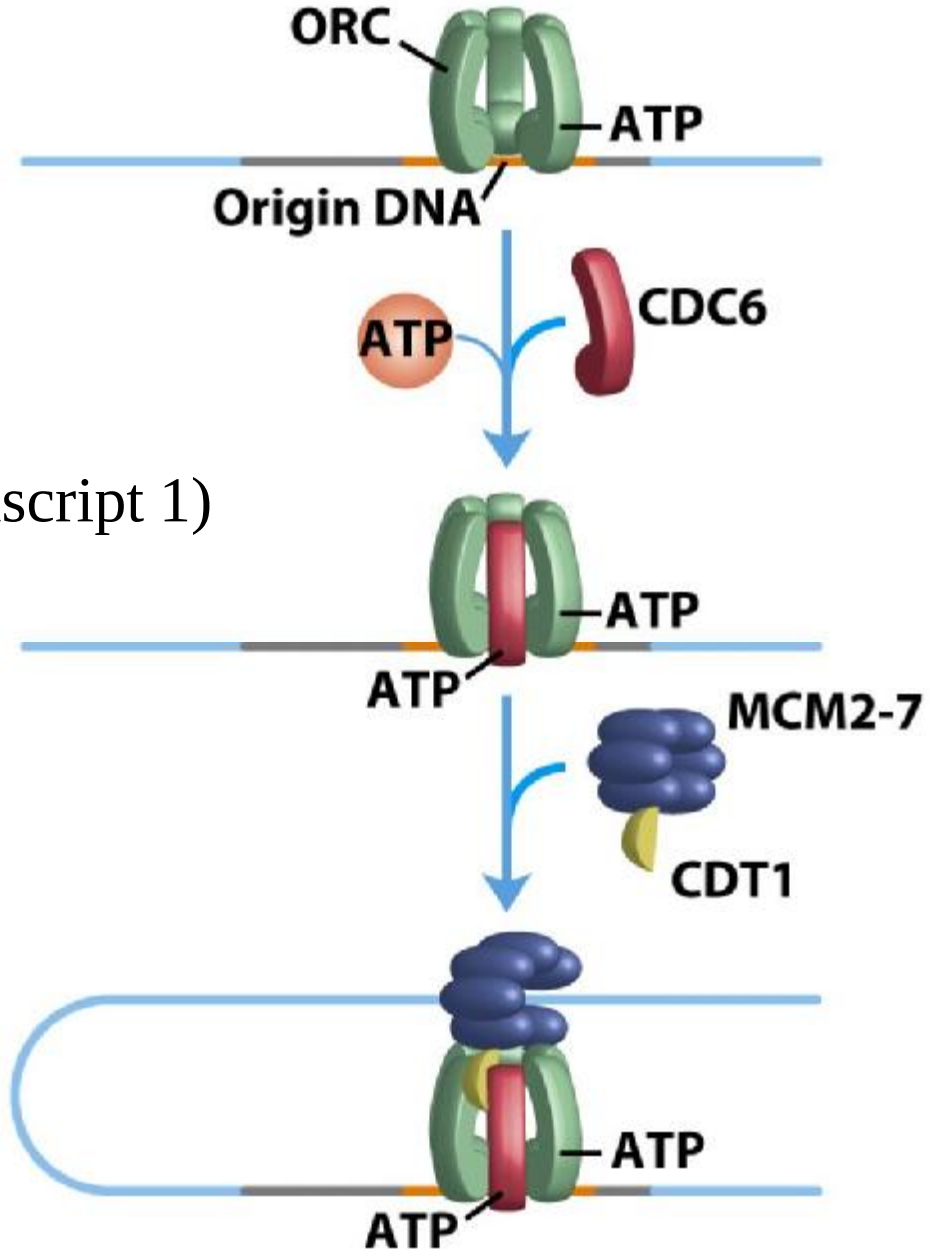
ORC
(origin recognition complex)

CDC6 (cell division cycle)

CDT (CDCl0-dependent transcript 1)



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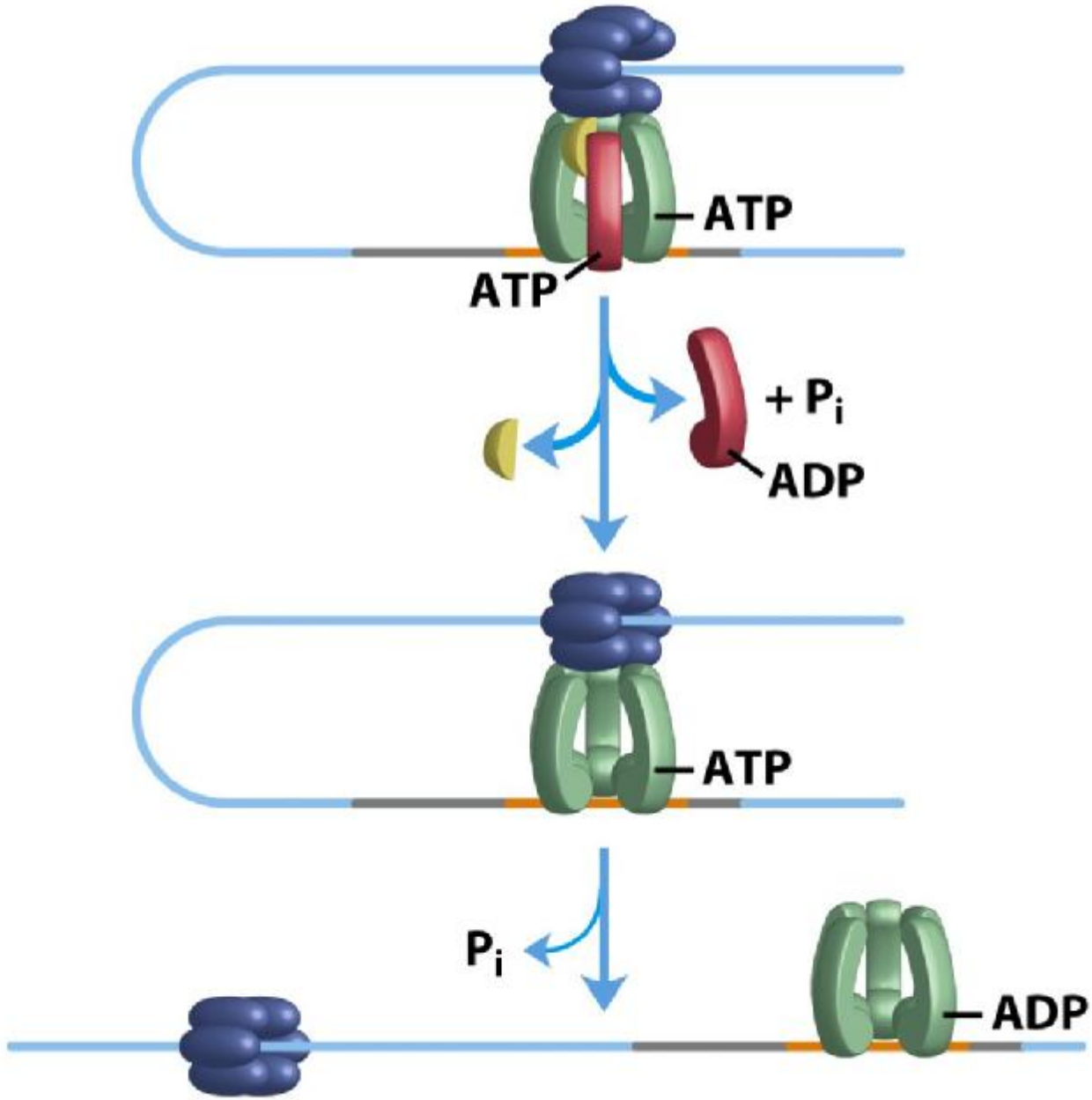

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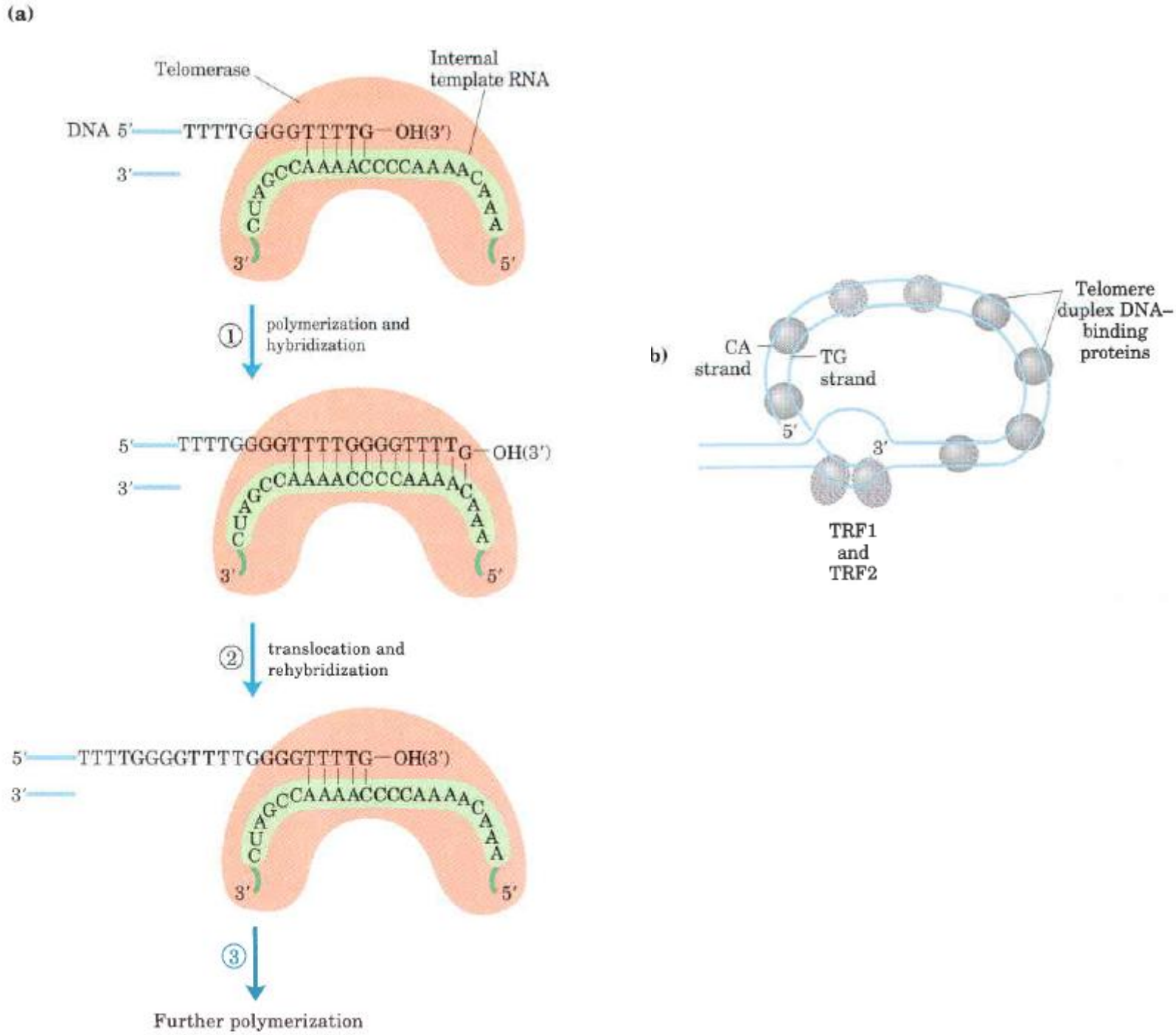
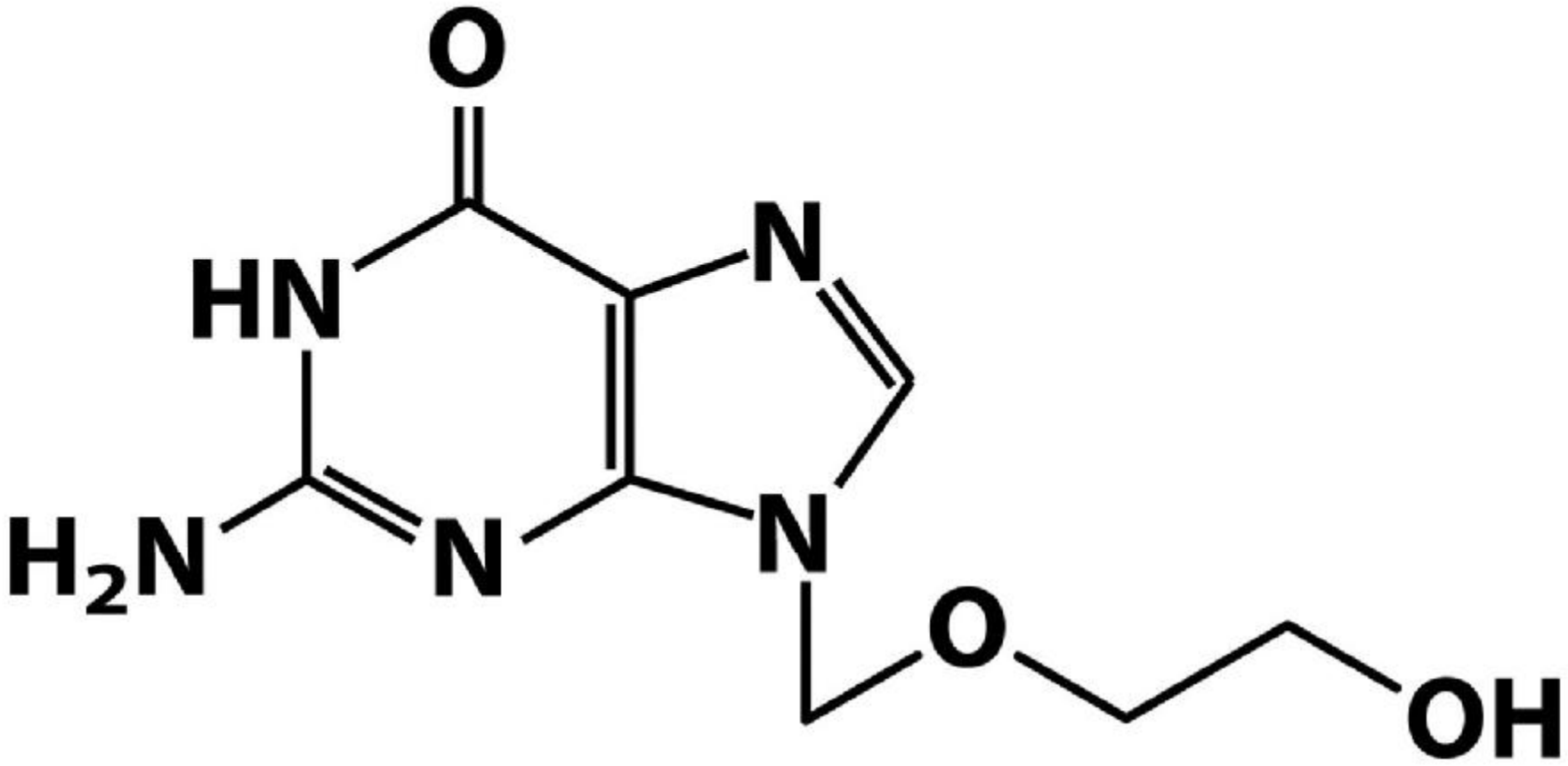

(a)
Telomerase
Internal template RNA
DNA 5′
TTTTGGGGTTTTG
OH(3′)
3′
AGCCAAAACCCCAAAACAAA
3′
5′
① polymerization and hybridization
5′
TTTTGGGGTTTTGGGGTTTTG
OH(3′)
3′
AGCCAAAACCCCAAAACAAA
3′
5′
② translocation and rehybridization
5′
TTTTGGGGTTTTGGGGTTTTG
OH(3′)
3′
AGCCAAAACCCCAAAACAAA
3′
5′
③
Further polymerization
b)
CA strand
TG strand
Telomere duplex DNA–binding proteins
5′
3′
TRF1 and TRF2



Acyclovir

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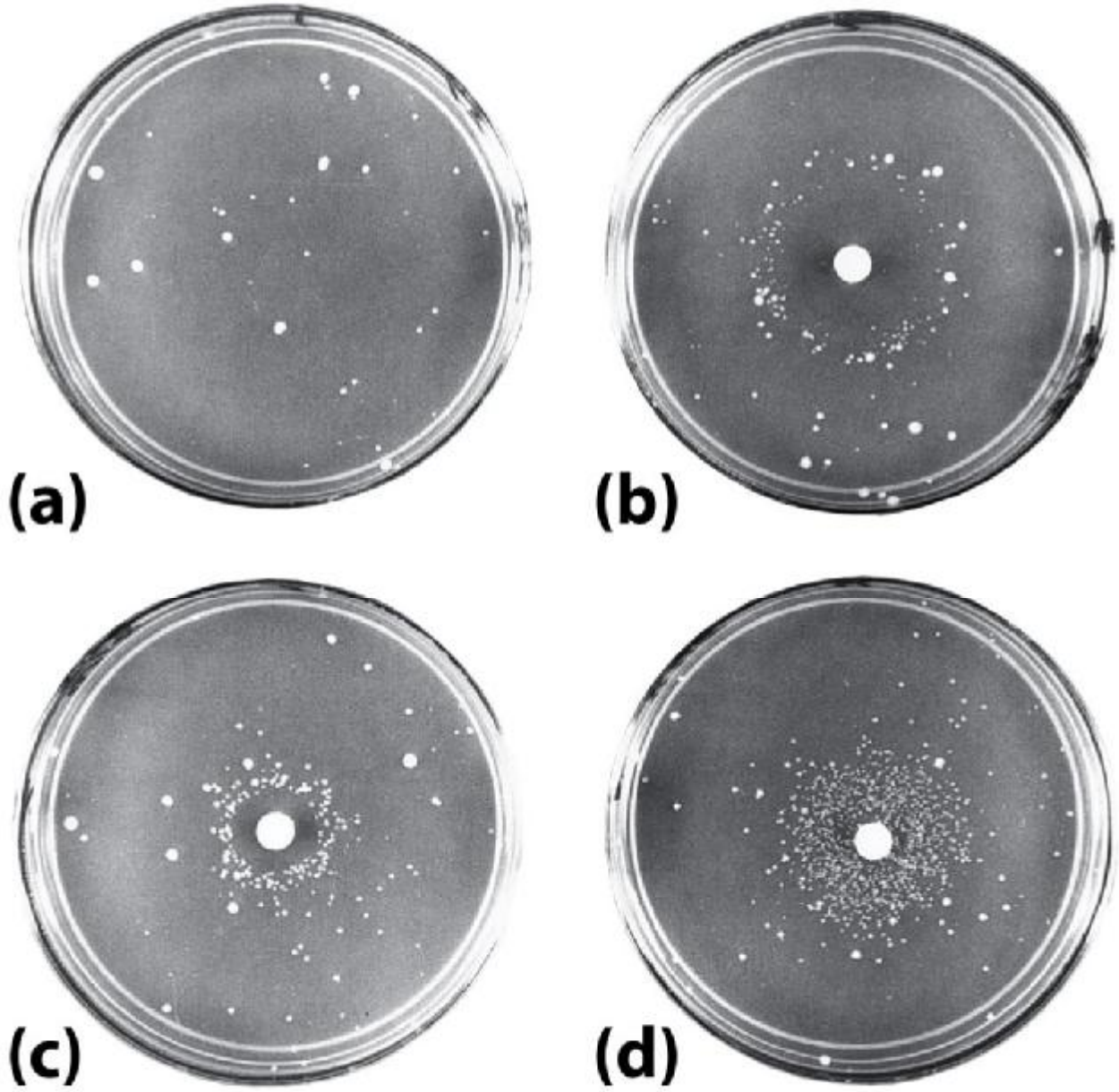

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TABLE 25–5 Types of DNA Repair Systems in *E. coli*

Enzymes/proteins	Type of damage
Mismatch repair	
Dam methylase MutH, MutL, MutS proteins DNA helicase II SSB DNA polymerase III Exonuclease I Exonuclease VII RecJ nuclease Exonuclease X DNA ligase	Mismatches
Base-excision repair	
DNA glycosylases AP endonucleases DNA polymerase I DNA ligase	Abnormal bases (uracil, hypoxanthine, xanthine); alkylated bases; in some other organisms, pyrimidine dimers
Nucleotide-excision repair	
ABC excinuclease DNA polymerase I DNA ligase	DNA lesions that cause large structural changes (e.g., pyrimidine dimers)
Direct repair	
DNA photolyases	Pyrimidine dimers
O^6-Methylguanine-DNA methyltransferase	O^6-Methylguanine
AlkB protein	1-Methylguanine, 3-methylcytosine

Table 25-5
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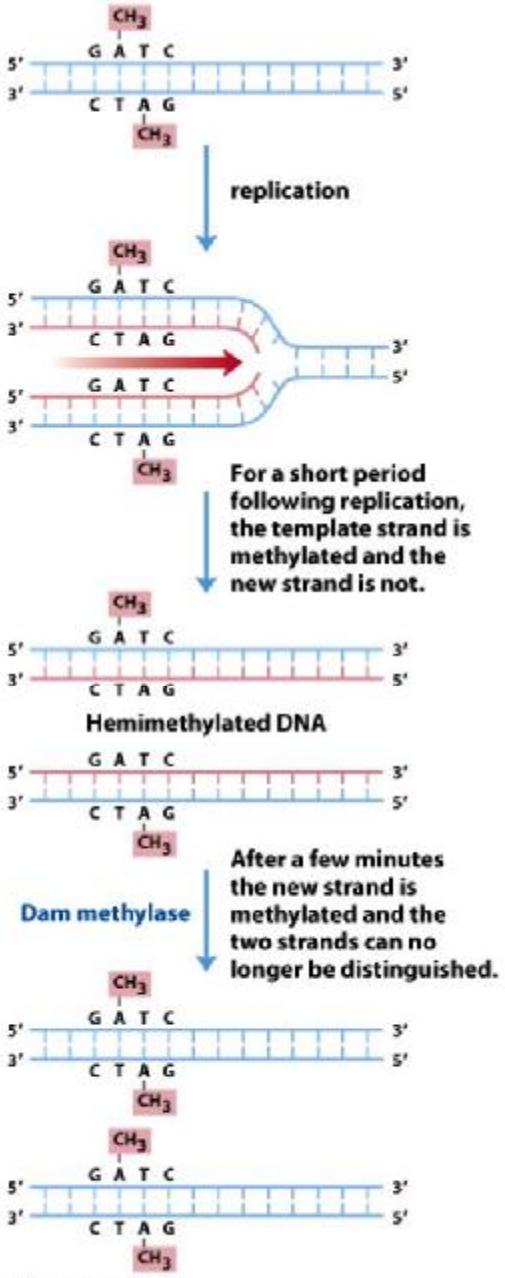

Figure 25-22

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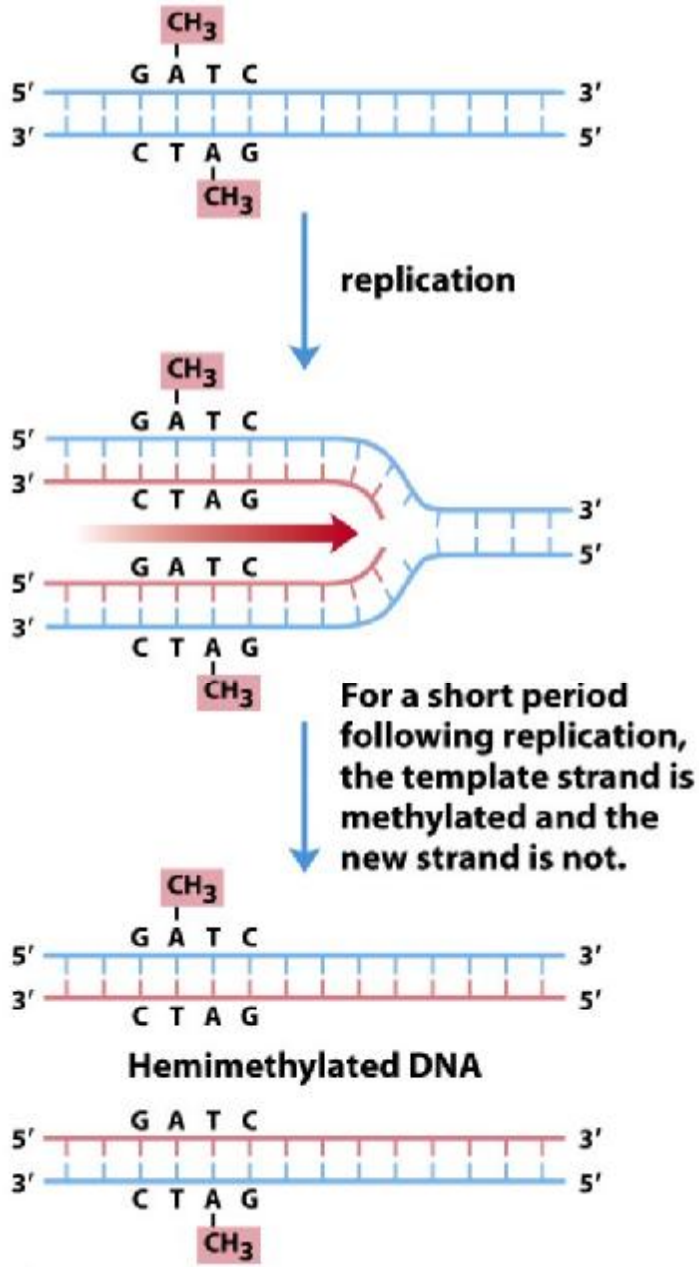

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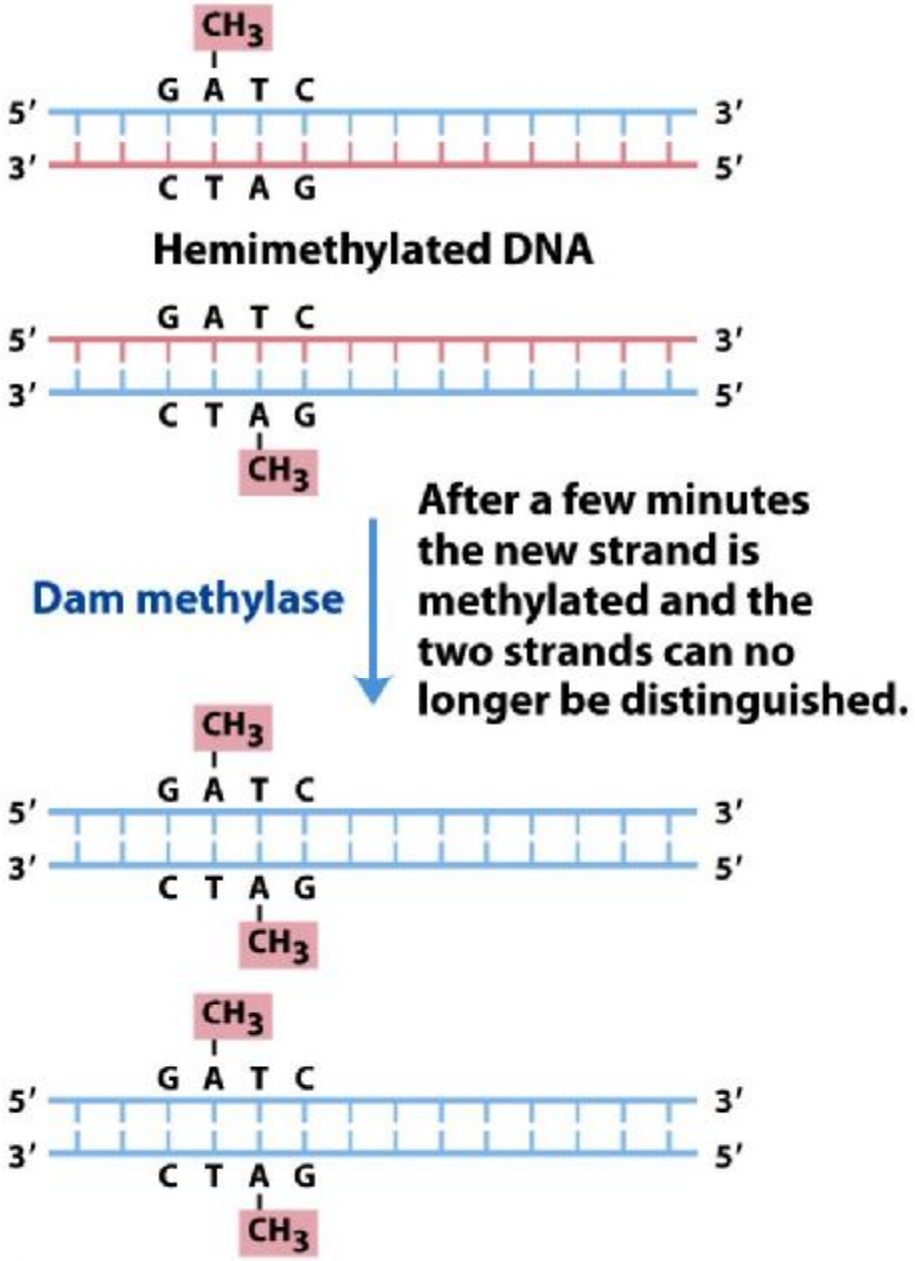

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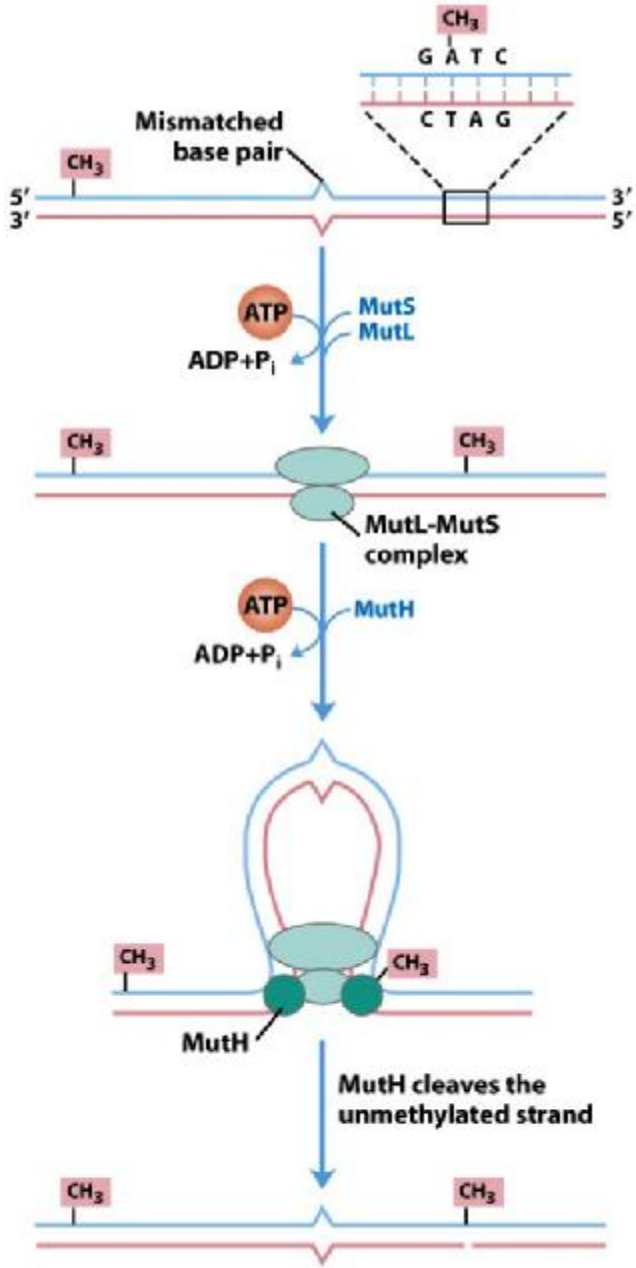

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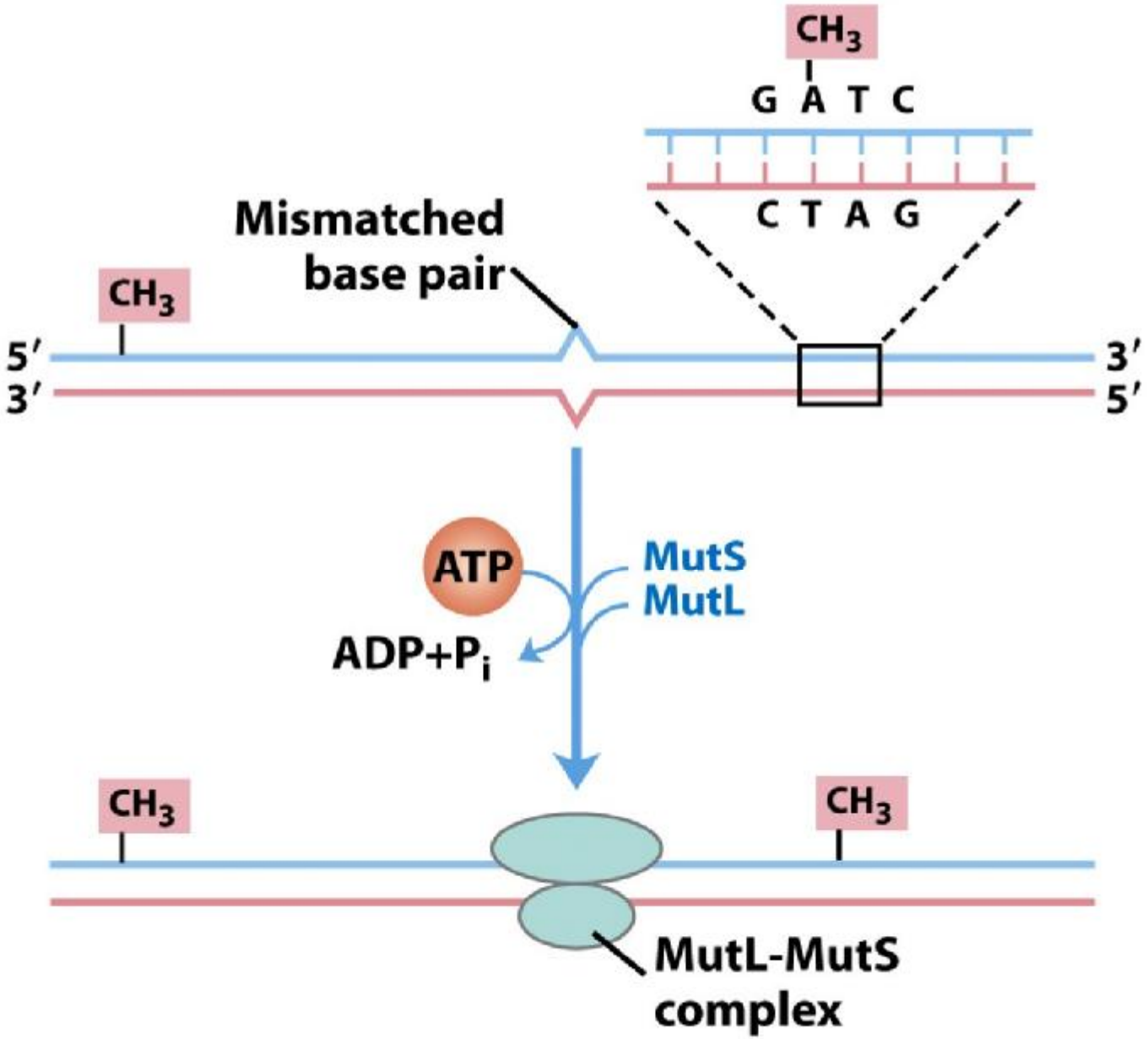

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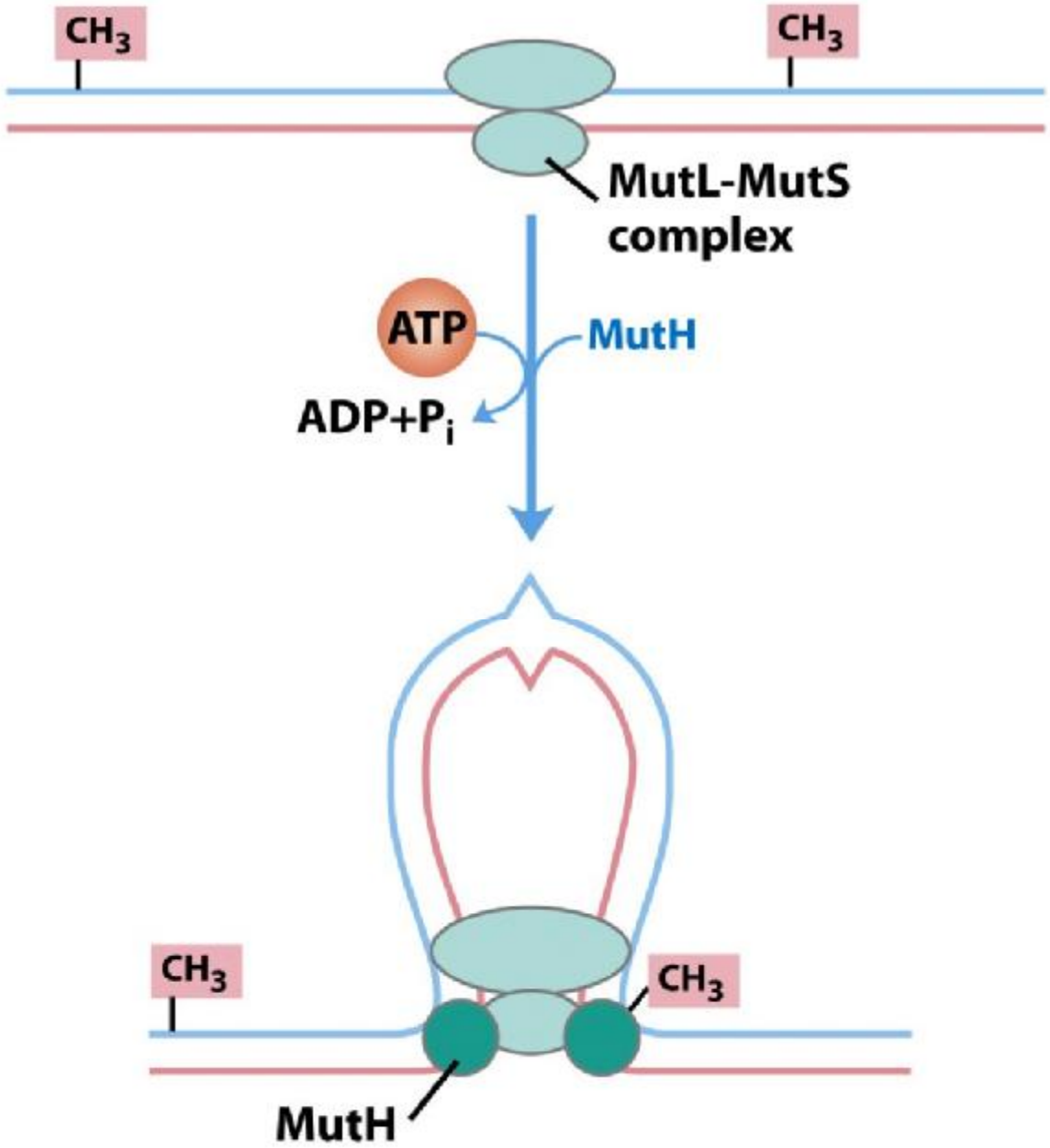

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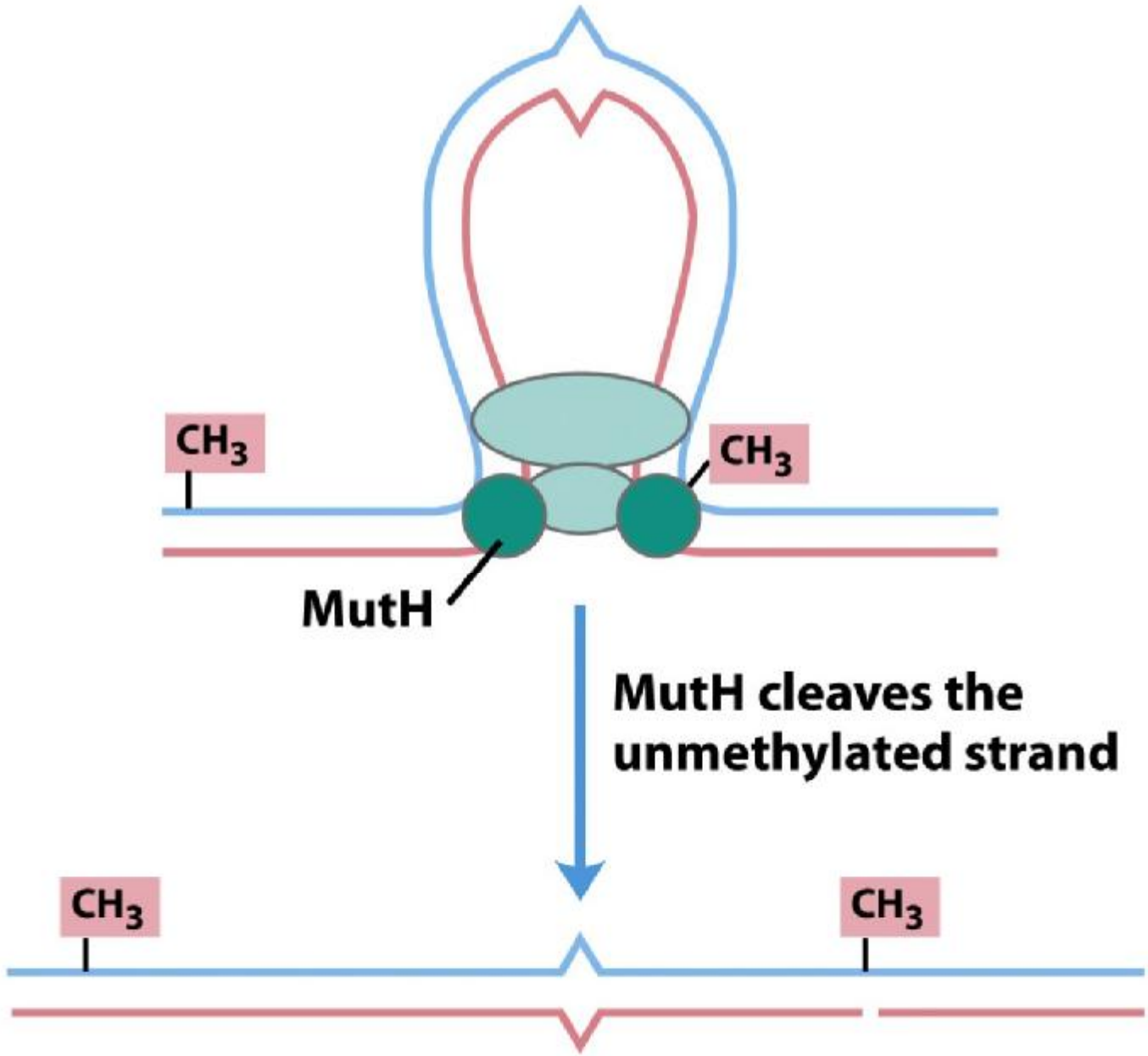

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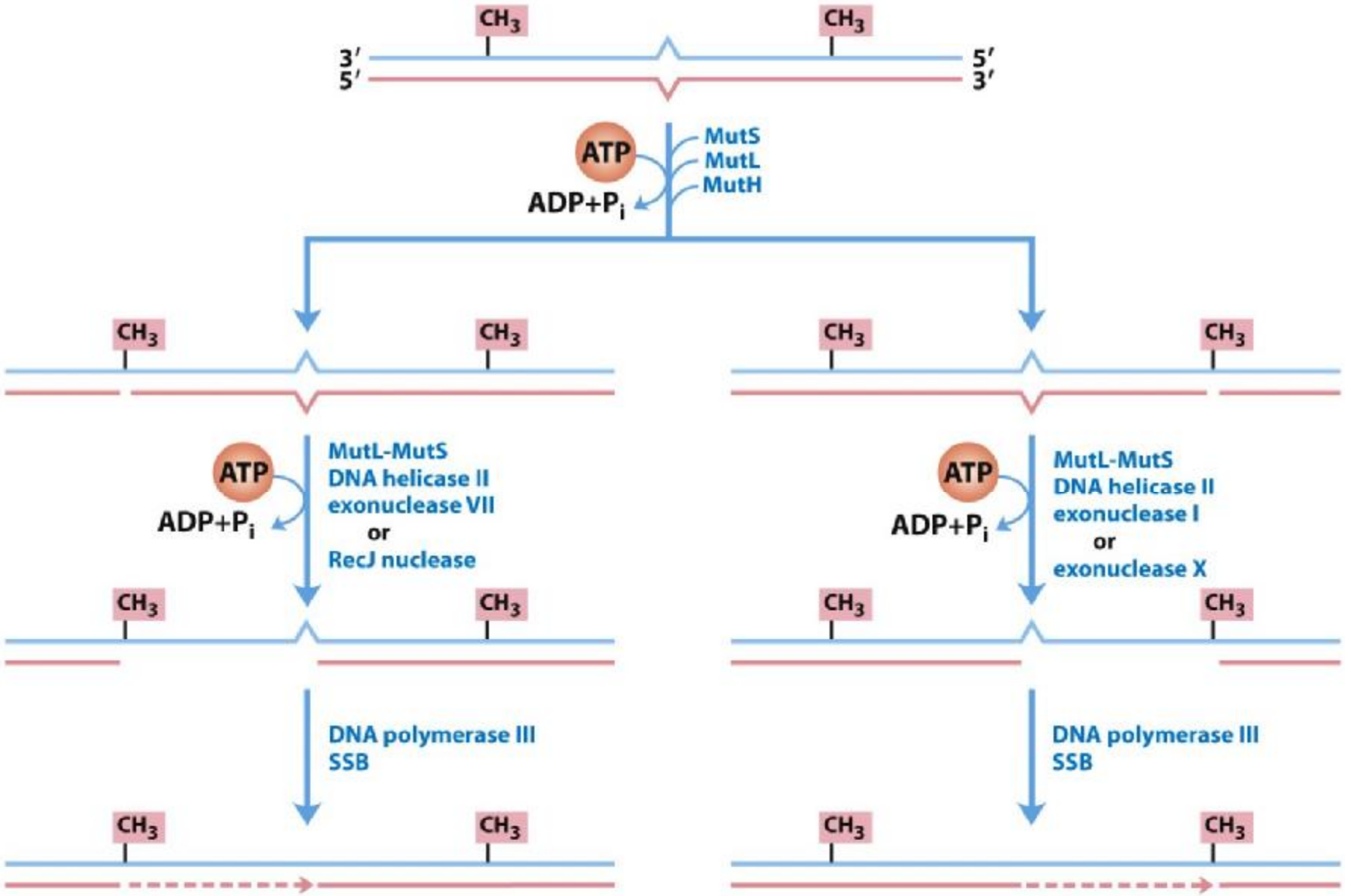

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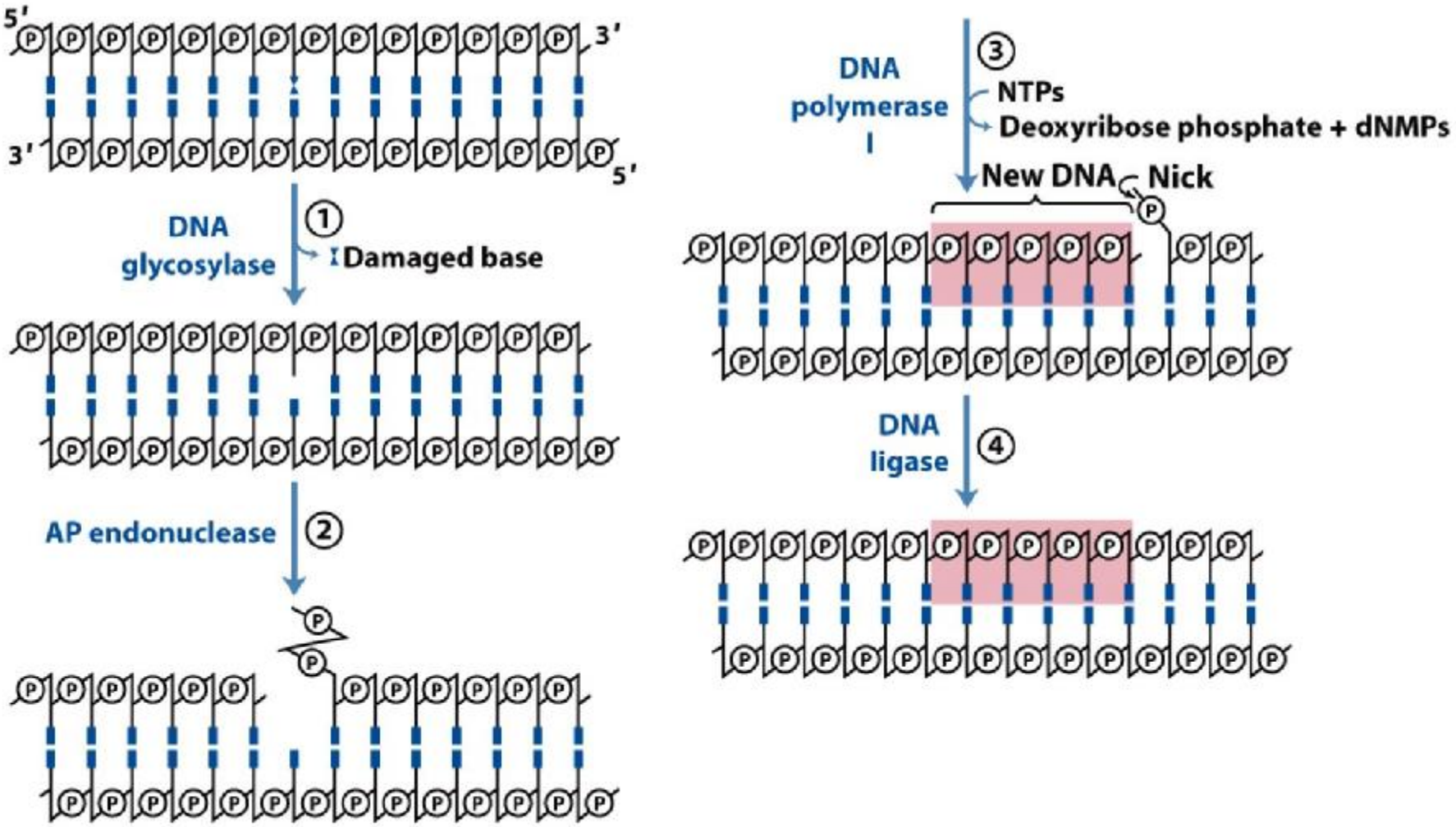

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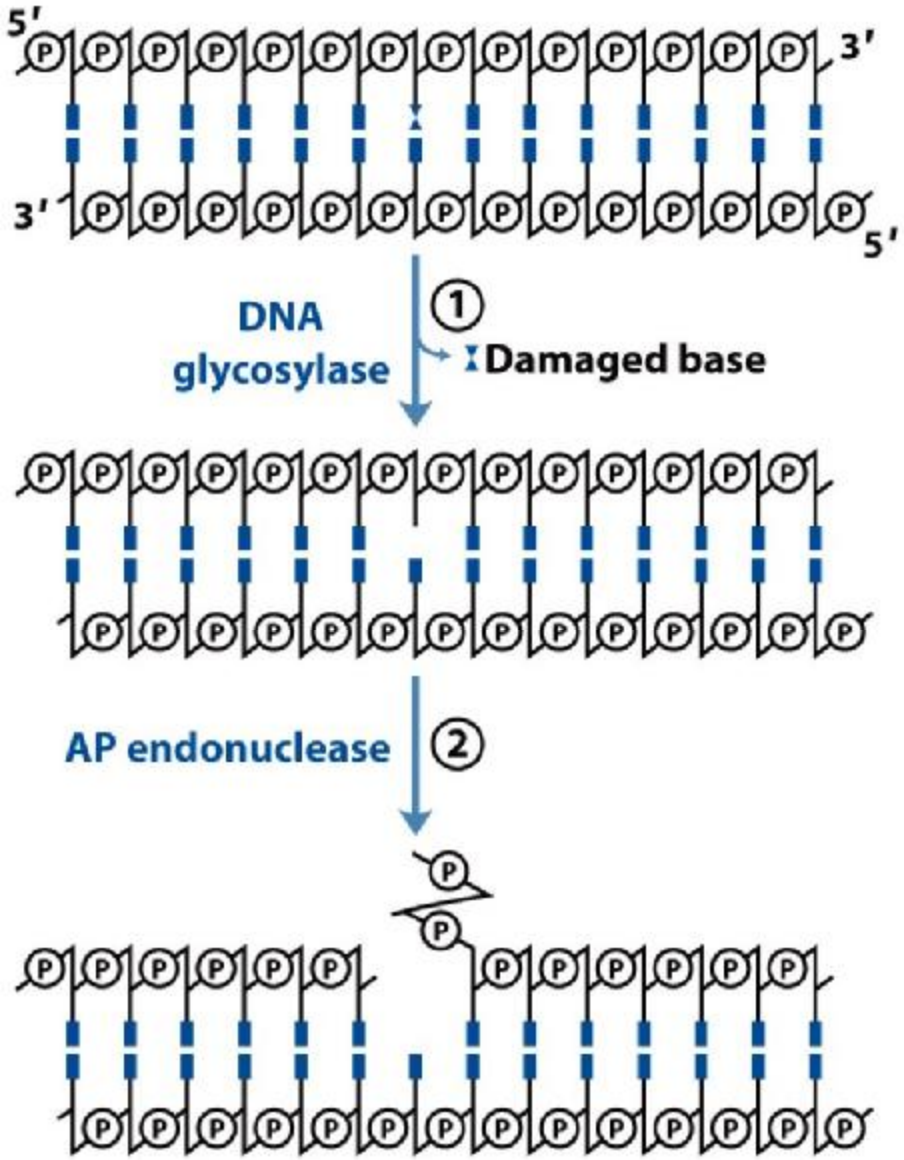

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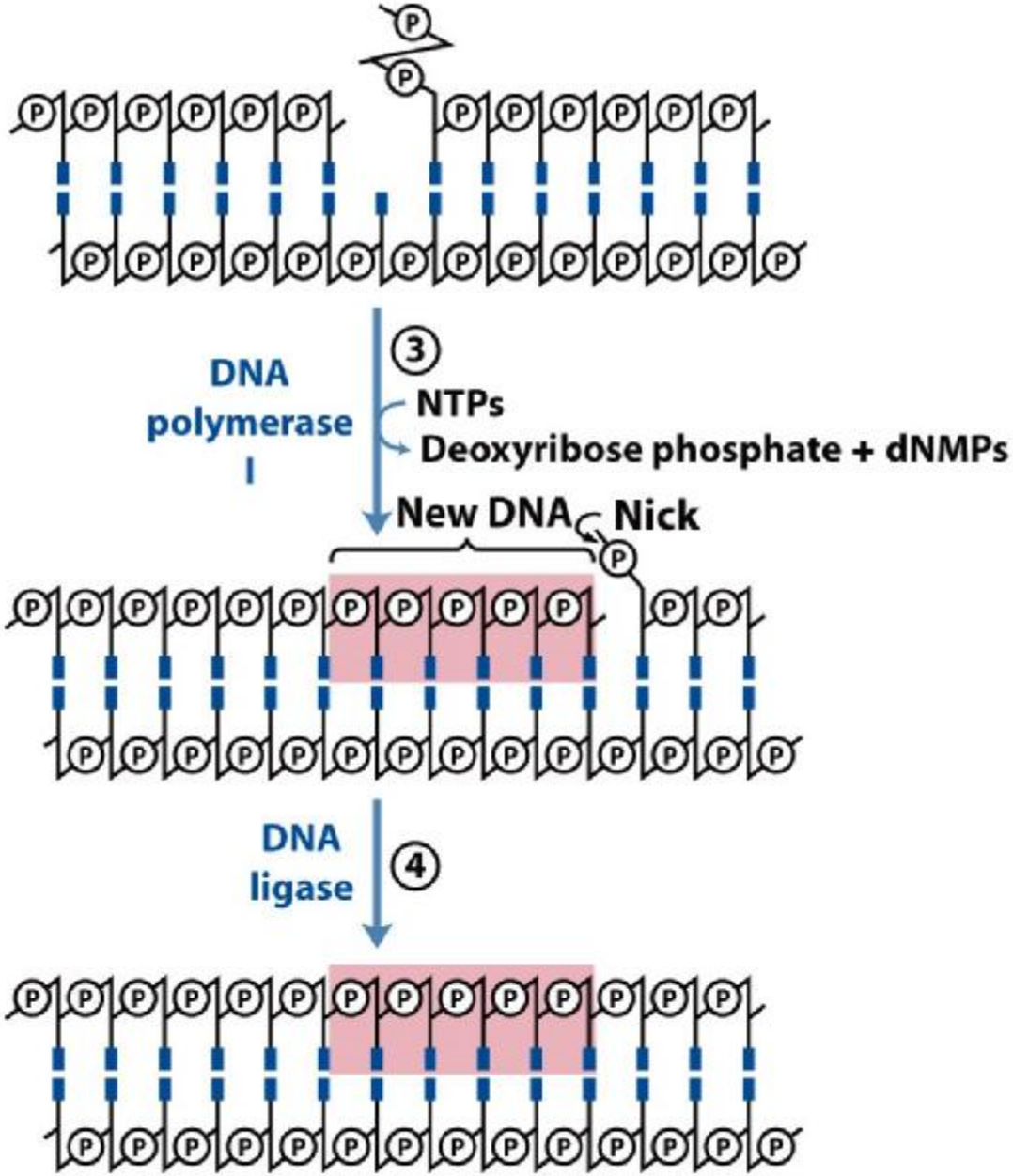

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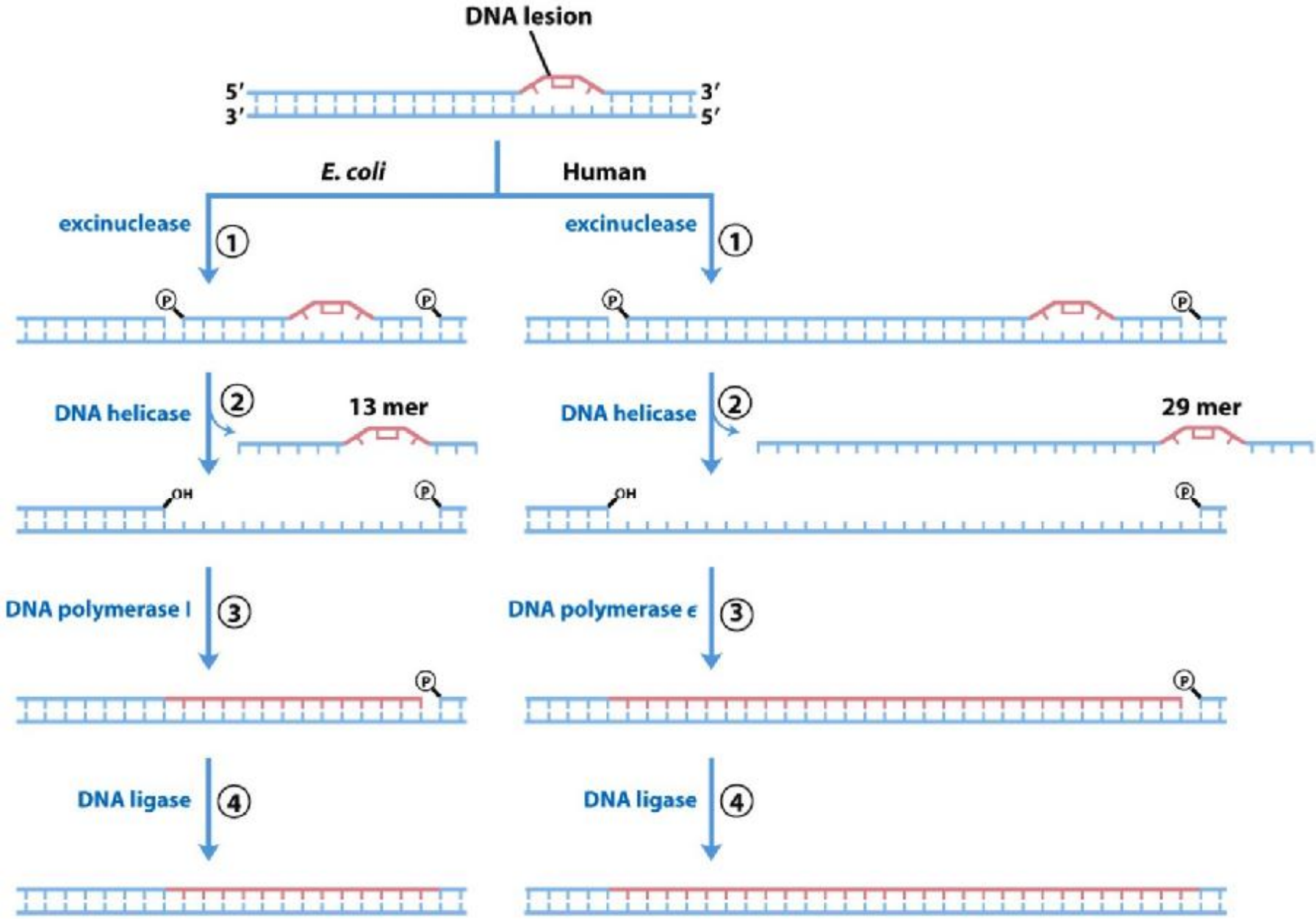

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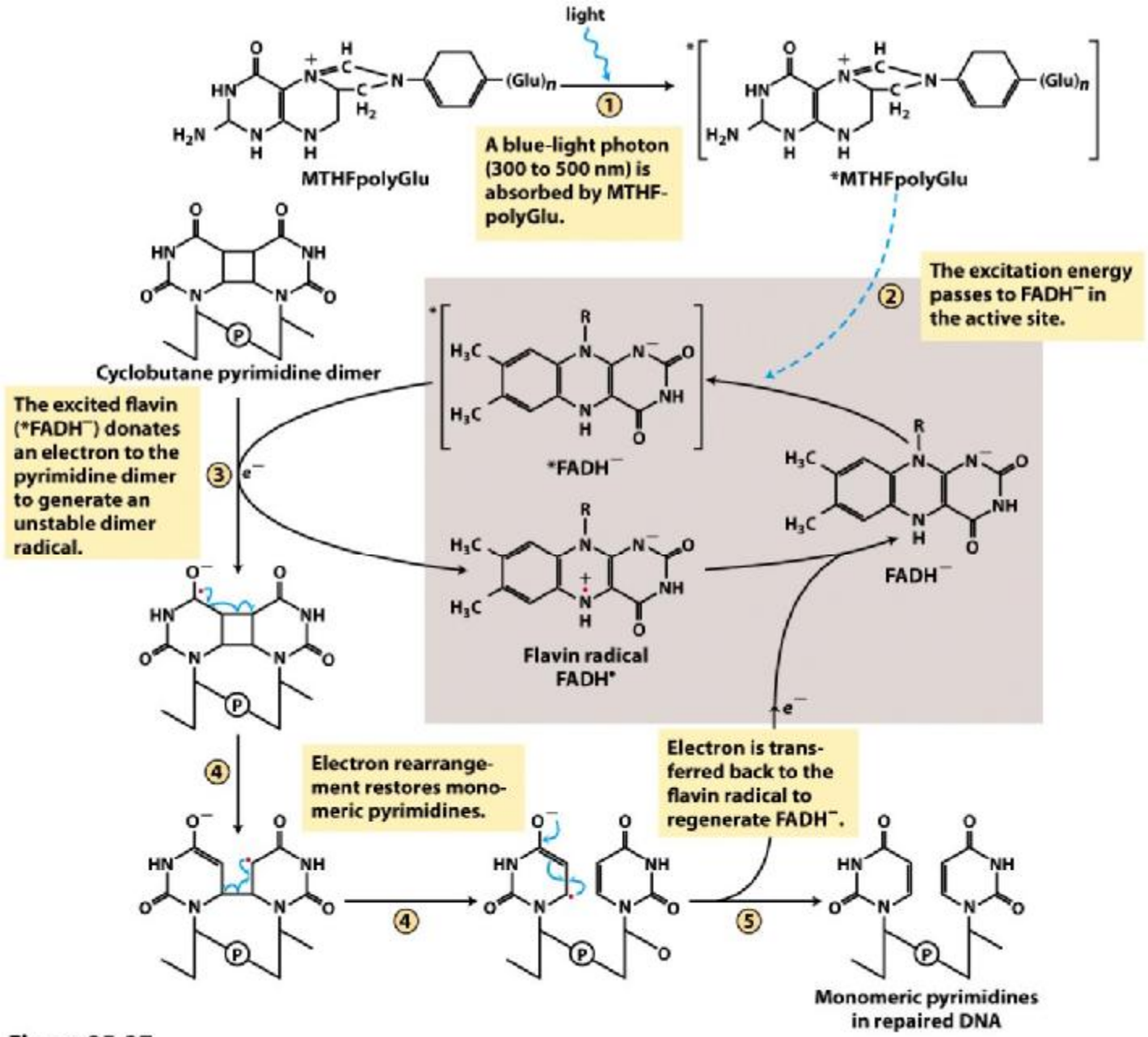

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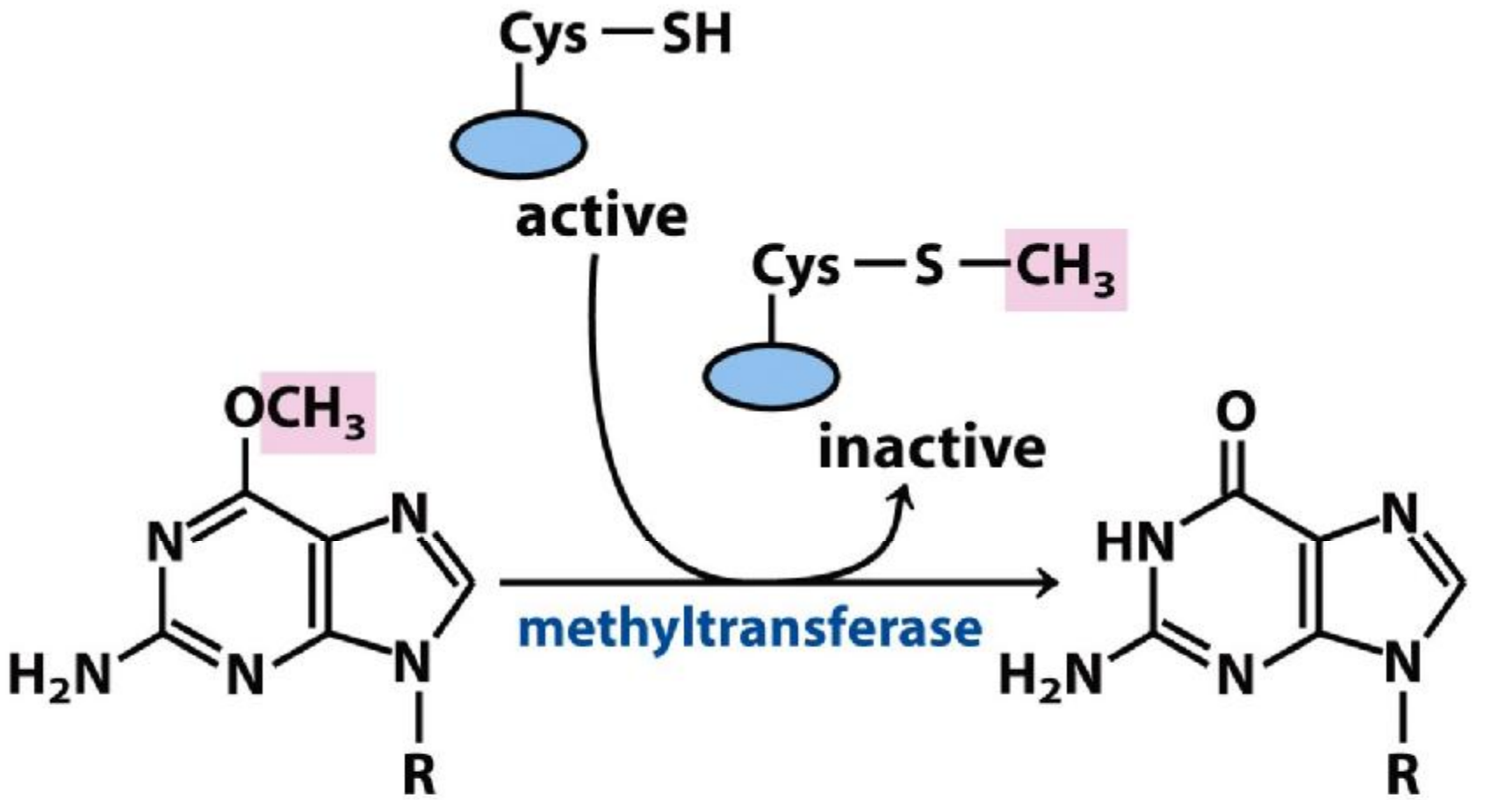

O^6-Methylguanine nucleotide

Guanine nucleotide

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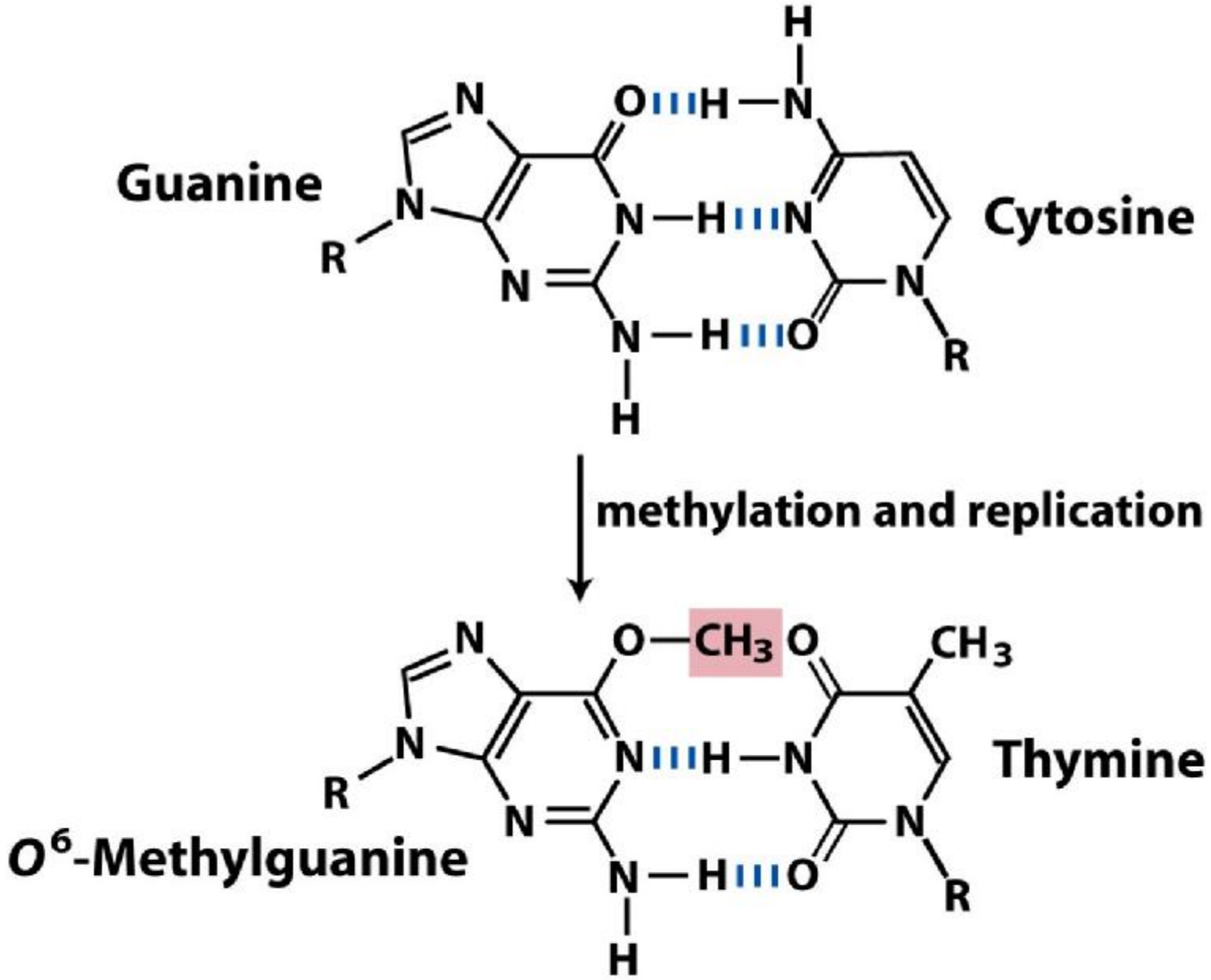

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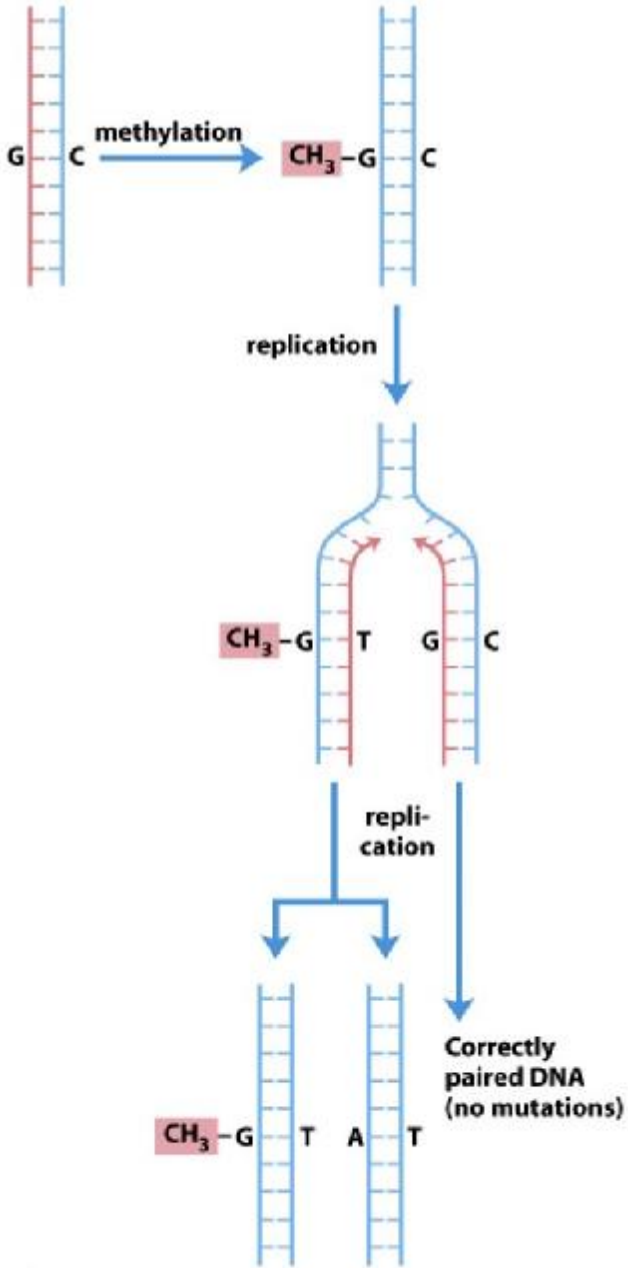

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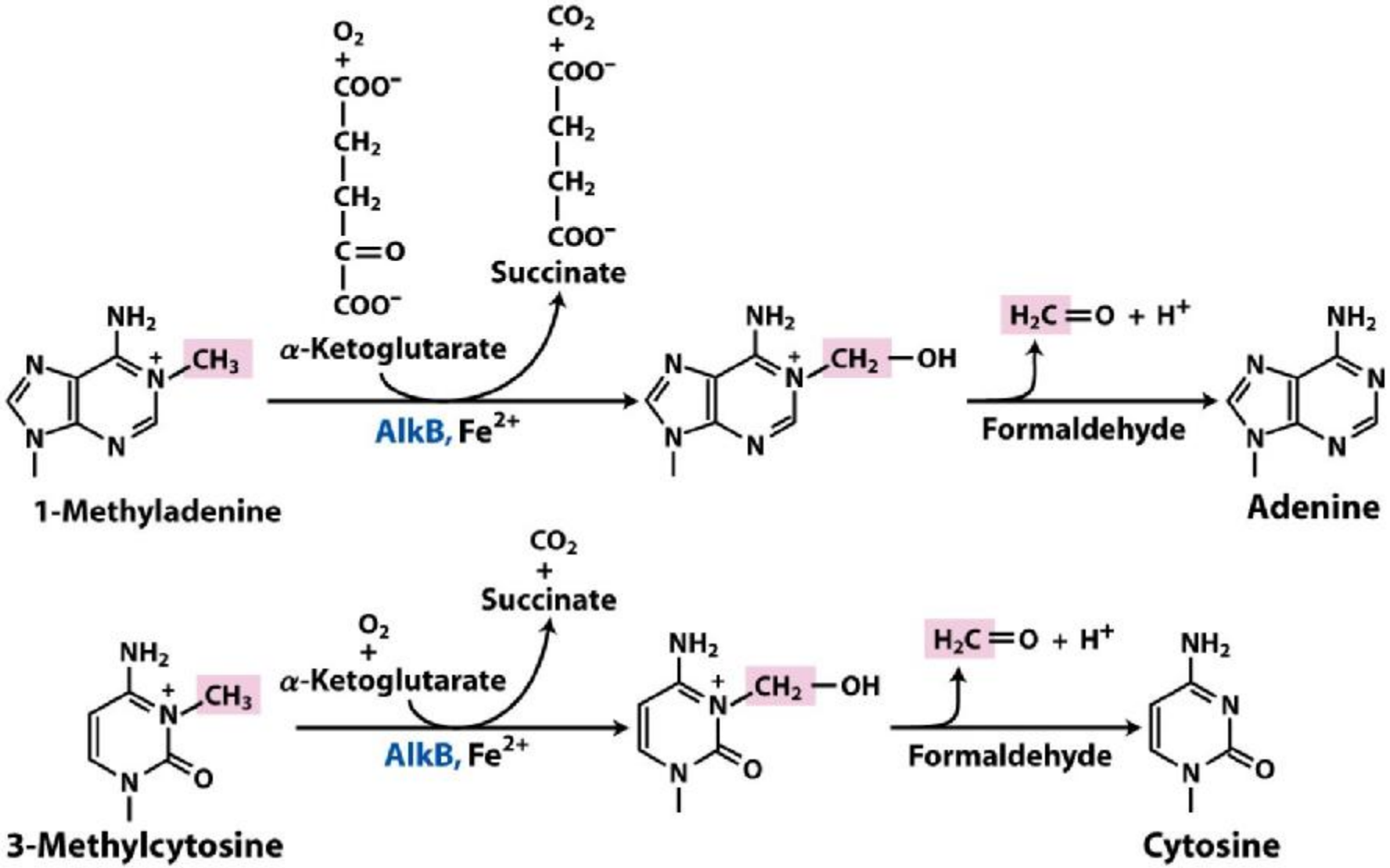

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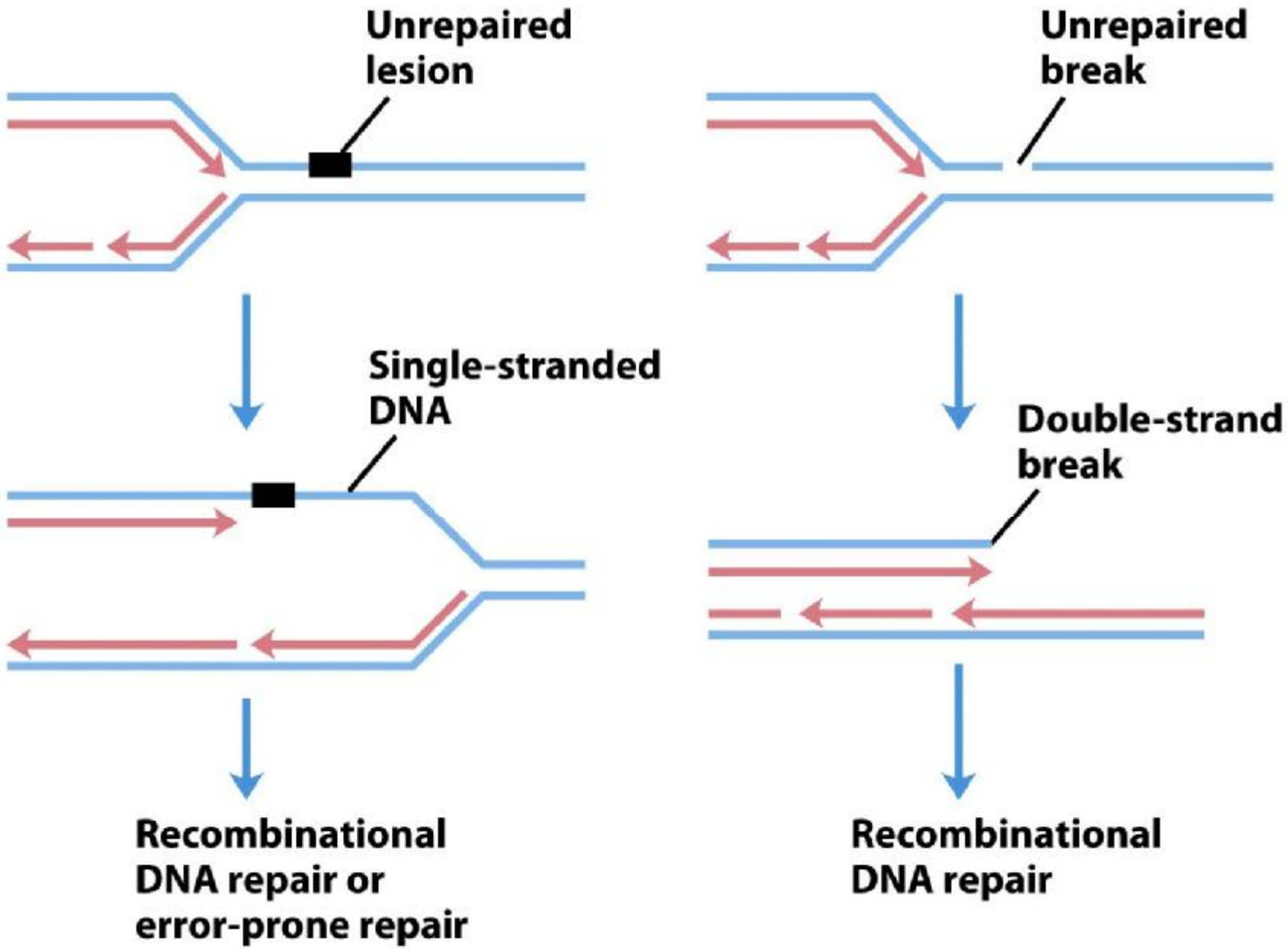

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TABLE 25–6 Genes Induced as Part of the SOS Response *in E. coli*

Gene name	Protein encoded and/or role in DNA repair
Genes of known function	
polB (dinA)	Encodes polymerization subunit of DNA polymerase II, required for replication restart in recombinational DNA repair
uvrA *uvrB*	Encode ABC excinuclease subunits UvrA and UvrB
umuC *umuD*	Encode DNA polymerase V
sulA	Encodes protein that inhibits cell division, possibly to allow time for DNA repair
recA	Encodes RecA protein, required for error-prone repair and recombinational repair
dinB	Encodes DNA polymerase IV
ssb	Encodes single-stranded DNA-binding protein (SSB)
himA	Encodes subunit of integration host factor (IHF), involved in site-specific recombination, replication, transposition, regulation of gene expression
Genes involved in DNA metabolism, but role in DNA repair unknown	
uvrD	Encodes DNA helicase II (DNA-unwinding protein)
recN	Required for recombinational repair
Genes of unknown function	
dinD	
dinF	

Note: Some of these genes and their functions are further discussed in Chapter 28.

Table 25-6
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Barbara McClintock
1902–1992

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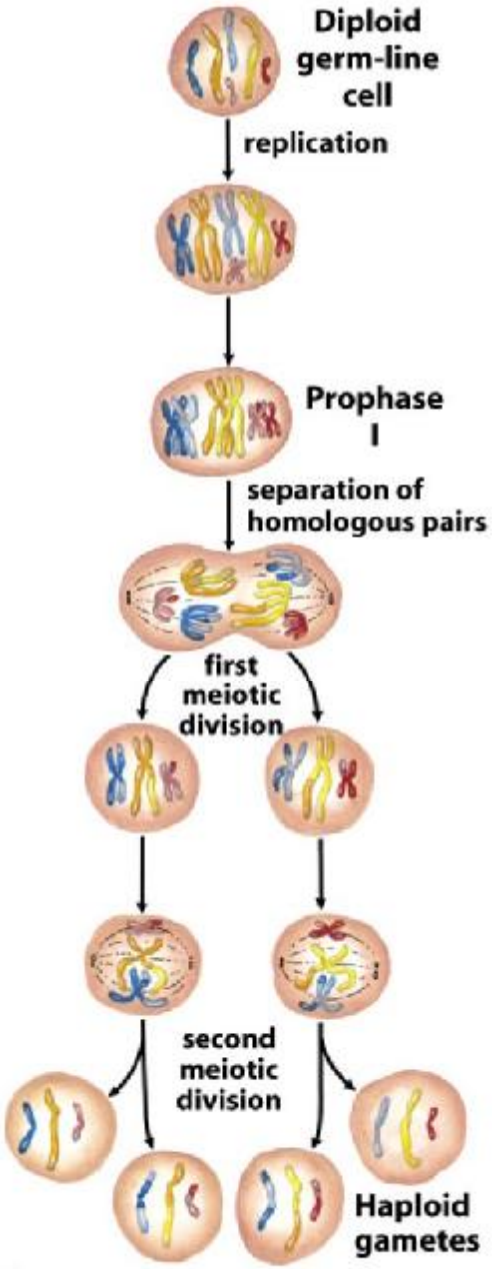

Figure 25-31

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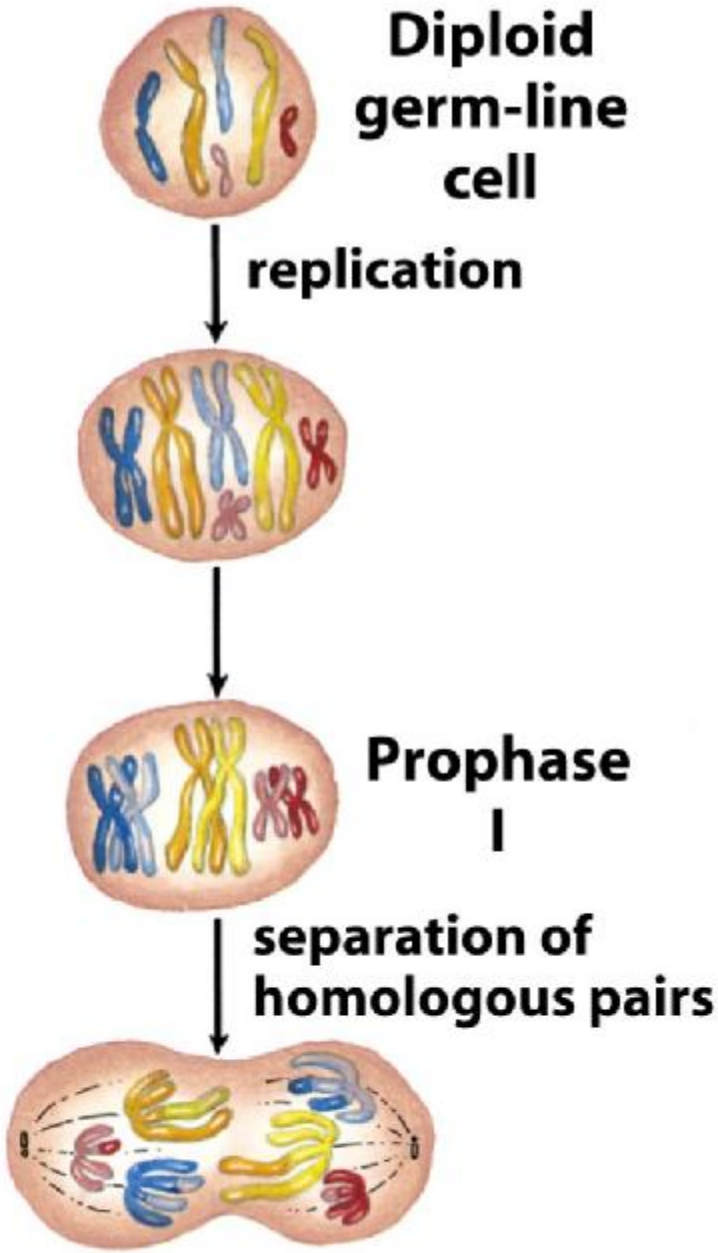

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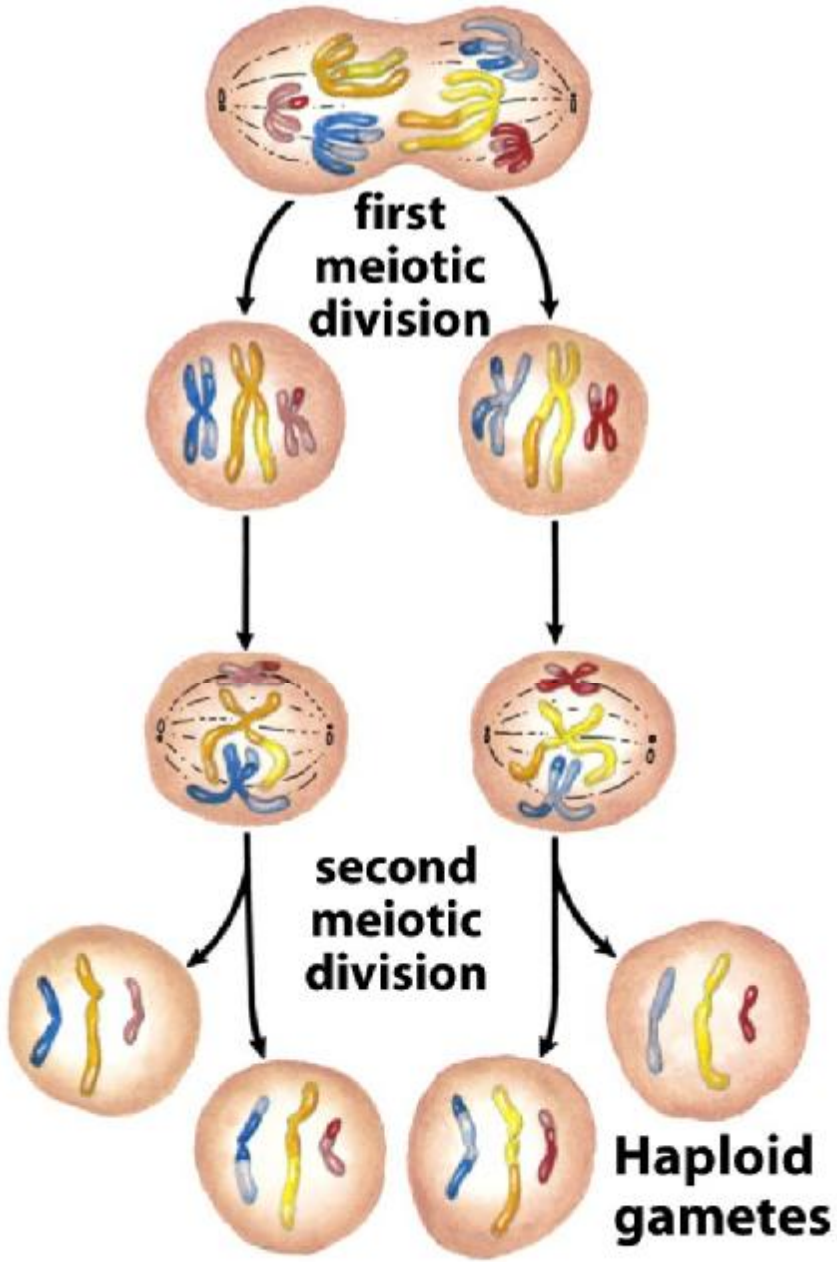

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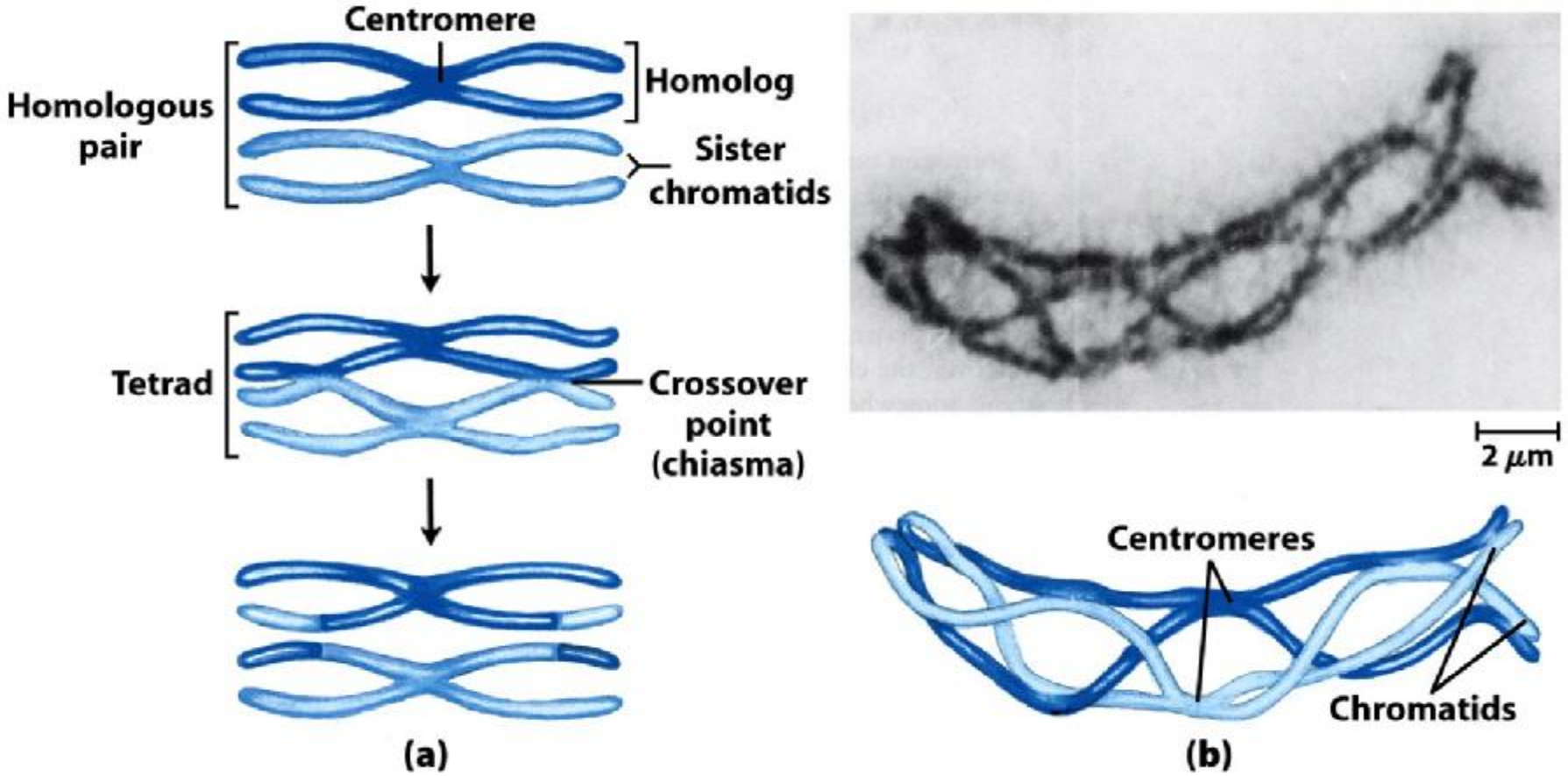

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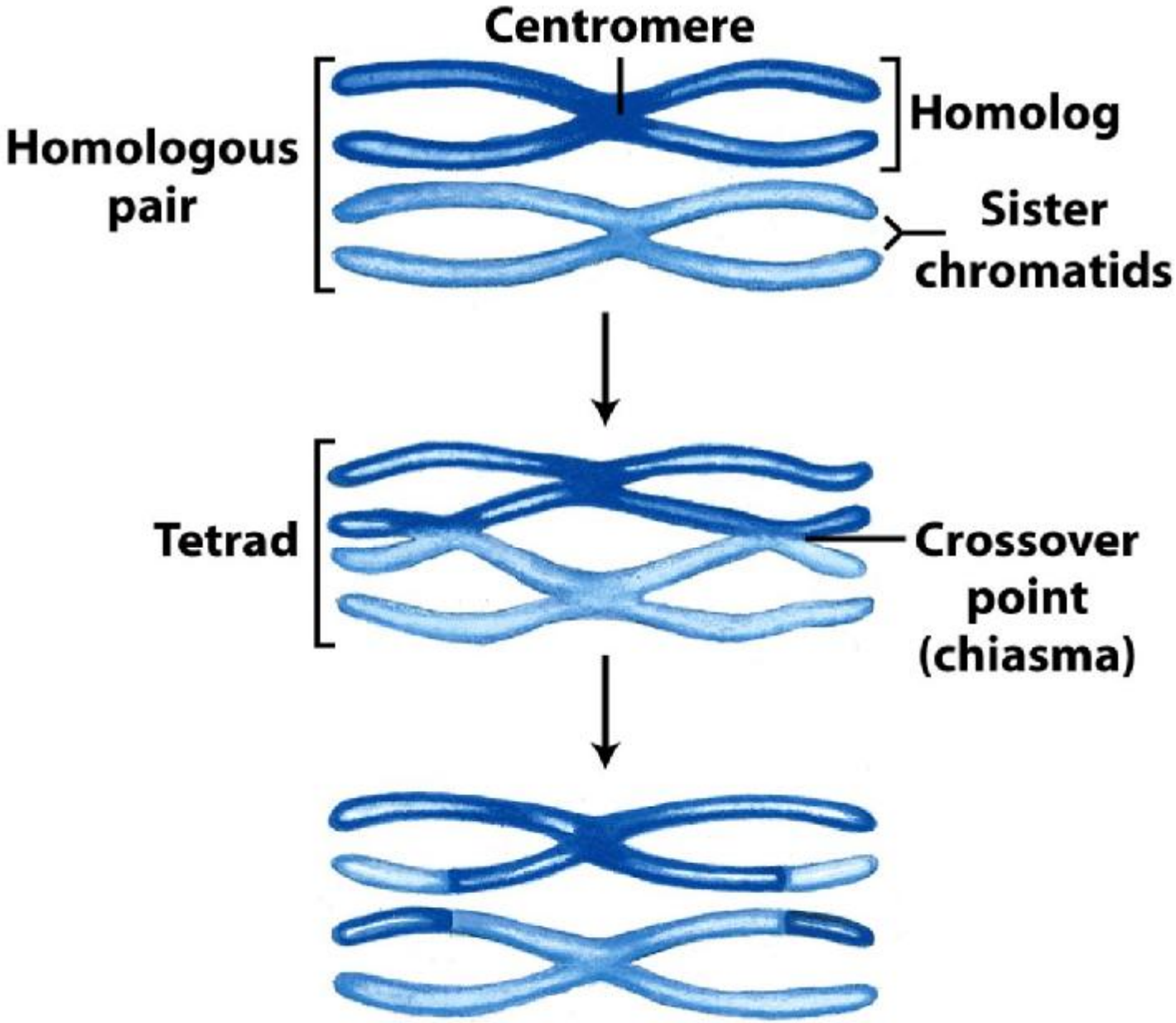

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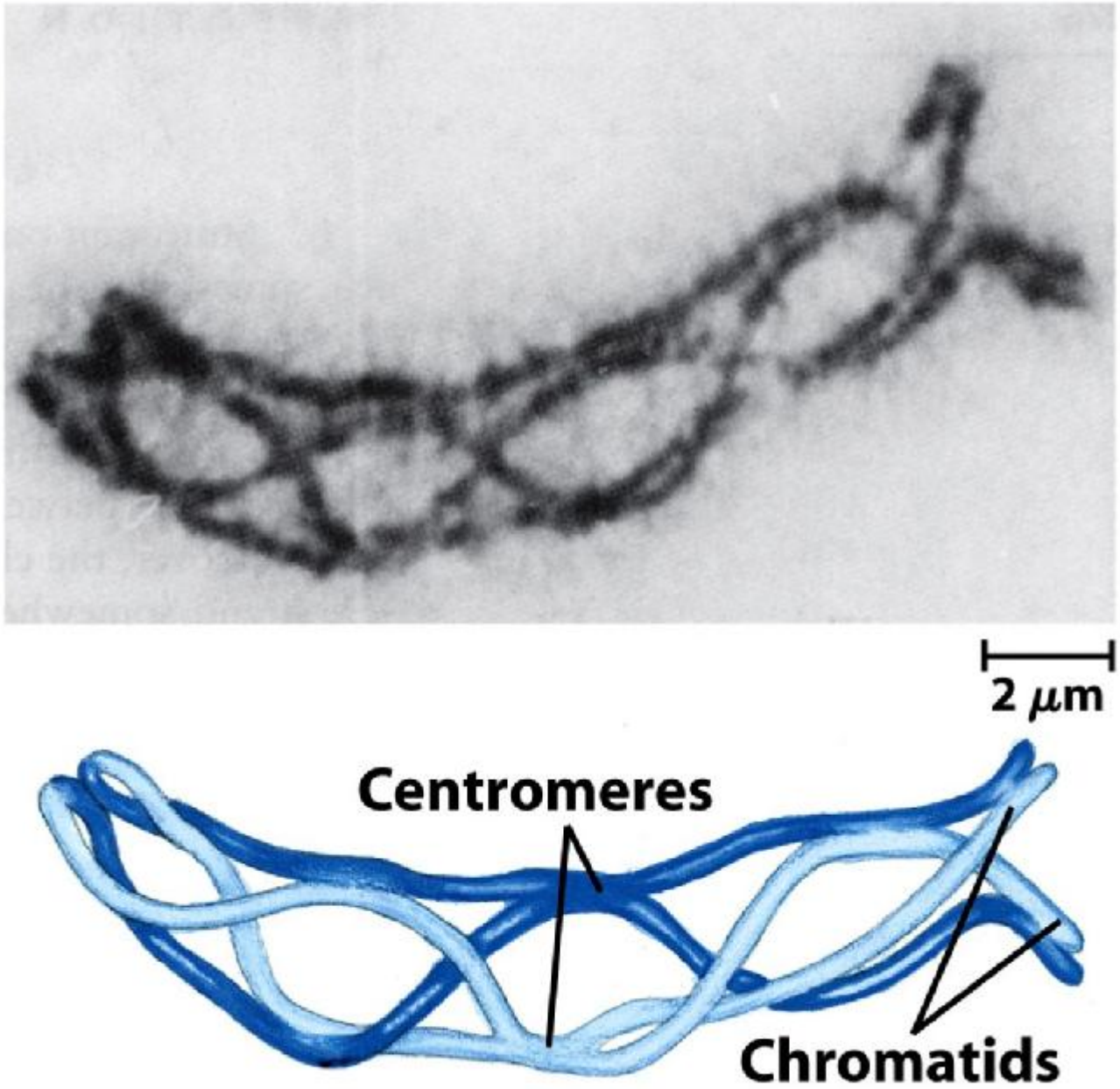

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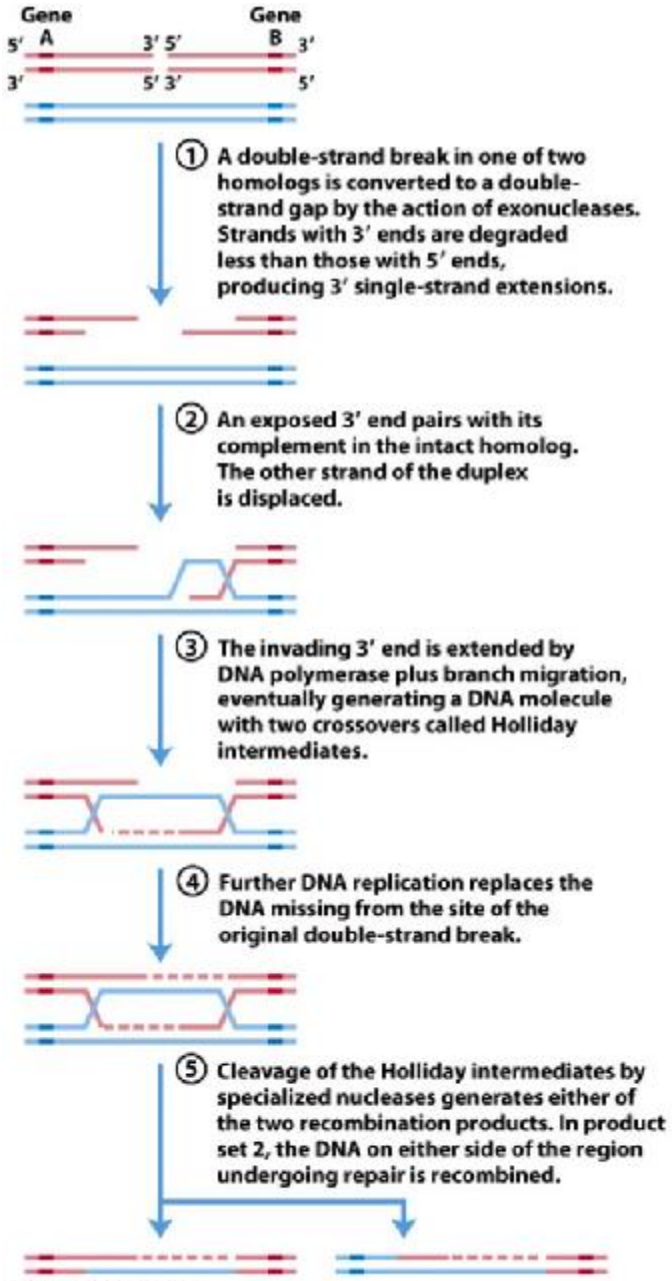

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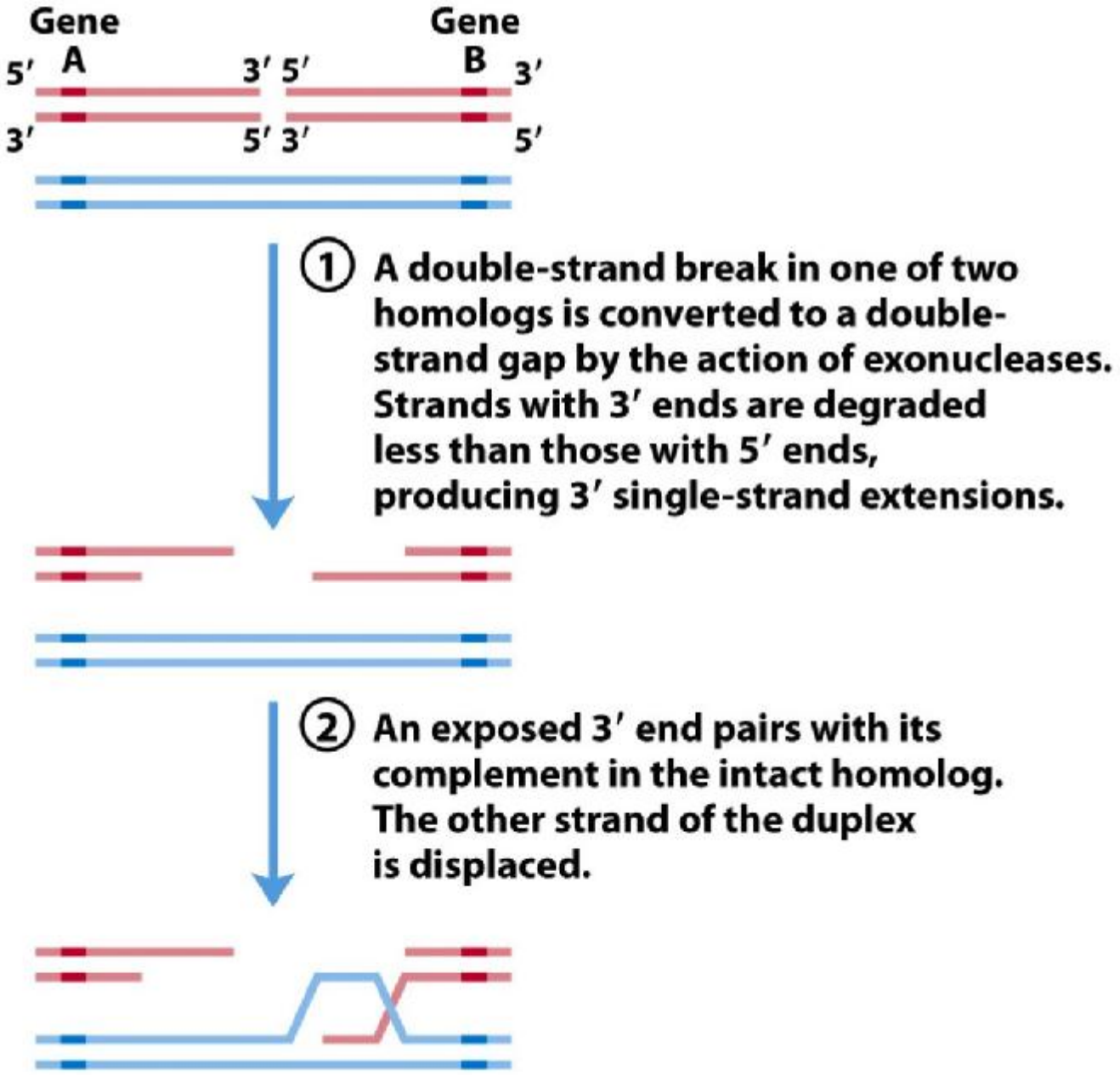

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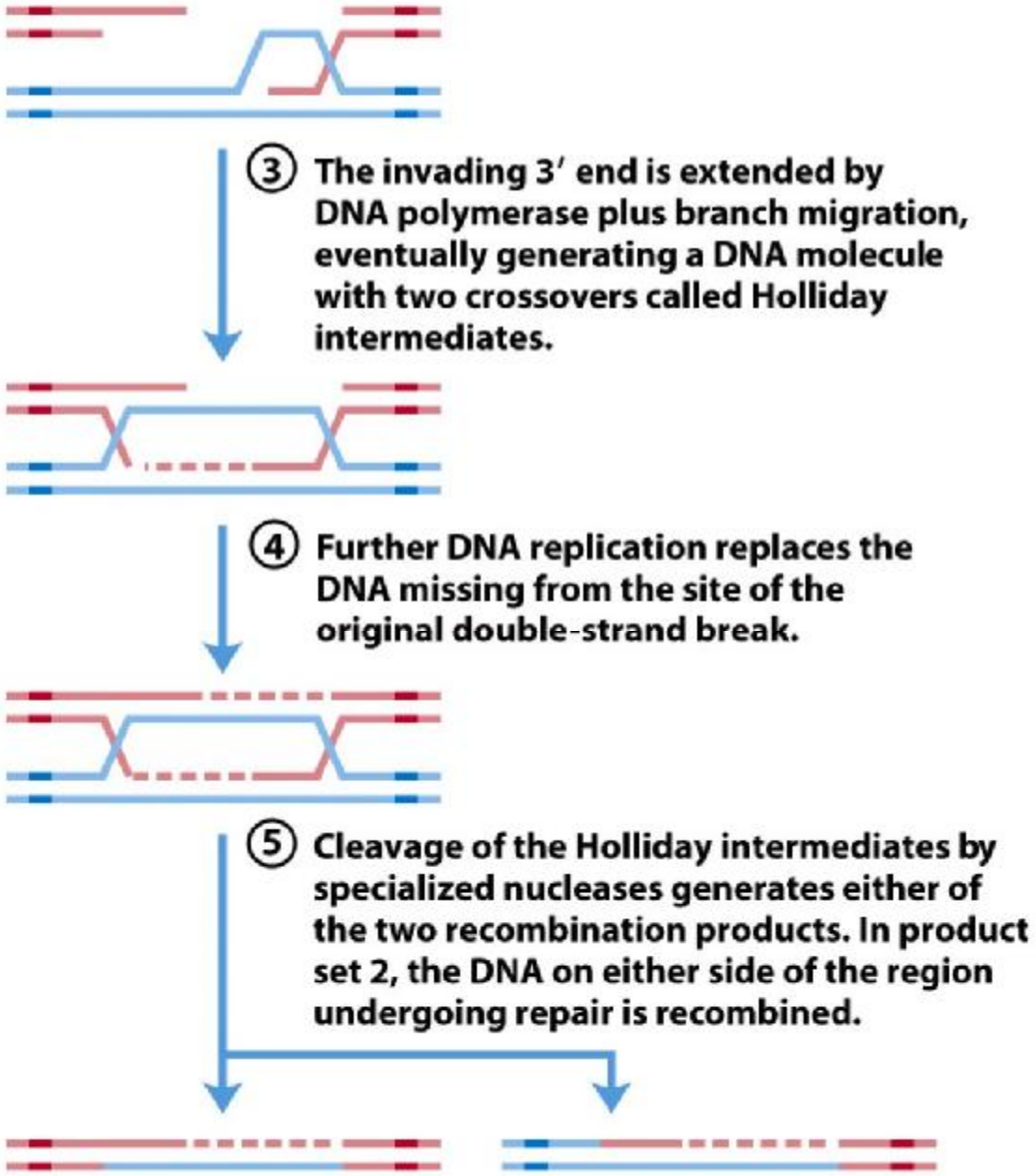

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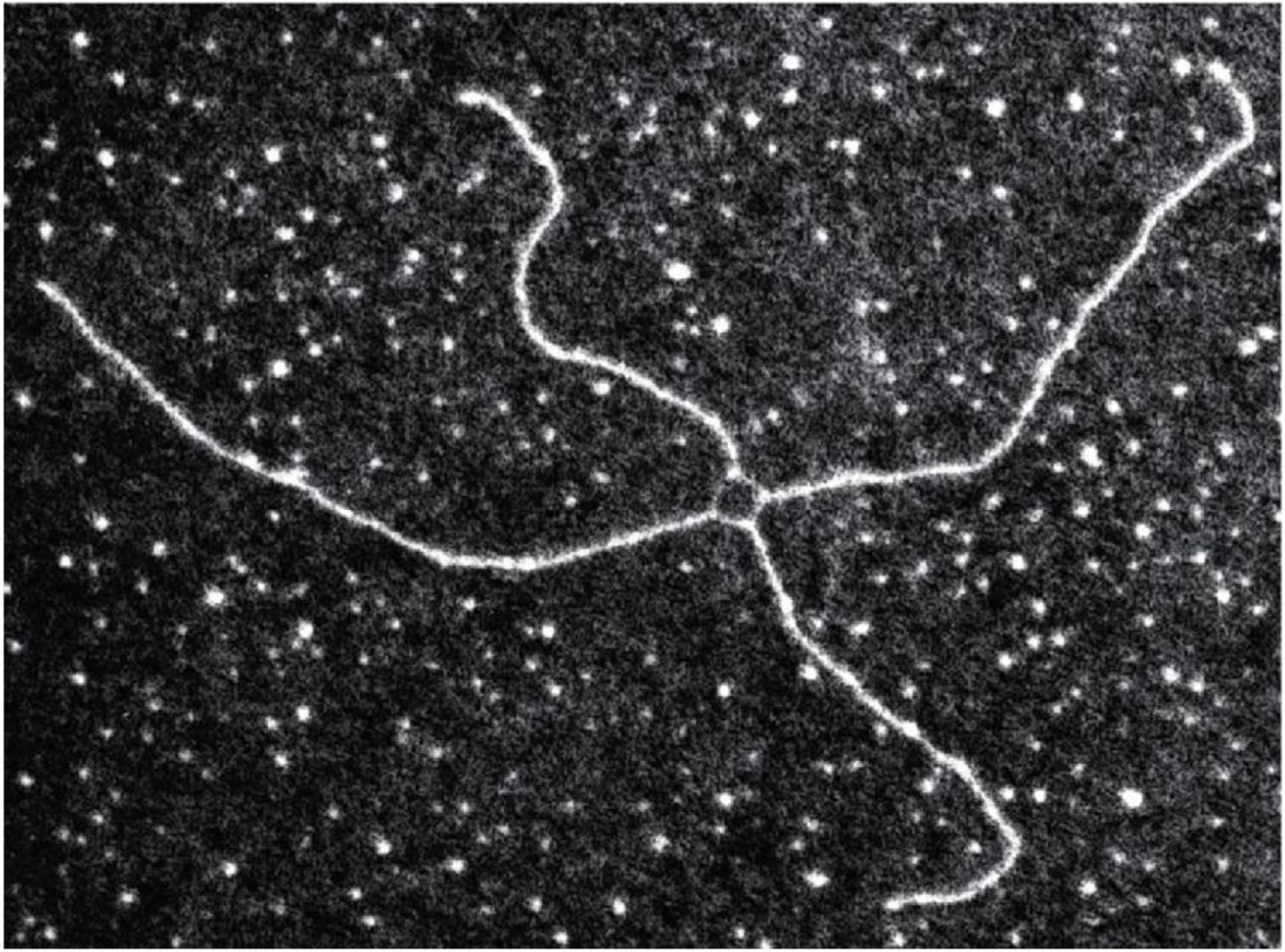

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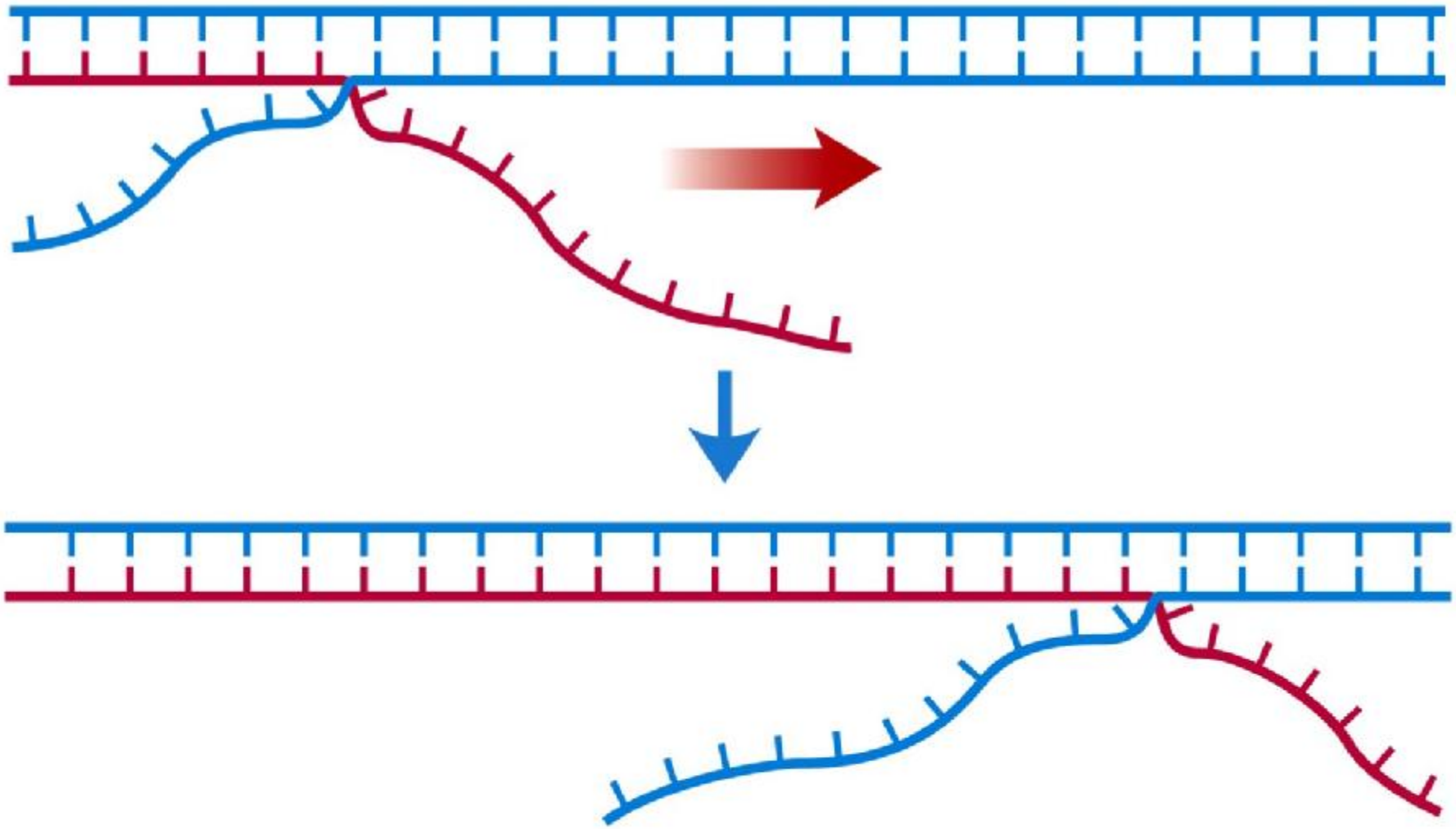

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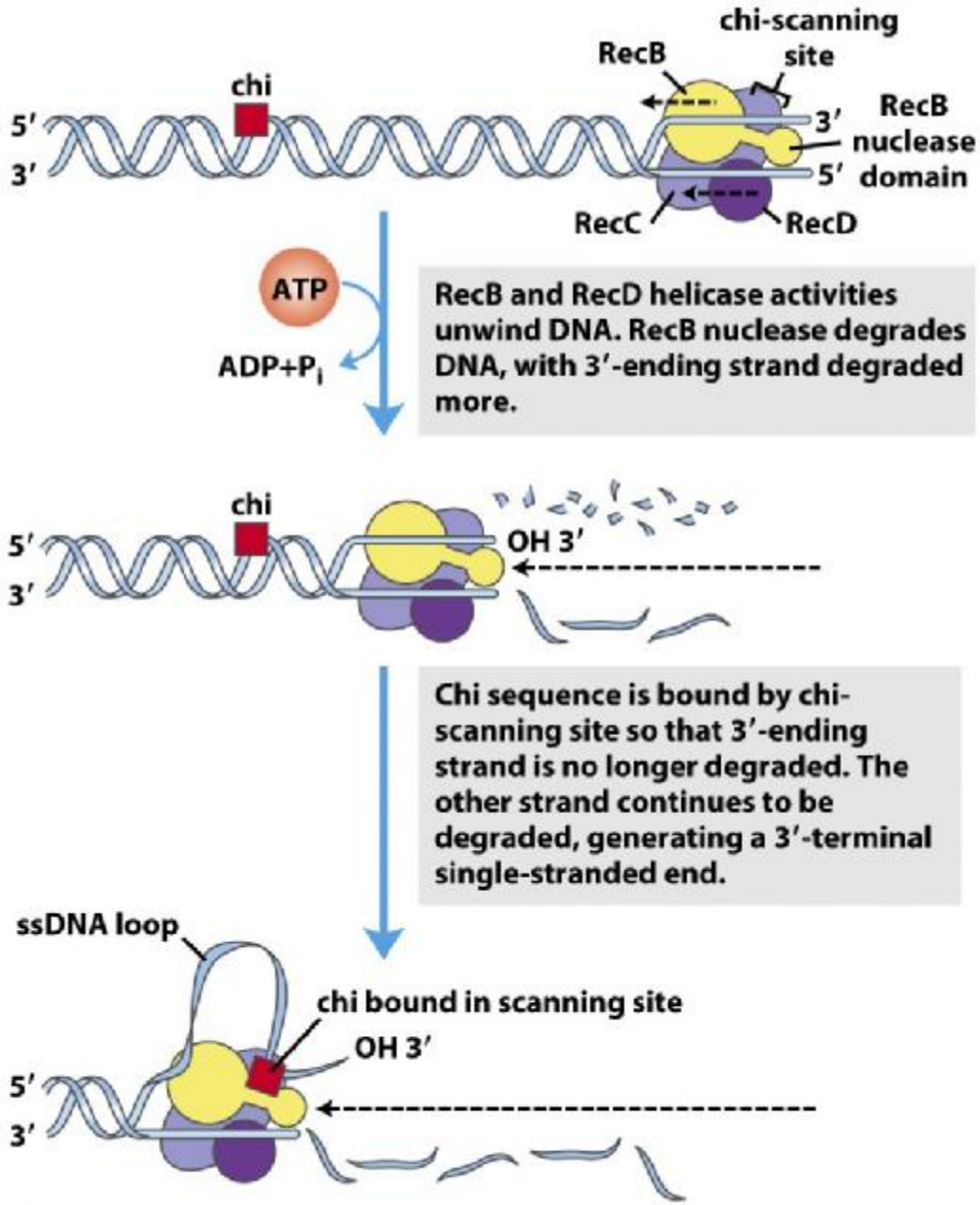

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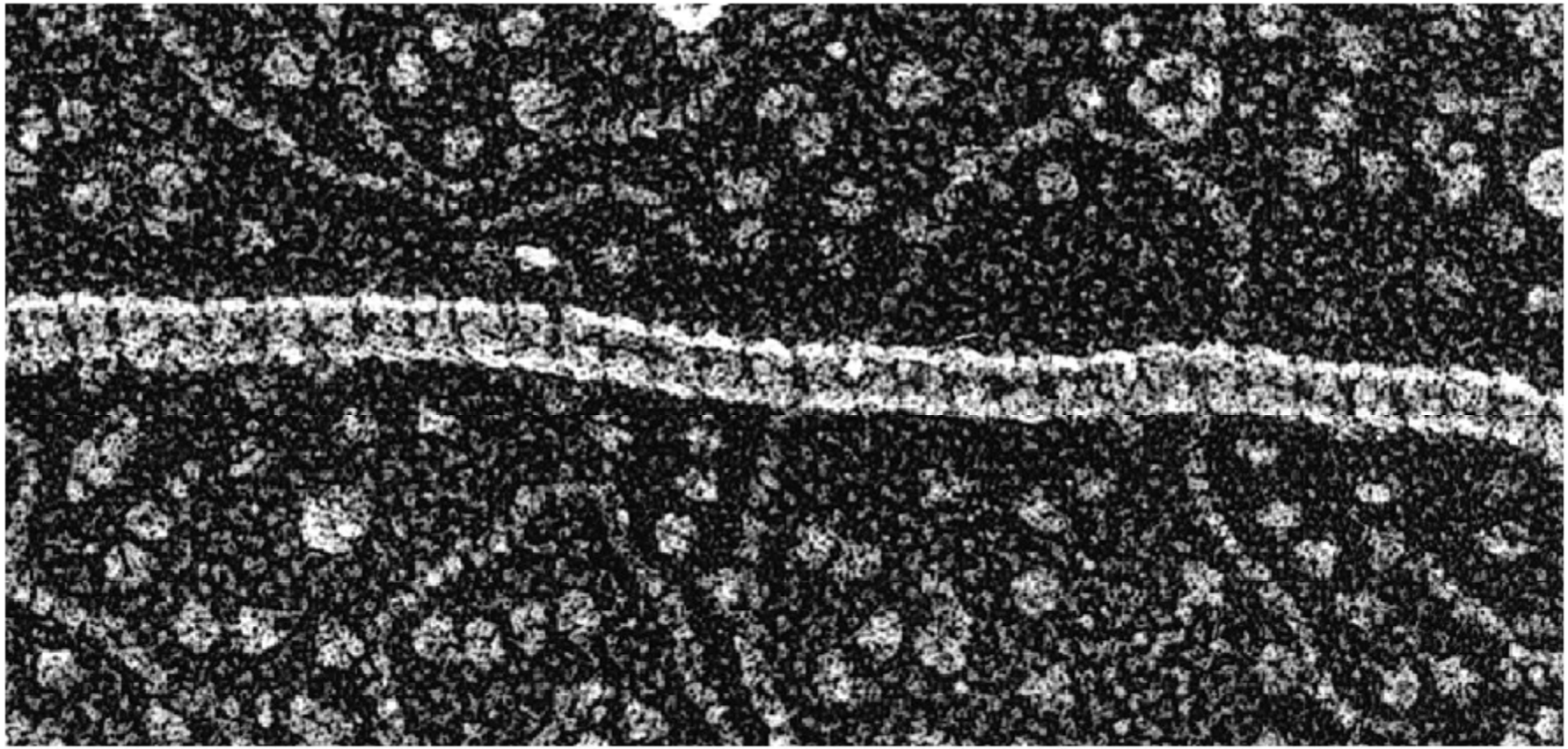

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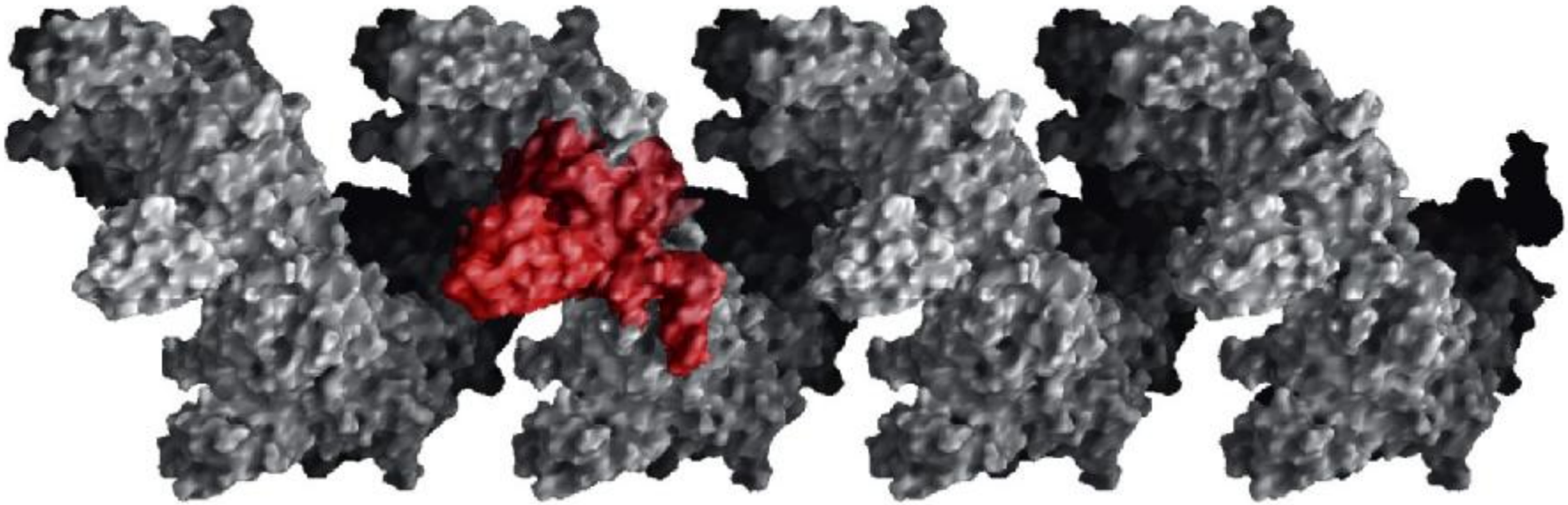

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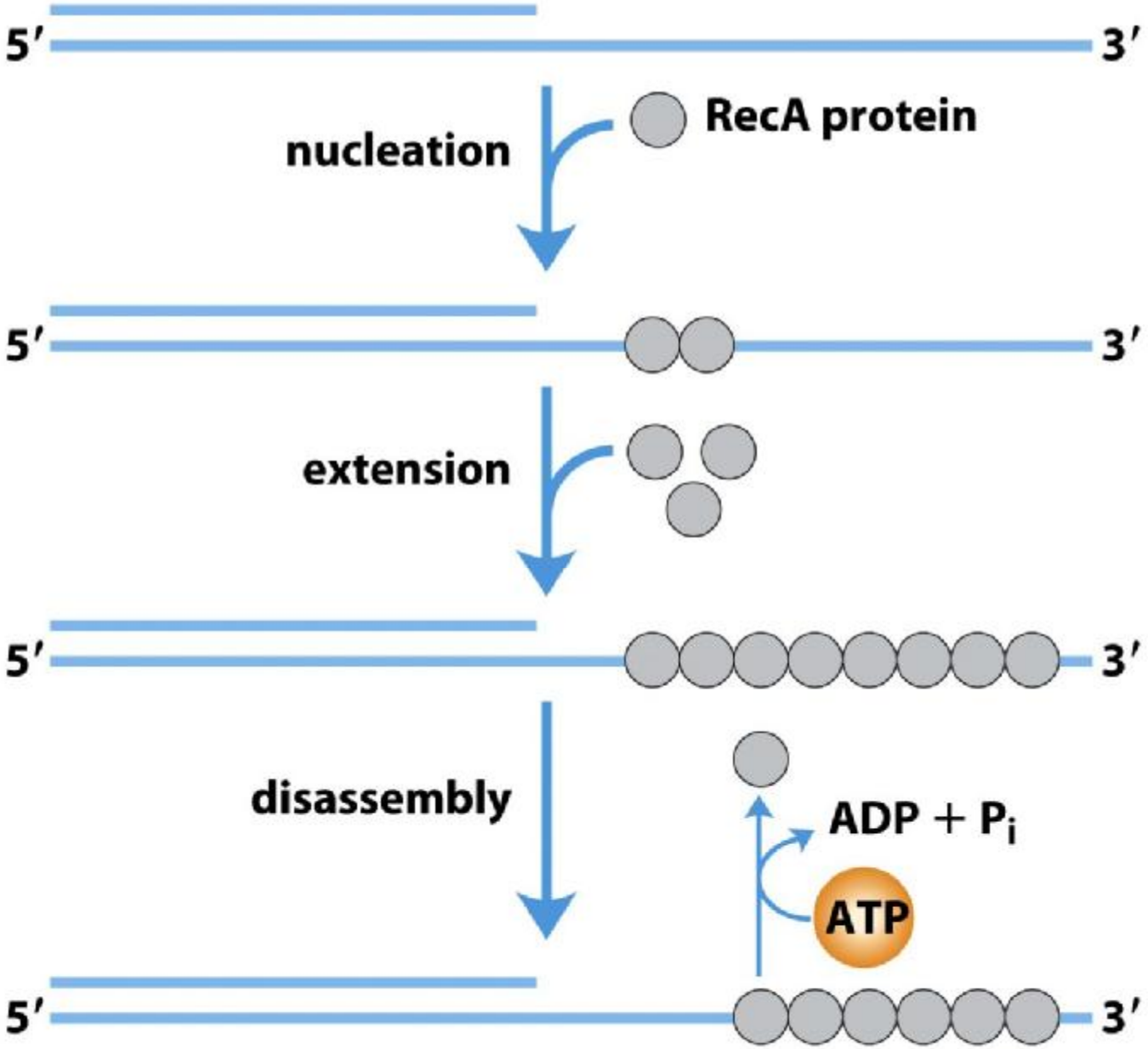

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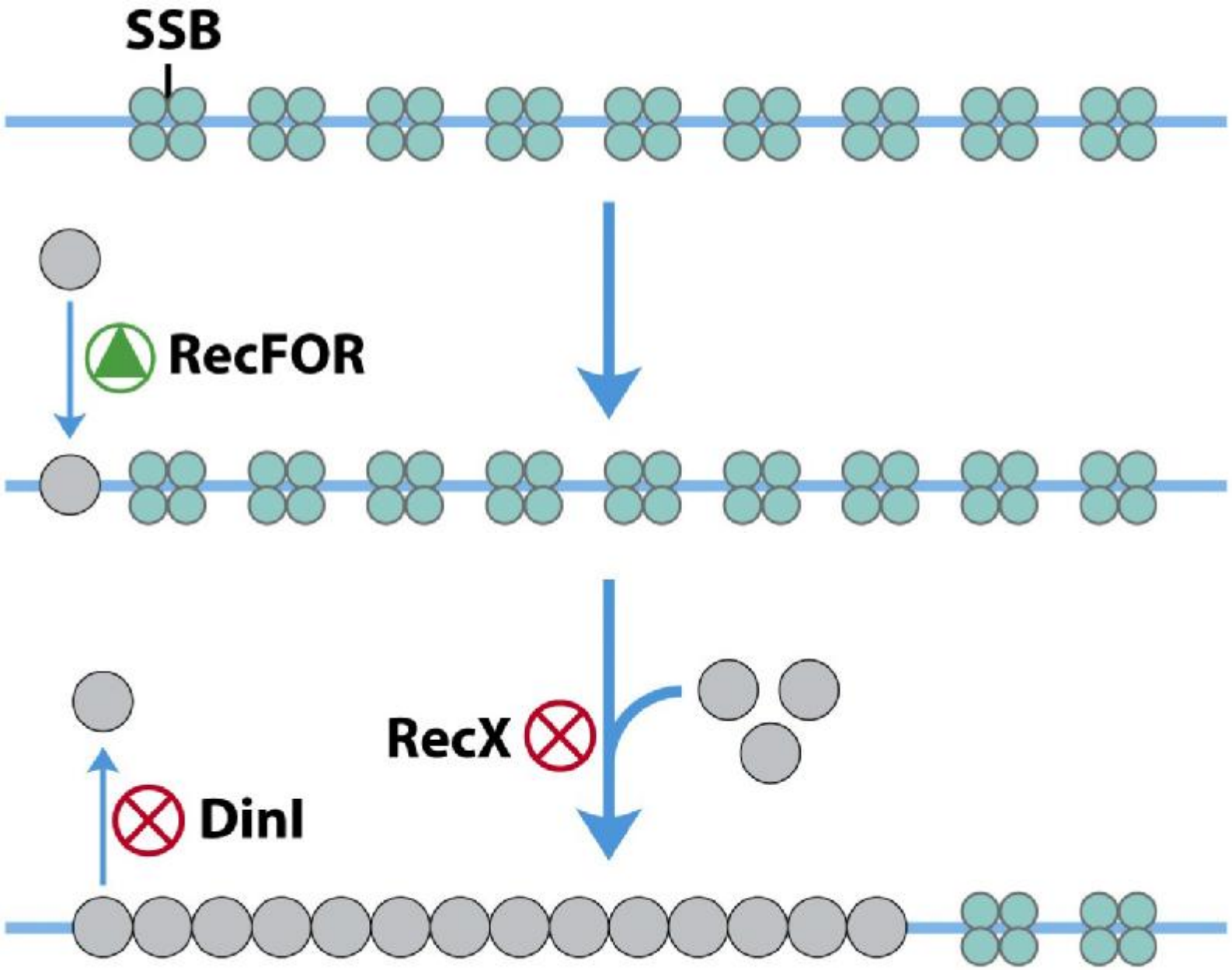

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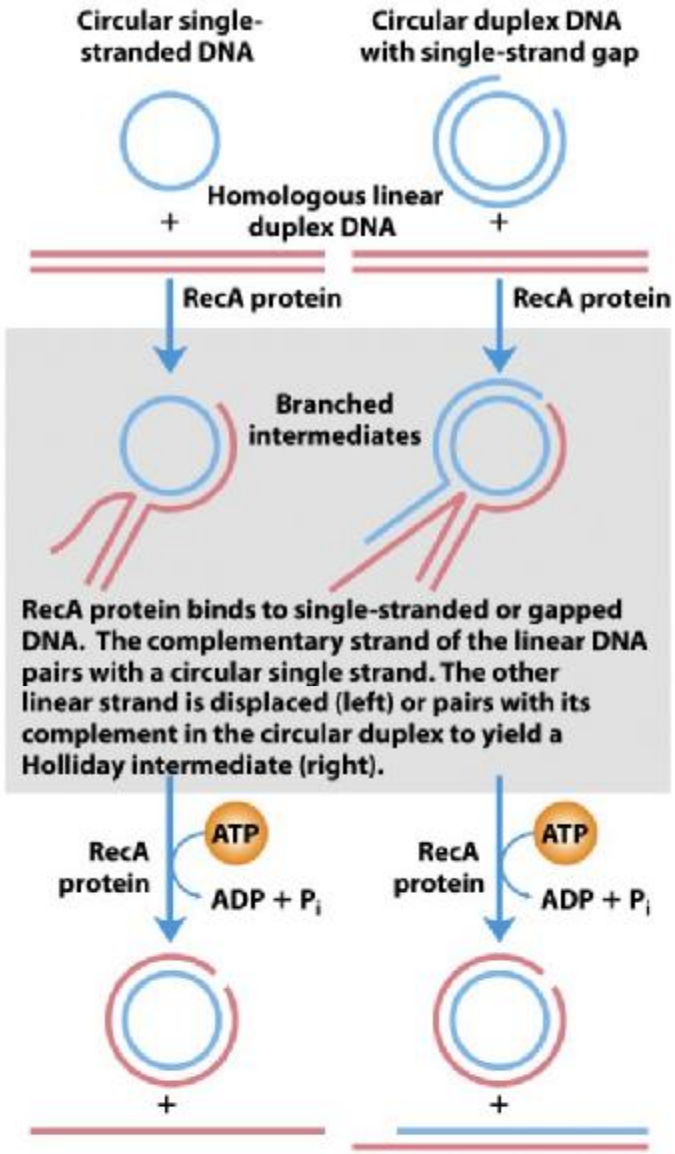

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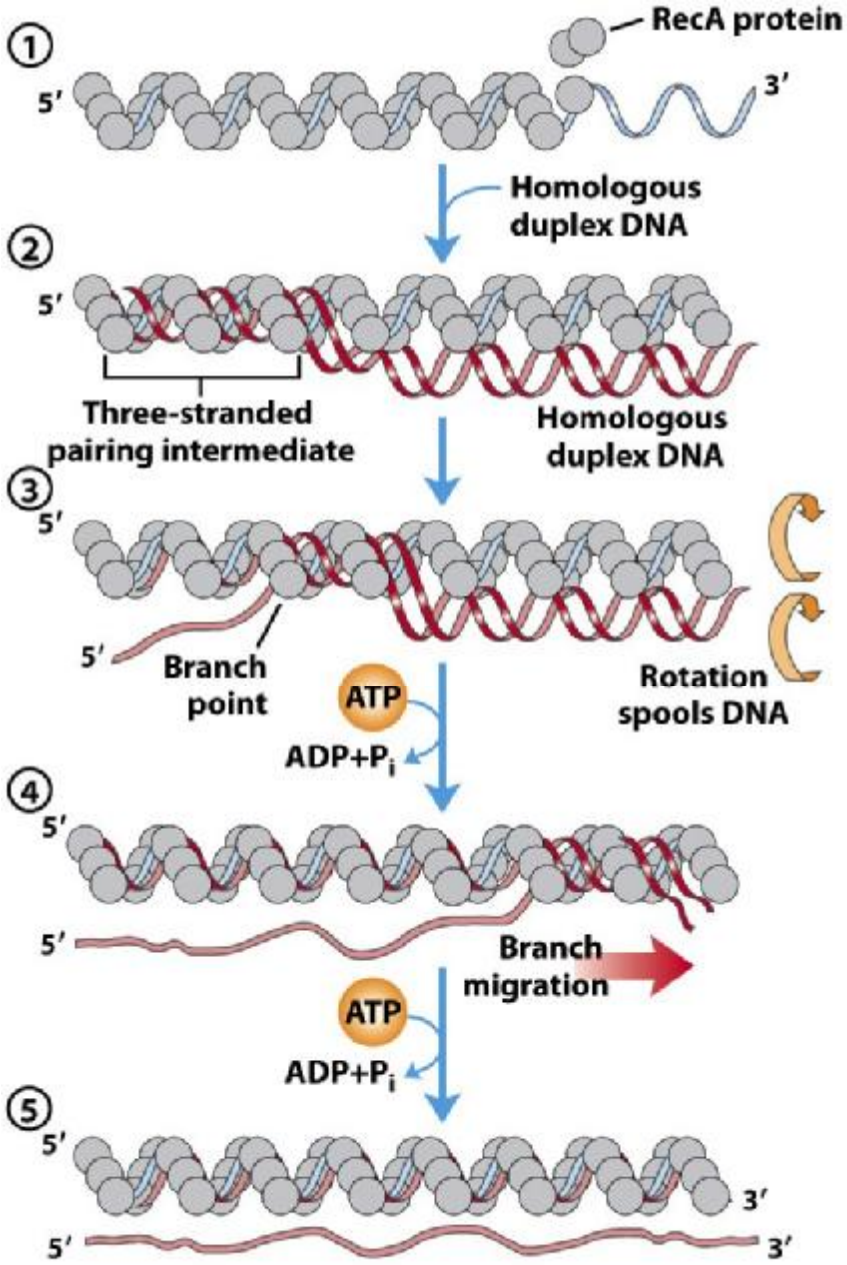

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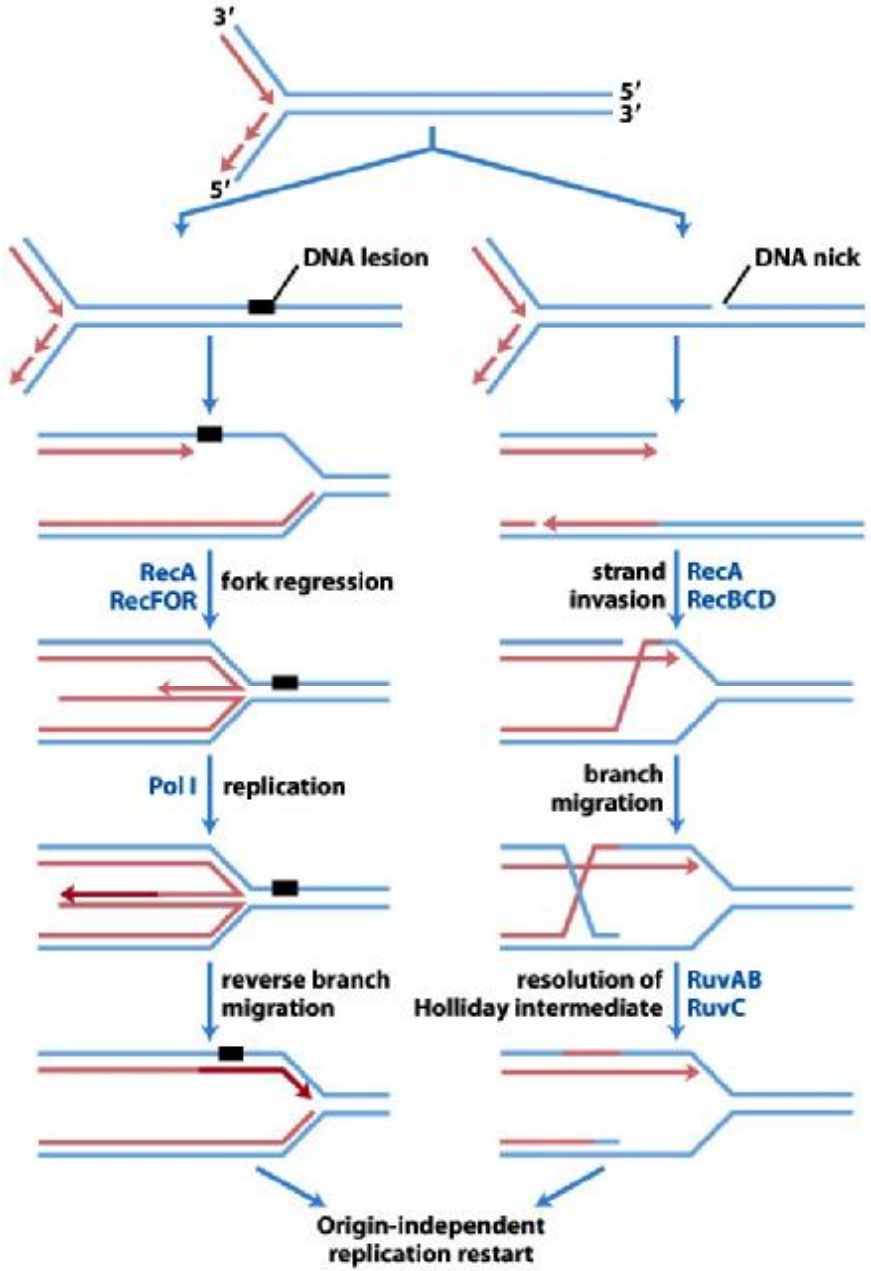

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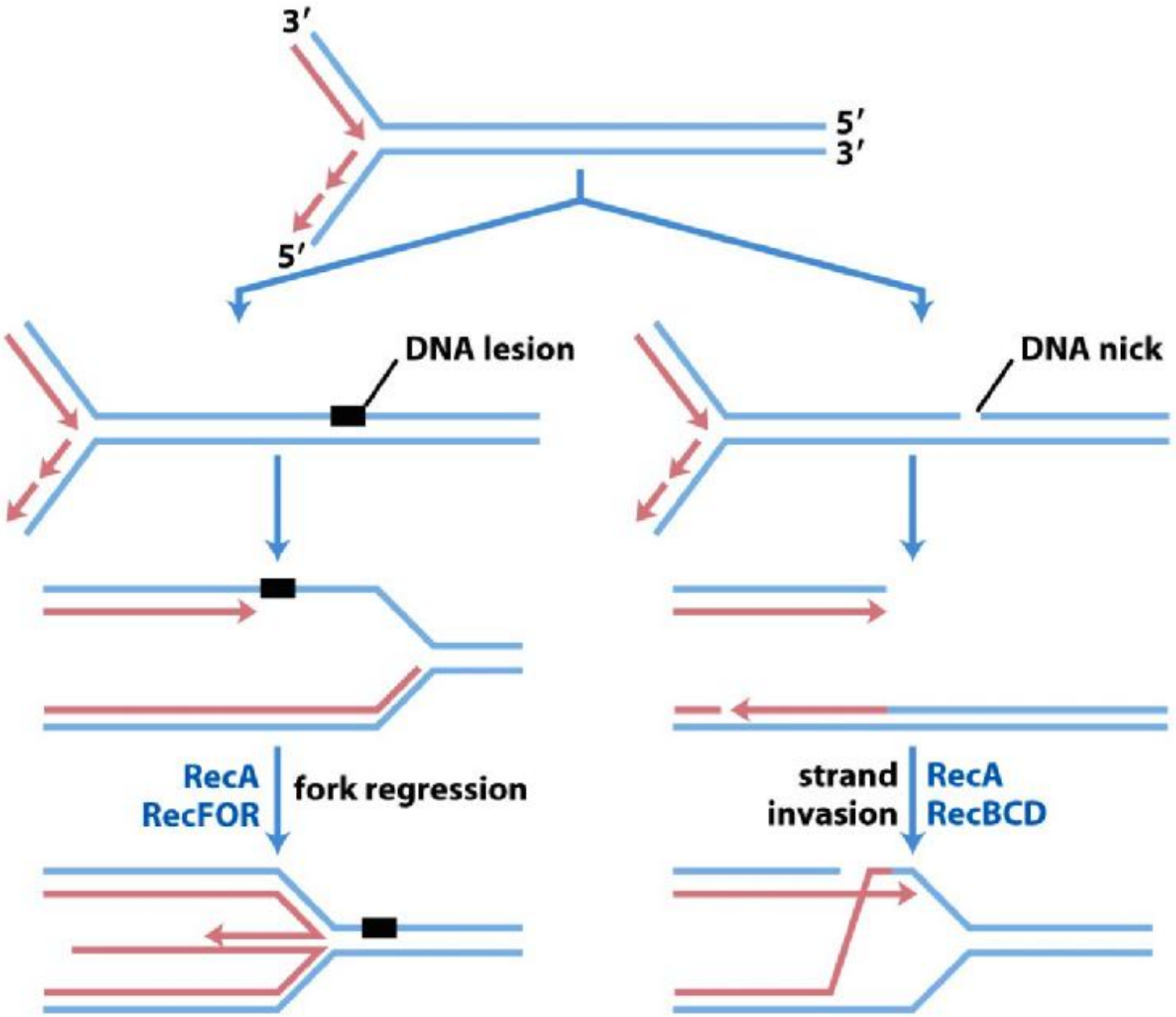

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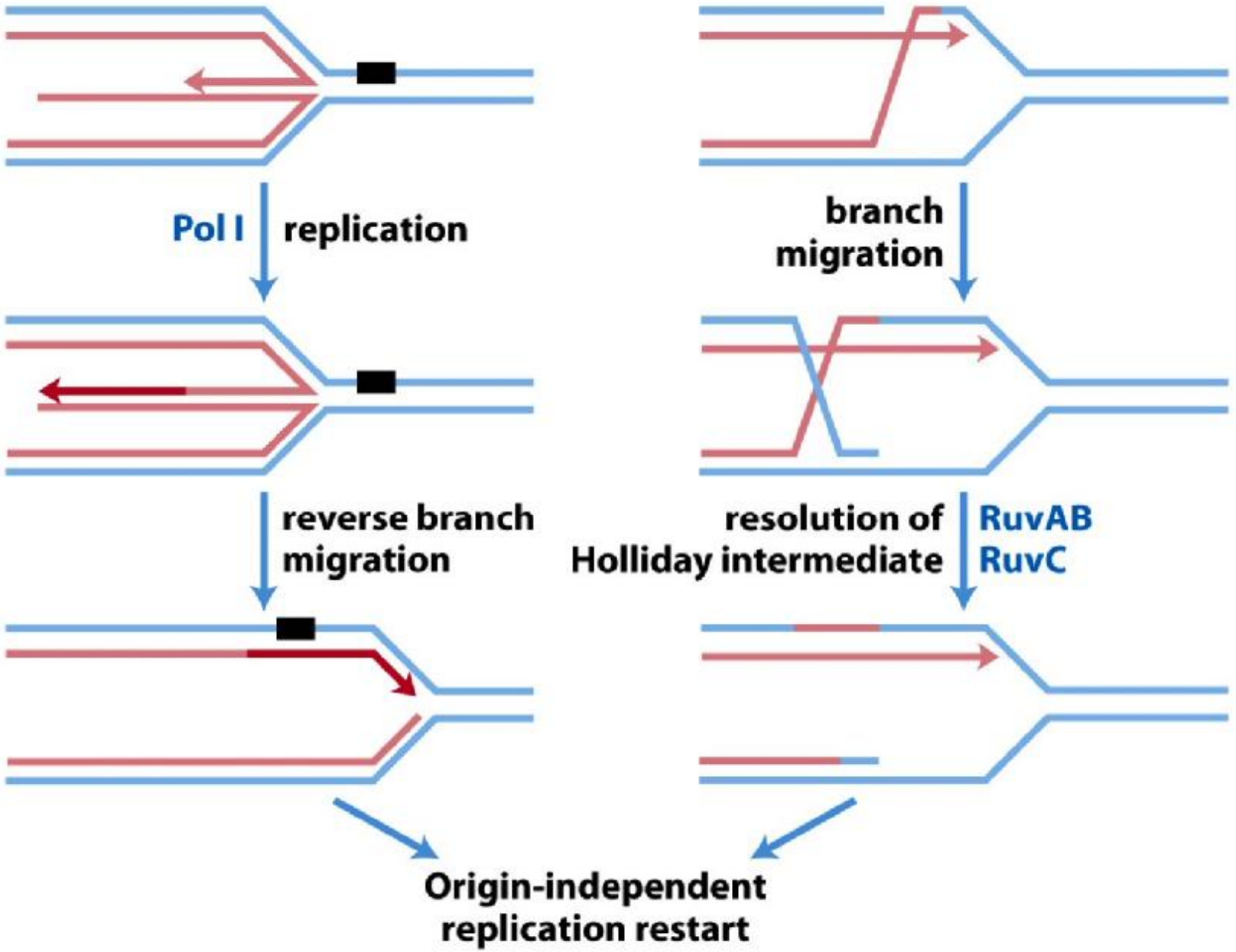

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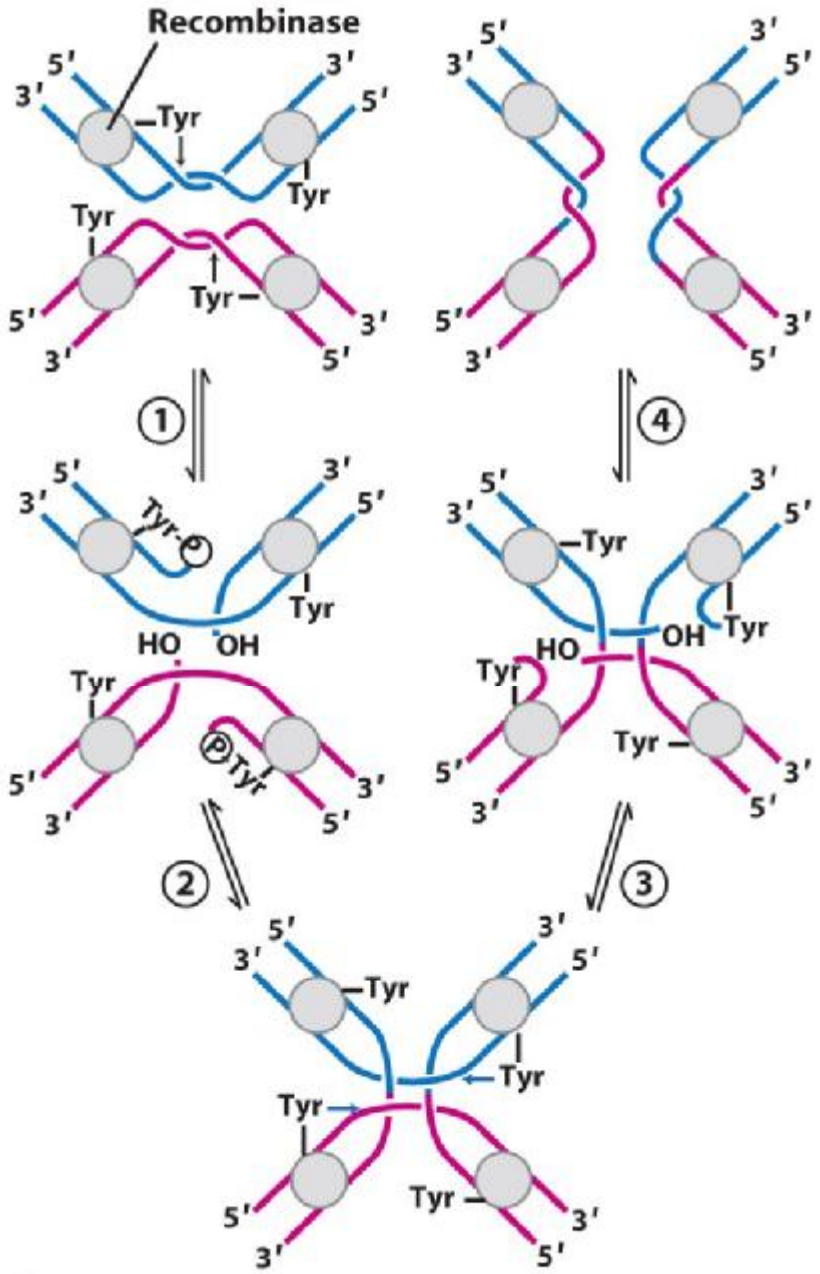

Figure 25-40a

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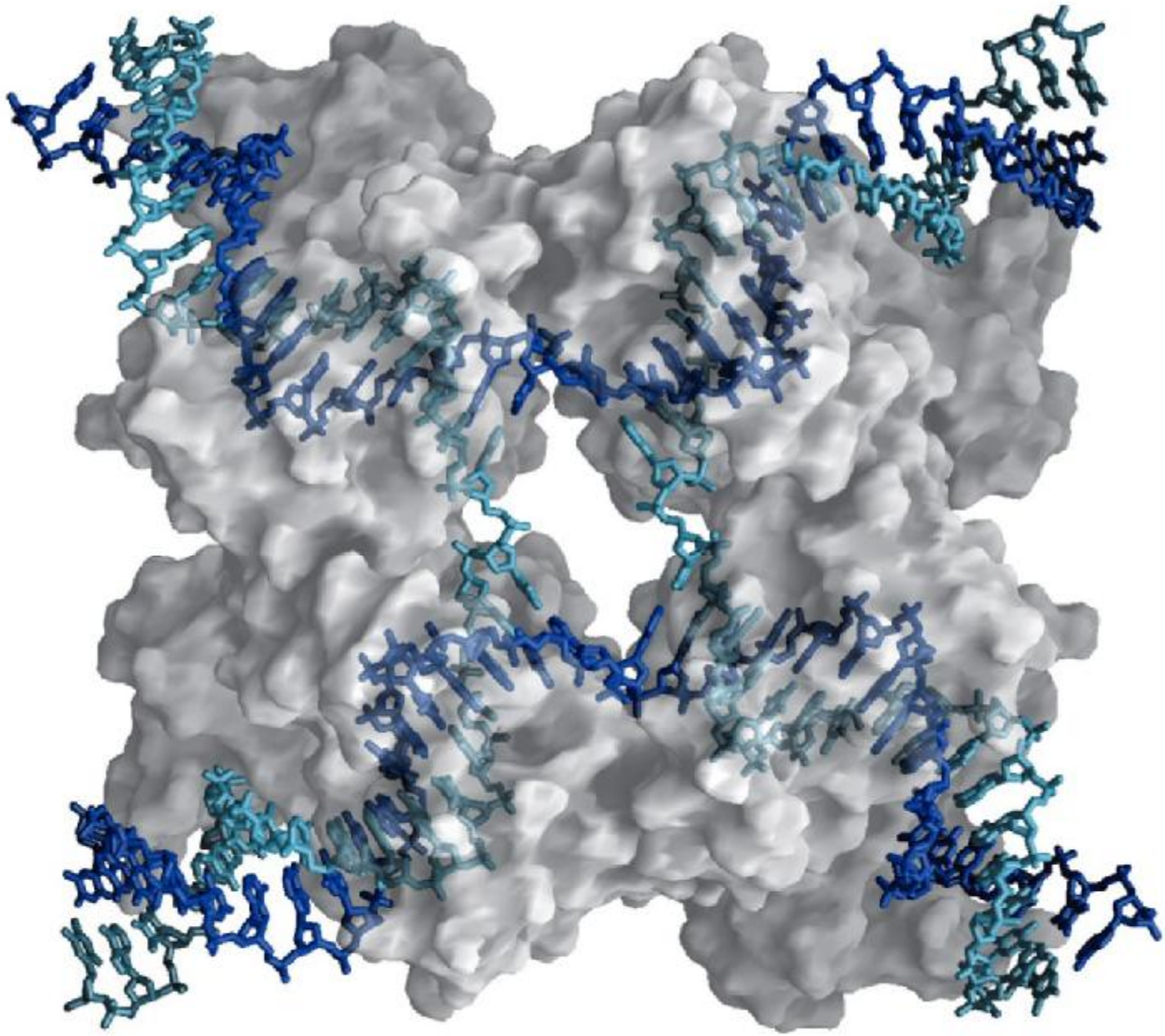

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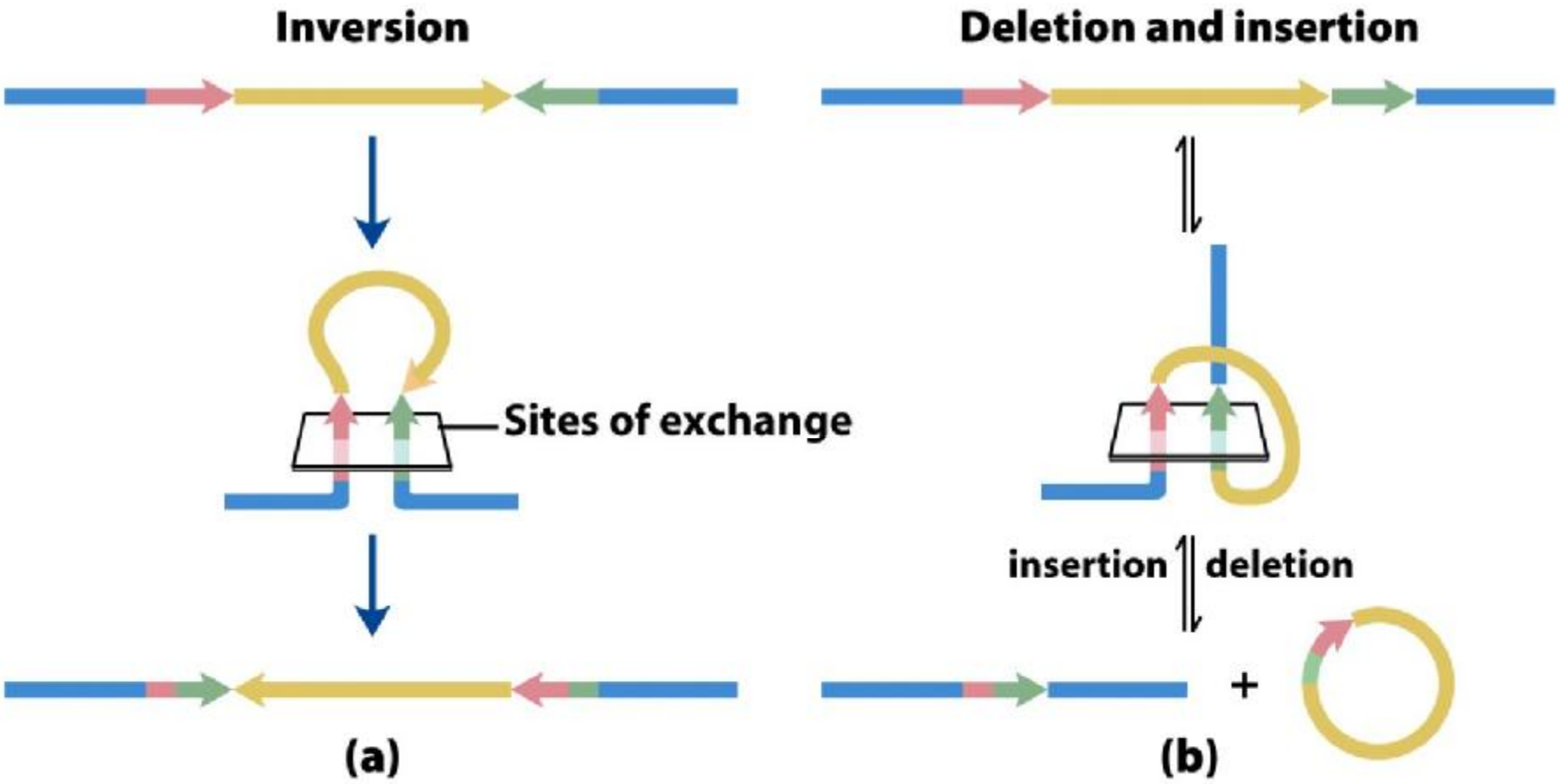

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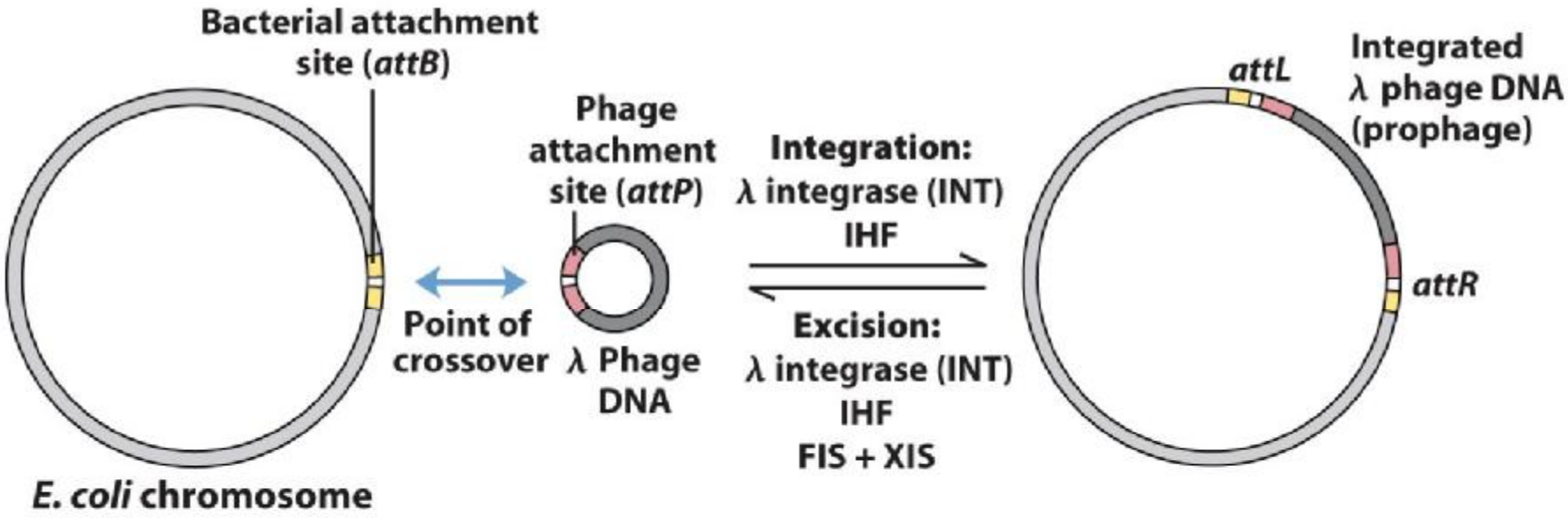

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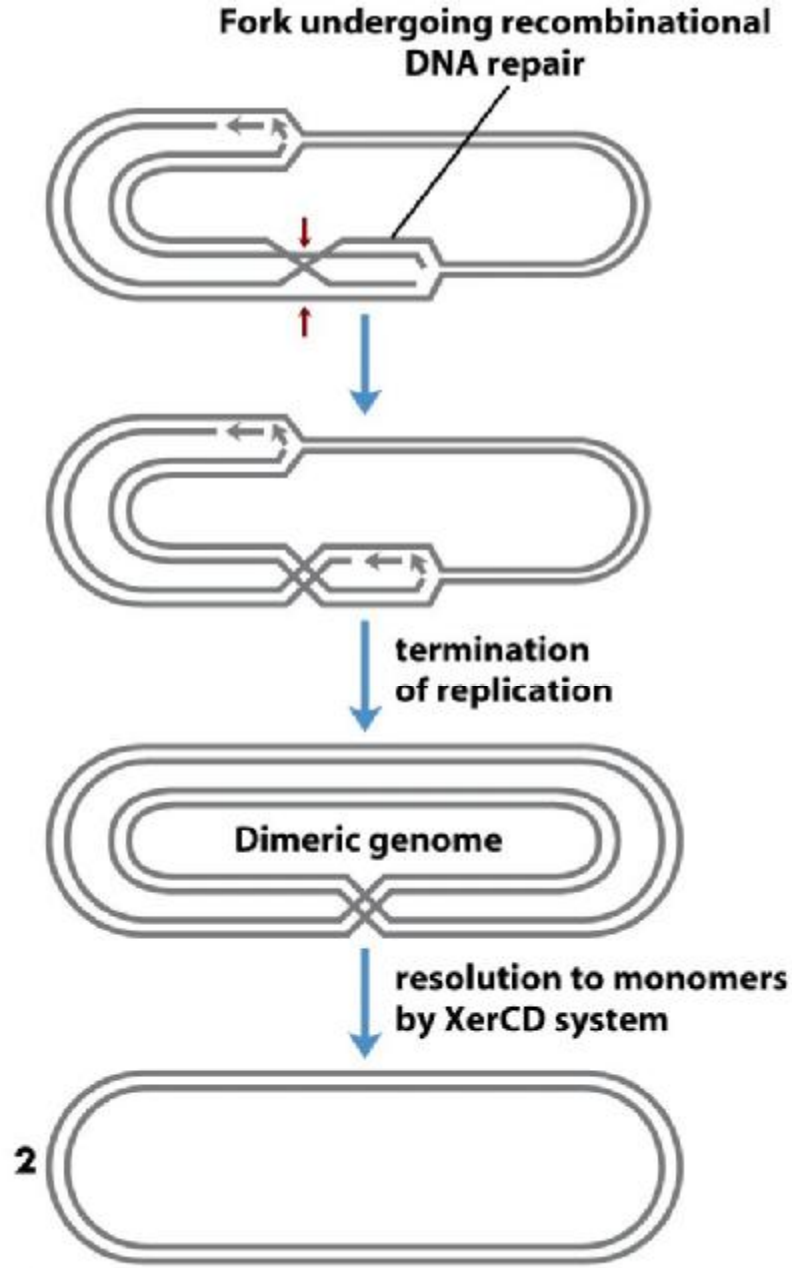

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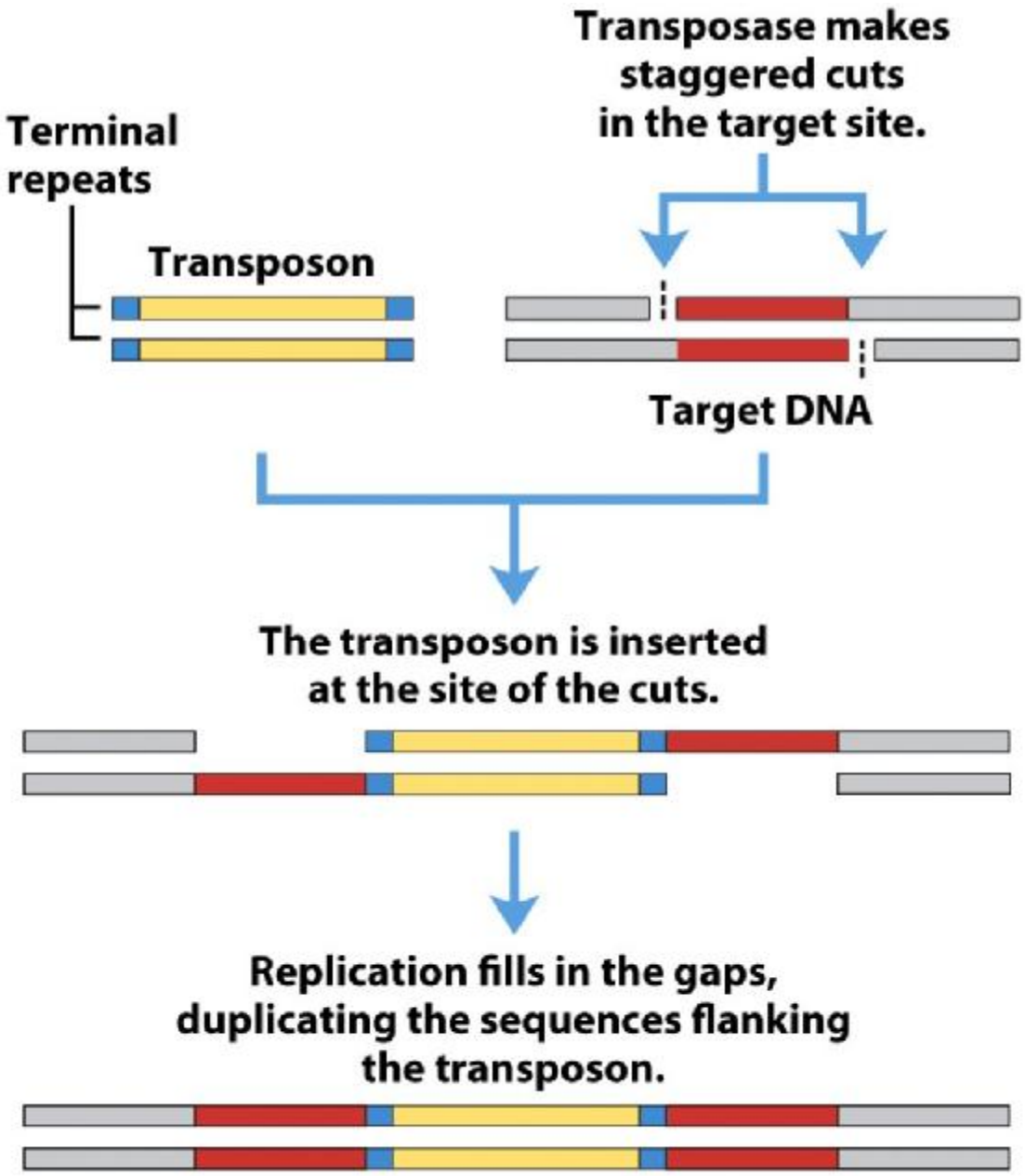

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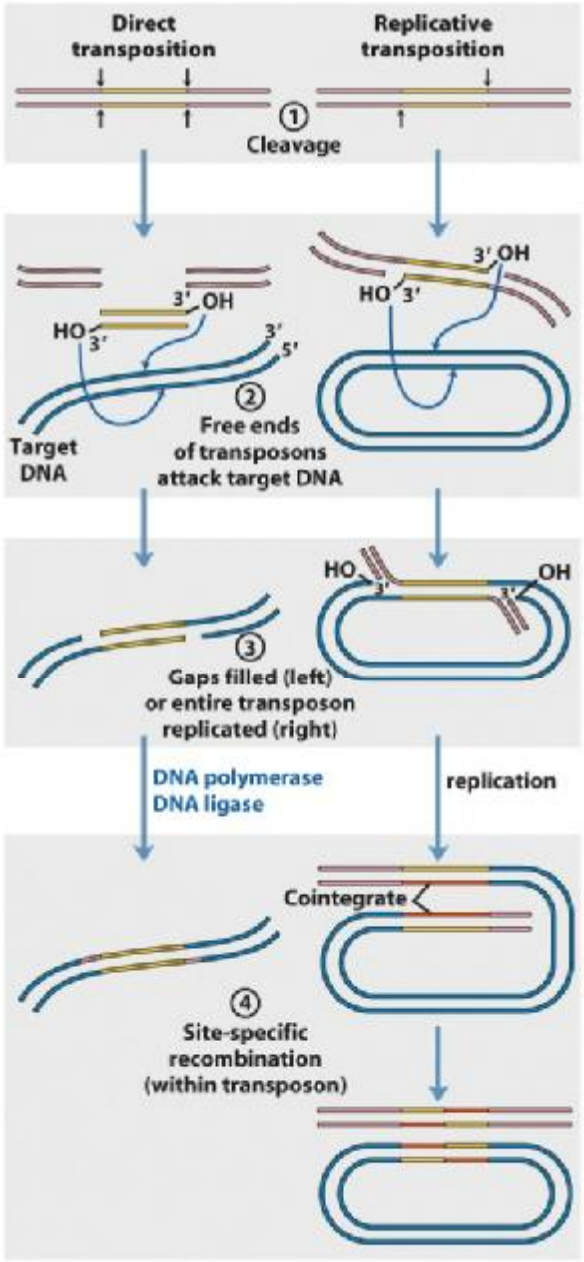

Figure 25-45

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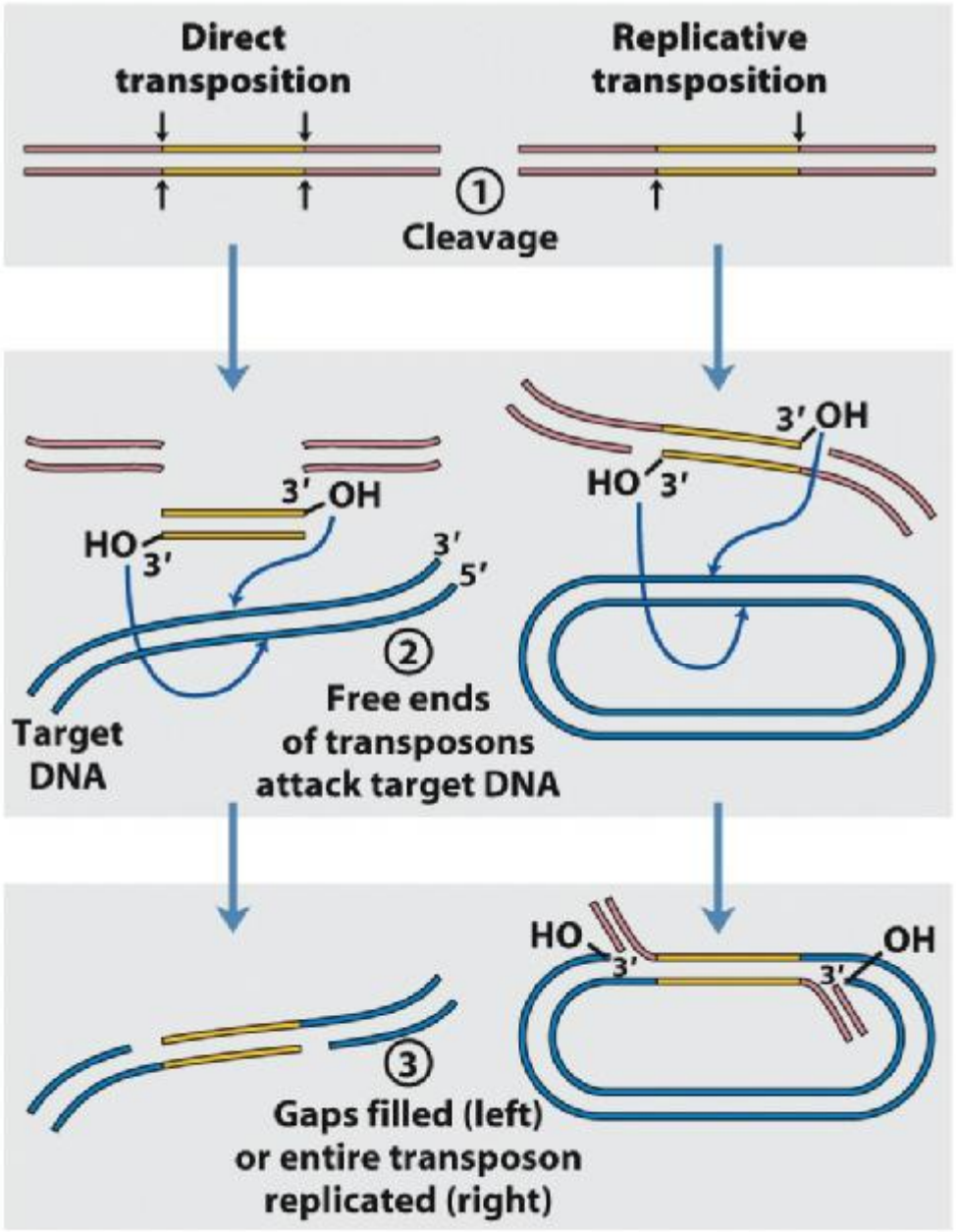

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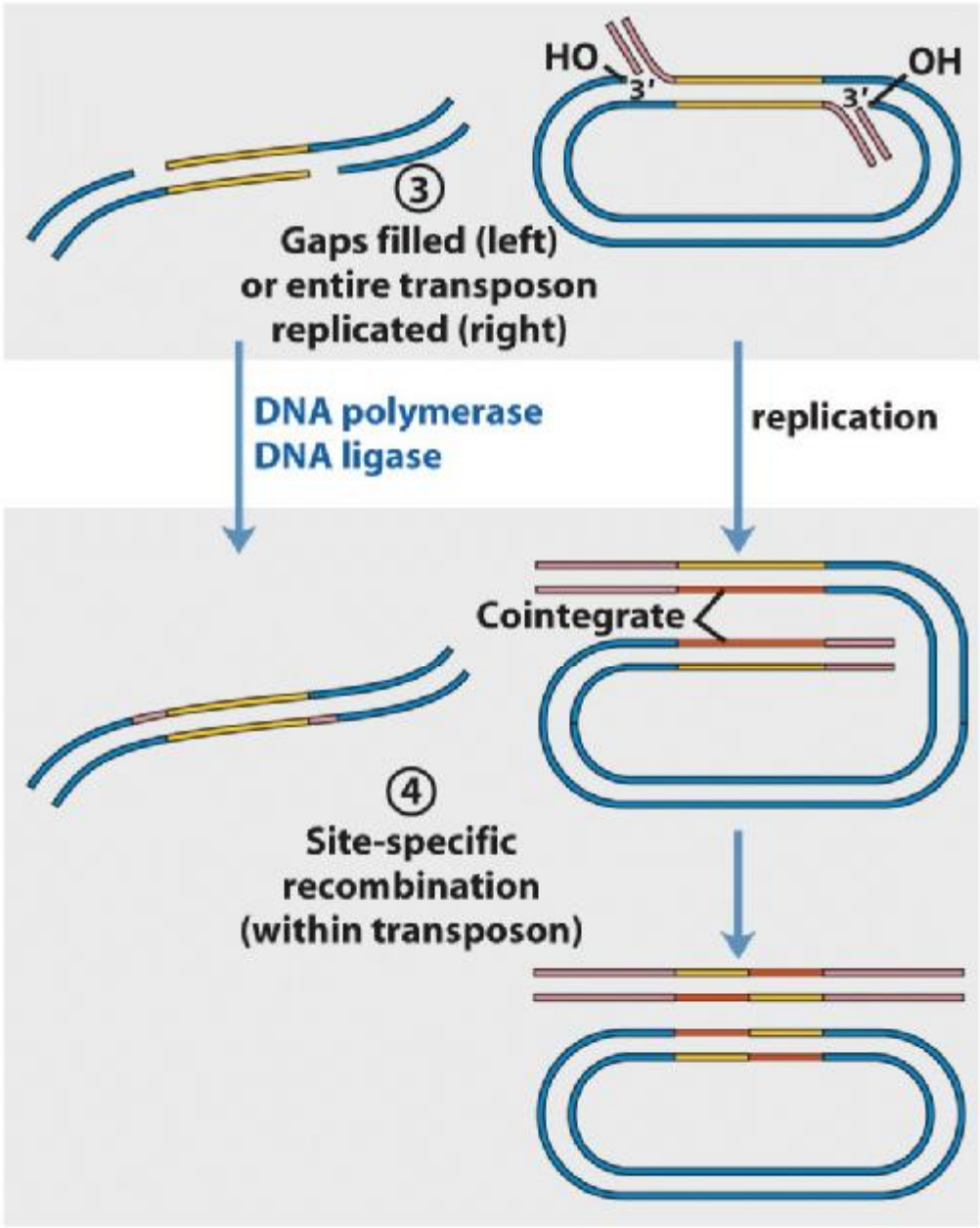

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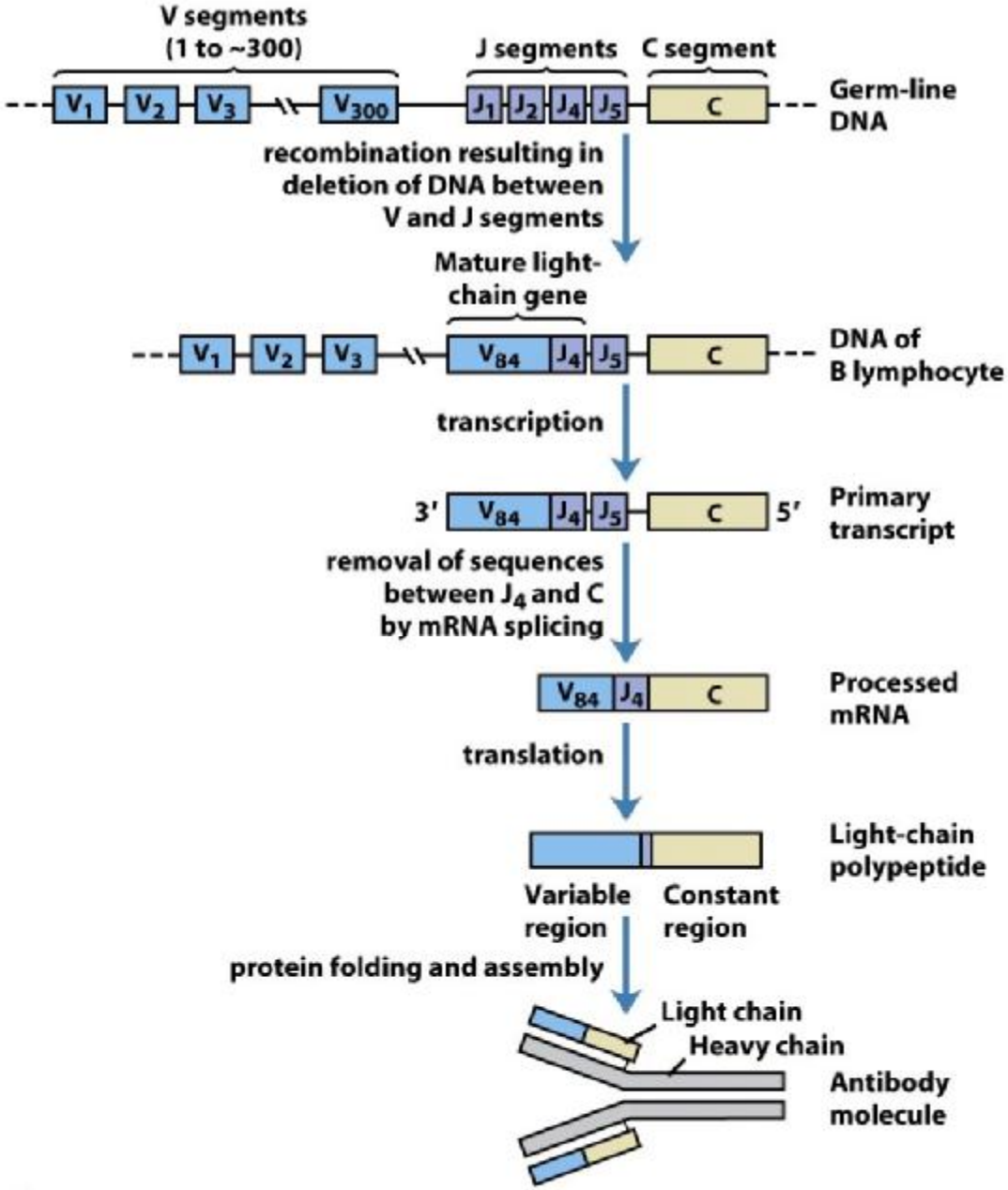

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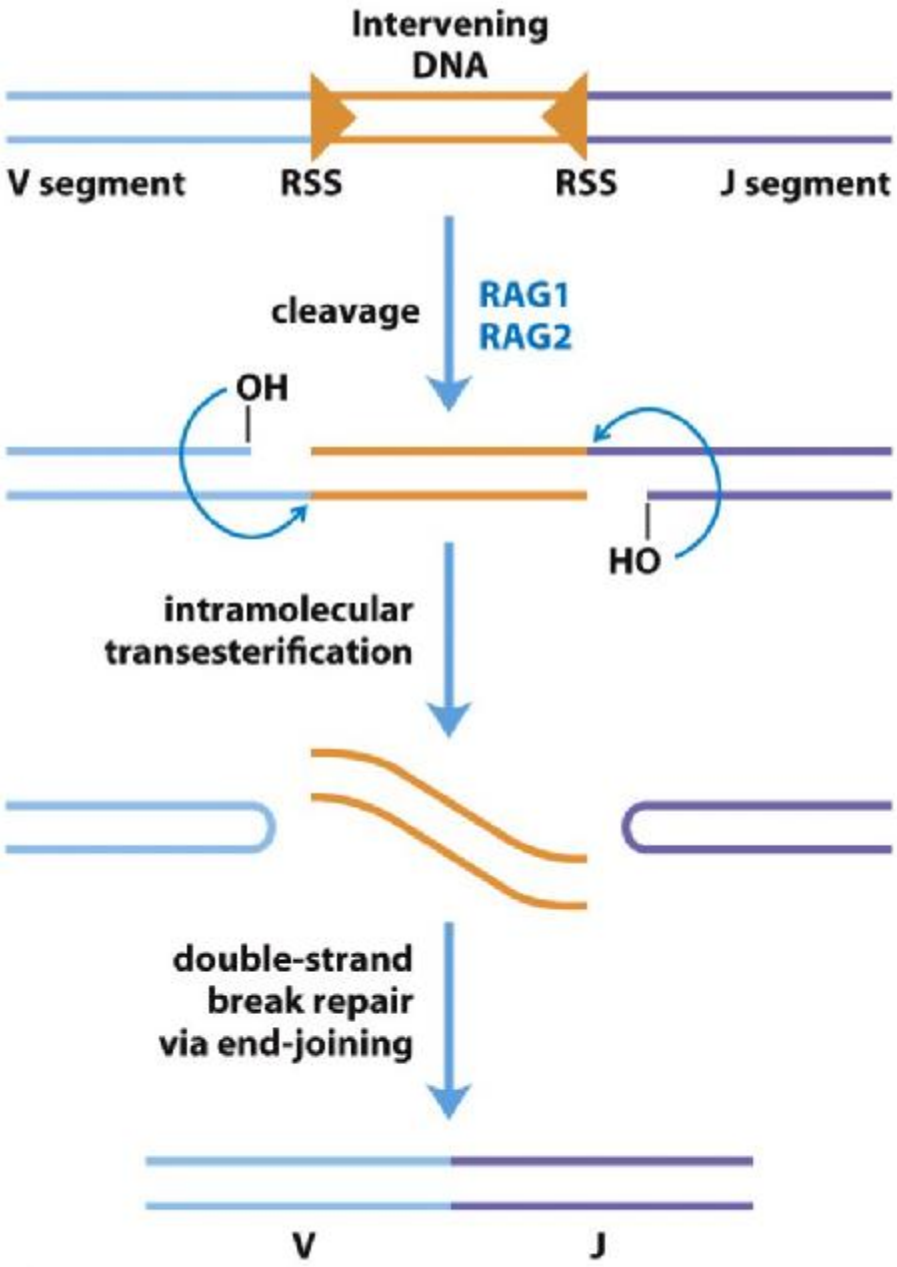

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